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Understanding and improving crop photosynthesis

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Introduction

It is widely recognised that photosynthesis in many important crops is well below its theoretical potential. With crop yields and stability under threat from the impact of climate change, there is now an urgent need to synthesise existing research on best practices for improving C_3 photosynthesis in crops to optimise sustainable crop production and yields. This volume reviews the wealth of current research that addresses this challenge.

The book is split into three parts: Part 1 chapters provide a general overview of C_3 photosynthesis, focusing specifically on its biochemistry and genetics in crop plants. Chapters in Part 2 focus on improving photosynthesis through the process of light harvesting, drawing attention to the relationship between photosynthesis and the circadian clock as well as modifying the photosystem antenna complex to improve light harvesting. Chapters also focus on relaxing non-photochemical quenching to improve photosynthesis, the modification of mesophyll conductance and the modification of leaf and canopy architecture to optimise photosynthesis in crops. Part 3 chapters focus on optimising chloroplast function and light conversion to improve photosynthesis, highlighting how modifying photorespiration, maximising the efficiency of ribulose biphosphate respiration and understanding and modifying protein function in plant chloroplasts can optimise crop performance.

Part 1 General

Part 1 opens with a chapter that focuses on understanding the biochemistry of C_3 photosynthesis in crop plants. Chapter 1 begins by first describing the carboxylation phase of the C_3 cycle, which is then followed by sections on the reduction phase and regeneration phase of the C_3 cycle. The chapter also addresses how C_3 cycle enzymes can be regulated, highlighting methods such as light activation and how analysing the crystal structure of the C_3 cycle enzymes can help to regulate them. It moves on to discuss approaches to determine which enzymes limit the flow of carbon through the C_3 cycle, such as empirical studies and modelling of the C_3 cycle. A section on future opportunities to improve the C_3 cycle is also included.

Moving on from Chapter 1, Chapter 2 draws specific attention to the genetics of C_3 photosynthesis in crop plants. The chapter introduces the photosynthesis-associated core genes encoded either in the nucleus or in the chloroplast and discusses how different internal (e.g. redox state, circadian rhythm) and external (e.g. abiotic stresses, light) signals regulate their transcription, particularly in crop plants. Since the molecular

mechanisms underlying the regulation of photosynthesis-associated genes is poorly understood, the chapter also discusses what is known regarding the transcriptional regulation of photosynthesis in C_3 crops, mainly rice and tomato. Among the regulators described, few were shown in the field to have the potential to improve photosynthesis. How the state-of-the-art knowledge can be used for photosynthesis improvement and future work perspectives, including the use of transplastomics, is also discussed.

Part 2 Improving photosynthesis: light harvesting

The first chapter of Part 2 discusses interactions between photosynthesis and the circadian system. Chapter 3 begins by describing how the circadian system regulates photosynthetic processes, as well as how it can regulate photosynthesis in C_4 and Crassulacean Acid Metabolism species. The chapter then draws specific attention to the interactions between photosynthates and the circadian system and highlights how starch metabolism is used as a consistent energy supply during the night. This is then followed by an analysis of the indicators of cellular energy status and its integration into the circadian system. The chapter also discusses the generation of reactive oxygen species during photosynthesis and how reactive oxygen species can also be integrated into circadian timing.

Chapter 4 looks at modifying photosystem antennas to improve light harvesting for photosynthesis in crops. The chapter first examines photopigments and their functions in light-harvesting complexes, then moves on to review several photosynthetic light harvesting protein complexes. A section on photoinhibition is also provided, which is then followed by an analysis of photosynthesis efficiency. Current challenges with modifying photosystem antennas to improve light harvesting are highlighted, which are then followed by the potential areas of research that can be developed in the future.

The next chapter focuses on relaxing non-photochemical quenching to improve photosynthesis in crops. Chapter 5 starts by reviewing light harvesting and photochemistry, then moves on to analyse the process of non-photochemical quenching, focusing specifically on dynamic regulation of light harvesting efficiency in the PSII antenna. The chapter also looks at assessing non-photochemical quenching via fluorescence measurements and how the photosystem II subunit S and zeaxanthin are important factors in controlling non-photochemical quenching formation and relaxation in higher plants. A section on manipulating non-photochemical quenching to improve photosynthetic efficiency is also provided.

