Photosynthesis solutions to enhance productivity

Christine H. Foyer[1], Alexander V. Ruban[2] and Peter J. Nixon[3]

[1]Centre of Plant Sciences, School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK
[2]School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK
[3]Faculty of Natural Sciences, Department of Life Sciences, Imperial College, South Kensington Campus, Exhibition Road, London SW7 2AZ, UK

CHF, 0000-0001-5989-6989; AVR, 0000-0001-8554-0249; PJN, 0000-0003-1952-6937

The concept that photosynthesis is a highly inefficient process in terms of conversion of light energy into biomass is embedded in the literature. It is only in the past decade that the processes limiting photosynthetic efficiency have been understood to an extent that allows a step change in our ability to manipulate light energy assimilation into carbon gain. We can therefore envisage that future increases in the grain yield potential of our major crops may depend largely on increasing the efficiency of photosynthesis. The papers in this issue provide new insights into the nature of current limitations on photosynthesis and identify new targets that can be used for crop improvement, together with information on the impacts of a changing environment on the productivity of photosynthesis on land and in our oceans.

This article is part of the themed issue 'Enhancing photosynthesis in crop plants: targets for improvement'.

1. Photosynthesis is geared for high productivity in resource-limited natural environments

Photosynthesis is a major driver of life on the Earth, introducing the energy from sunlight into the biosphere and releasing oxygen from water. Significant progress has been made in our understanding of the functional operation of photosynthesis over the past 50 years, particularly in terms of our knowledge of the molecular physiology of the component pathways and the ecology of photosynthesis in a world where the atmosphere is becoming increasingly enriched in carbon dioxide [1–5]. Despite the overwhelming weight of evidence from research on atmospheric CO_2 enrichment highlighting the close link between increased photosynthesis and yield, the application of our mechanistic knowledge of photosynthesis until recently has been largely unsuccessful. The early assumption that selection on the basis of photosynthesis would lead to increased productivity in crop plants has resulted in failure and frustration. Although cereal grain yields were almost doubled in the past century through the application of knowledge in plant breeding and genetic manipulation, there was no change in the rate of photosynthesis per unit leaf area.

Evolution entrained and perfected photosynthesis for high productivity in resource-limited natural environments. Given the sessile nature of land plants that requires a high level of stabilization of metabolism in a greatly fluctuating environment, the photosynthetic processes have evolved to be highly plastic and flexible at the expense of efficiency. The driving force for photosynthesis, sunlight, is an almost limitless supply compared to the sugars and carbon skeletons that drive respiration. Hence, the processes that underpin energy conservation in the former are much less stringent in the former than the latter. Moreover, energy dissipation mechanisms are intrinsic to the operation of light harvesting linked to electron transport in photosynthesis, allowing

effective protection of excess irradiance. The improvement of photosynthetic efficiency now appears to offer a major opportunity for achieving the sustainable yield increases required to meet future demands for food. The papers in this volume not only present an overview of photosynthetic mechanisms and their regulation, but they are also designed to promote discussion of how more efficient photosynthesis may be developed in crop plants to improve both crop yields and nutritional value.