The subject of Chapter 6 is modifying mesophyll conductance to optimise photosynthesis in crops. The chapter first describes the points of resistance to diffusion of carbon dioxide in plants, which in turn, influences mesophyll

conductance. It then moves on to review the interaction between mesophyll cell anatomy, light and mesophyll conductance. The link between leaf age and mesophyll conductance is also examined, which is followed by an analysis of cell wall diffusion, how cellular membranes can be used to diffuse carbon dioxide and how mesophyll conductance can be improved via the use of aquaporins as carbon dioxide channels. The chapter reviews carbon dioxide solubility in liquids, the improvement of mesophyll conductance through using carbonic anhydrases and how mesophyll conductance can be estimated. Strategies for altering mesophyll conductance are also highlighted in the chapter.

The final chapter of Part 2 looks at modifying canopy architecture to optimise photosynthesis in crops. Chapter 7 begins by reviewing how light is modelled within crop canopies and how breeding has impacted modern crop canopy architecture. It moves on to examine potential targets for canopy improvement, such as optimising leaf area, leaf traits as well as leaf optical properties to improve radiation use efficiency. Finally, the chapter discusses considerations for the adoption of canopies better suited to their environment and management practices.

Part 3 Improving photosynthesis: optimising chloroplast function/light conversion

The first chapter of Part 3 discusses modifying photorespiration to optimise crop performance. Chapter 8 first highlights both the advantages and disadvantages of using photorespiration, focusing on how carbon and energy is lost during the process and how future climates could affect photorespiration. The chapter moves on to examine recent efforts to improve photorespiration, highlighting the importance of keeping things moving to prevent inhibition as well as discussing current photorespiratory bypass approaches. A section on how photorespiration can beat rising temperatures is also included, which is then followed by an overview of how improving photorespiration under non-steady-state conditions could improve carbon and nitrogen budgets.

The subject of Chapter 9 is maximising the efficiency of ribulose bisphosphate regeneration to optimise photosynthesis in crops. It begins by first describing the various component processes of photosynthesis, such as the use of enzymes, photosynthetic responses to light and carbon dioxide as well as optimising the use of resources important for photosynthesis. The chapter then moves on to review ways of optimising ribulose bisphosphate regeneration through resource investment, light use efficiency and interactions between light use and carbon metabolism. Examples of improving ribulose bisphosphate regeneration are also provided, such as sedoheptulose bisphosphatase and sucrose-phosphate synthase.

The final chapter of the book draws attention to understanding and modifying protein function in plant chloroplasts to optimise photosynthesis. Chapter 10 starts by describing a general carbon dioxide concentrating mechanism, focusing on cyanobacterial carbon dioxide and green algal carbon dioxide models first. It then goes on to examine the differences between the cyanobacterial carbon dioxide concentrating mechanism and the Chlamydomonas carbon dioxide concentrating mechanism, as well as how algal carbon dioxide concentrating mechanism components can be put into crops. The chapter dedicates individual sections to the various strategies currently available, specifically the envelope transporter-based, thylakoid-based, protopyrenoid-based, pyrenoid-based and finally the carboxysome-based strategies. It also highlights currently technical challenges associated with targeting inorganic carbon as well as the challenges of replacing and relocating carbonic anhydrases.

Chapter 1

Understanding the biochemistry of C_3 photosynthesis in crop plants

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1 Introduction

All photosynthetic organisms use the C_3 (Calvin-Benson) cycle to fix atmospheric CO_2 into organic compounds needed for the development and growth of the plant. In higher plants, the reactions of this pathway in plants take place in the chloroplast stroma of green tissues, predominantly in the leaves. Energy in the form of ATP and NADPH, needed to drive this cycle, is generated by the light reactions of photosynthesis that take place on the thylakoid membranes. The steps in this cycle were first elucidated in the 1950s by Calvin, Benson, Bassham and colleagues (see for a recent historical perspective Sharkey, 2019), and the enzymes involved were identified and catalytic properties determined during the 1970s and 1980s (Leegood, 1990). In photosynthetic eukaryotes, there are 11 different enzymes in the C_3 cycle catalysing 13 reactions, and the cycle can be divided in response to 3 phases: carboxylation, reduction and regeneration. Carbon compounds produced in this cycle are essential for growth and

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development of the plant and while the majority (five-sixths) of the triose phosphate produced in the C_3 cycle remains within the cycle to regenerate RuBP, one-sixth of the carbon exits the cycle for biosynthesis of a range of compounds (Fig. 1). The balance carbon being delivered to these different biosynthesis pathways is not fixed but is likely to change during development, under different environmental conditions and also to changes in the rate of photosynthesis. However, what is fixed is the need to retain five out of every six carbons fixed in the pathway to prevent the cycle becoming depleted.

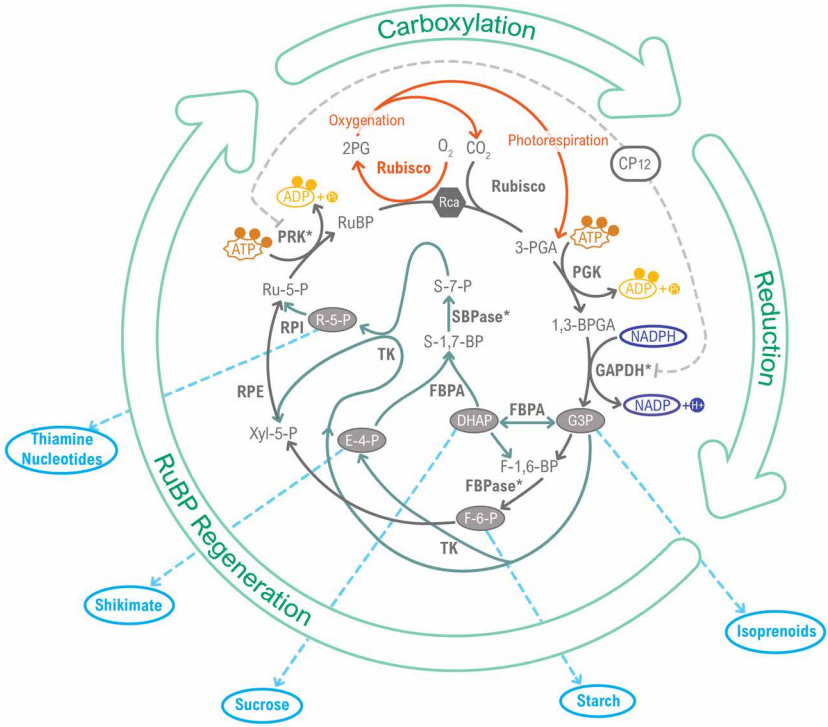

Figure 1 The reactions of the C_3 cycle. The first step in the fixation of atmospheric CO_2 is catalysed by the enzyme Rubisco which results in the formation of 3-PGA, the first stable compound in the cycle. The next two reactions form the reductive phase and are catalysed by PGK, forming BPGA using ATP and GAPDH which forms G-3-P consuming NADPH. The enzyme TPI produced DHAP. G-3-P and DHAP, known as TPs, enter the regenerative phase of the C_3 cycle catalysed by FBPA, forming S1,7-BP and F1,6-BP. SBPase and FBPase then produce S7-P and F6-P which are then converted to 5C compounds in reactions catalysed by TK, RPI and RPE resulting in the formation of Ru5P. The final step in the cycle is catalysed by PRK producing the CO_2 acceptor molecule Ru1,5-BP. The C_3 cycle produces compounds which are exported to a number of biosynthetic pathways for the synthesis of isoprenoids, starch, sucrose, shikimate, thiamine and nucleotides. Rubisco also has an oxygenase reaction which results in the formation of 2-phospoglycerate which enters the photorespiratory pathway.

The first two phases of the C_3 cycle, carboxylation and reduction, form the linear, assimilatory part of the cycle catalysed by the enzymes phosphoribulokinase (PRK), ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco), phosphoglycerate kinase (PGK) and glyceraldehyde 1,3-dehydrogenase (GAPDH) resulting in the formation of triose phosphates (TPs). These TPs can be exported from the pathway out to the cytosol for sucrose and isoprenoid synthesis, or they can be retained in the cycle and enter the branched, regeneration phase of the cycle. This regenerative phase results in the formation of the CO_2 acceptor molecule ribulose 1,5-bisphosphate (RuBP), and it also produces a number of different carbon compounds which exit the cycle and form the basis of the biosynthetic pathways for starch (fructose 6-phosphate), thiamine, nucleotides (ribose 5-phosphate) and phenylpropanoids (ertyhrose-4-phosphate) (Fig. 1).

1.1 CO_2 assimilation in C_3 photosynthesis

The initial carboxylation reaction of the C_3 cycle is catalysed by the enzyme Rubisco, in which atmospheric CO_2 is added to the acceptor molecule, ribulose 1,5-bisphosphate (RuBP). This results in the formation of an unstable six-carbon compound, 2-carboxy-3-ketoarabinotol-1,5-bisphosphate, which splits in half forming two molecules of 3-phosphoglycerate (3-PGA). This three-carbon molecule is the first stable product following carboxylation, giving this pathway the name the C_3 cycle. This 3-PGA then enters the reduction phase of the cycle and is converted to glycerate 1,3-bisphosphate (G1,3-BP) using a molecule of ATP. In the second step in this reductive phase, NADPH is consumed and G1,3-BP is converted to glyceraldeyde-3-phosphate (G3-P), which is then converted to dihydroxyacetone phosphate (DHAP) by triose phosphate isomerase (TPI). These two 3C compounds, G1,3-P and DHAP, are then converted to the 6C and 7C compounds fructose 1,6-bisphosphate (F1,6-BP), sedoheptulose 1,7-bisphosphate (S1,7-BP), by fructose 1,6-bisphosphate/sedoheptulose 1,7-bisphosphate aldolase (FBPA). Dephosphorylation of F1,6-BP and S1,7-BP to fructose 6-phosphate (F6-P) and sedoheptulose 7-phosphate (S7-P) is catalysed by fructose 1,6-bisphosphatase (FBPase) and sedoheptulose 1,7-bisphosphate (SBPase). Both of these reactions are essentially irreversible *in vivo* due to the high-energy requirement for phosphorylation, which commits these carbon compounds to the regenerative phase of the C_3 cycle. A series of reactions convert F6-P and S7-P into 4C and 5C carbon compounds resulting in the formation of the CO_2-acceptor molecule ribulose 1,5-bisphosphate (RuBP) (Fig. 1). Three of these reactions are catalysed by transketolase (TK) (1) removes 2C from F6-P, forming erythrose 4-phosphate (E4-P), (2) transfers the 2C to G3-P forming xylulose 5-phosphate (Xyl5-P) and (3) removes to 2C from S7-P forming ribose 5-phosphate (R5-P). The last steps in the branched regenerative

phase of the cycle are catalysed by ribulose 5-phosphate epimerase (RPE), which converts Xyl 5-P to ribulose 5-P (Ru5-P) and ribose 5-P isomerase (RPI) catalysing the conversion of ribose 5-phosphate (R5-P) to Ru5-P. The final regeneration reaction is the start of the linear section of the C_3 cycle, and Ru5-P is phosphorylated by PRK to form the CO_2 acceptor RuBP (Fig. 1).

The carbon fixed through the C_3 in the daytime is partitioned between immediate use for biosynthesis, sustaining growth and maintenance costs, and reserves for the night time (concept reviewed in Smith and Stitt, 2007). The regulation of carbon utilisation is a complex process involving the integration of environmental cues, multiple signalling networks, and circadian regulation of carbon availability and demand across various plant tissues (see examples for the model plant Arabidopsis) (Flis et al., 2019; Graf et al., 2010; Mengin et al., 2017; Pilkington et al., 2015; Sulpice et al., 2014; Scialdone et al., 2013). Improving both photosynthesis and downstream physiological processes will be a critical part of strategies aiming to improve the high efficiency of our crops. To this end in recent years a major focus of research on the C_3 cycle has been on identifying bottlenecks to provide strategies for improving crop yield. There have been one or two notable successes from this work but as yet this has mainly been in model species or in controlled environment conditions (López-Calcagno et al., 2020; Simkin et al., 2019; Driever et al., 2017; Raines, 2022). However, given that the C_3 cycle is highly conserved, it is reasonable to predict that lessons learned from model plants will be transferable to crops, and there are now reports on improvements in wheat, tomato and brassica that this is a feasible route to improve yield (Long et al., 2006). This chapter provides an update on the current understanding of the biochemistry and regulation of the C_3 cycle enzymes, their role as limiting factors in the C_3 cycle and strategies to modify the C_3 cycle for crop improvement.

2 The carboxylation phase

The carboxylation phase of C_3 cycle is facilitated by the photosynthetic carbon fixing enzyme Rubisco (EC 4.1.1.39), and its ubiquity among photosynthetic organisms makes Rubisco the most abundant protein on Earth, with an estimated global terrestrial mass of 0.7 gigatons (Bar-On and Milo, 2019). Rubisco is often considered the rate-limiting step for photosynthetic carbon assimilation and is characterised by four biochemical features considered to be evidence of the enzyme's inefficiency. Firstly, Rubisco has a turnover rate of 2–10 s^{-1} orders of magnitude lower than other so-called 'perfect catalysts' which are limited only by the rate of diffusion of the substrate to the catalytic site. Secondly, the Rubisco carboxylation reaction is inhibited by a competing RuBP oxygenation reaction, which catalyses the first step of the energetically demanding photorespiratory pathway. Finally, Rubisco is heavily regulated,

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