2. Enhancing photosynthesis in microorganisms

When chloroplasts evolved from cyanobacteria via endosymbiosis they brought photosynthesis into eukaryotic cells. As well as having many advantages, this incorporation brought the hazards associated with photon-powered energy conversion and electron transport and reduction/oxidation (redox) regulation and signalling. A recent study on the proteome of the diatom *Phaeodactylum tricornutum*, suggests that the introduction of the photosynthetic electron transport chain into photosynthesis was accompanied by an increase in cysteine residues in proteins responding to the physiological state of the cell [6]. The presence of photosynthesis causes a substantial increase in the production of reactive oxygen species (ROS), causing a significant expansion of the redox-sensitive proteome, giving redox regulatory networks the ability to cope with fluctuating environmental conditions. Moreover, the high cysteine content of the diatom proteome may allow the cell to monitor photosynthetic electron flow better in the presence of molecular oxygen and so prevent over-oxidation [7]. Within this volume, Falkowski *et al.* [8] discuss how photosynthetic efficiency might be improved within the oceans. The phytoplankton community is shown to operate at only half maximal photosynthetic energy conversion efficiency because of poor nutrient availability that limits the synthesis or function of essential components in the photosynthetic apparatus. The intrinsic photo-protective mechanisms that operate in the reaction centres of the photosynthetic bacterium *Rhodobacter sphaeroides* to prevent formation of the long-lived triplet or singlet excited electronic states under fluctuating environmental conditions were analysed by Ma *et al.* [9]. These authors found that the spectroscopic signature of charge separation in preparations of partially oxidized reaction centres was replaced by that of an energy dissipation process. Krieger-Liszkay and co-workers [10] describe how photosystem (PS) II electron transport capacity in the cyanobacterium *Synechocystis* sp. PCC 6803 was altered relative to PSI by constitutive expression of the plastid terminal oxidase, which oxidizes plastoquinol and reduces oxygen to water. The observed alteration in the PSI to PSII stoichiometry was linked to effects on cellular redox status, particularly of the $NAD(P)H/NAD(P)^+$ pool leading to altered gene expression. The role of thylakoid-embedded FtsH protease complexes in the selective degradation of PSII subunits during the repair cycle in *Synechocystis* sp. PCC 6803 was explored by Nixon and co-workers [11]. These authors show that the PSII Psb29 subunit is required for the accumulation of the FtsH2/FtsH3 hetero-oligomeric complex that is involved in PSII repair. Moreover, the Psb29 protein from *Thermosynecho-coccus elongatus* was shown to have a highly conserved region that the authors suggest binds to FtsH. Decreased FtsH

function leading to loss of PSII repair cycle activity via THF1 is suggested to contribute to ROS production and the loss of chloroplast functions. A bioarchitectonic approach to the engineering of metabolism is described in considerable details by Kerfield [12], who breaks down the complexity of metabolic processes into modules such as subcellular compartments, domains within proteins, co-regulated groups of functionally associated genes and metabolic pathways. This intrinsically interesting overview not only considers the lessons learned from studies seeking to install new metabolic modules into cells, but also how bioarchitectonics is being applied to generate microbial cell factories that can be used to increase primary productivity.

3. How to develop more efficient photosynthesis in crop plants

Ruban [13] provides a comprehensive overview of the assessment of the protective effectiveness of non-photochemical fluorescence quenching (NPQ: [14,15]). This insightful perspective of NPQ information concerning the extent of photodamage and photoprotection (figure 1) about plant productivity is discussed in relation to environmental variables. The novel methodology described by this author is shown to provide a firm foundation for gaining a tool for quantification of light tolerance by photosynthetic organisms and, therefore, offering a comprehensive understanding of light responses in plants. A thought-provoking analysis of how manipulation of the thylakoid proton motive force (pmf) might be used to improve photosynthesis is provided by Kramer and co-workers [16]. However, it is likely that some of the proposed modifications to the photosynthetic machinery may have negative impacts on overall metabolism and also other processes such as stress tolerance. Within this context, Aro and co-workers [17] discuss how susceptibility of PSI to photoinhibition, particularly at low temperatures or under high light, should be taken into account in consideration of the manipulation of photosynthesis. Using the *pgr5* mutant, which lacks ΔpH-dependent regulation of photosynthetic electron transport, the authors outline the consequences of high light-mediated PSI photoinhibition for downstream chloroplast processes such as carbon fixation and starch accumulation, as well as effects on cell signalling.

4. Enhancing photosynthetic electron transport: carbon assimilation and chloroplast–nucleus interactions to improve plant productivity

The acquisition of photosynthetic capacity requires extensive cooperation between organelles, encompassing coordinated light perception, expression of nuclear and plastid genes, biosynthesis of lipids, proteins and pigments, as well as transport and appropriate localization and insertion of components. This cooperation between organelles that underpins chloroplast functions extends throughout the life of the chloroplast and underpins the role of the chloroplast as a cellular sensor of environmental changes. The signalling function of chloroplasts encompasses photosynthesis but extends to systemic signals and the production of phytohormones that mediate plant stress responses and
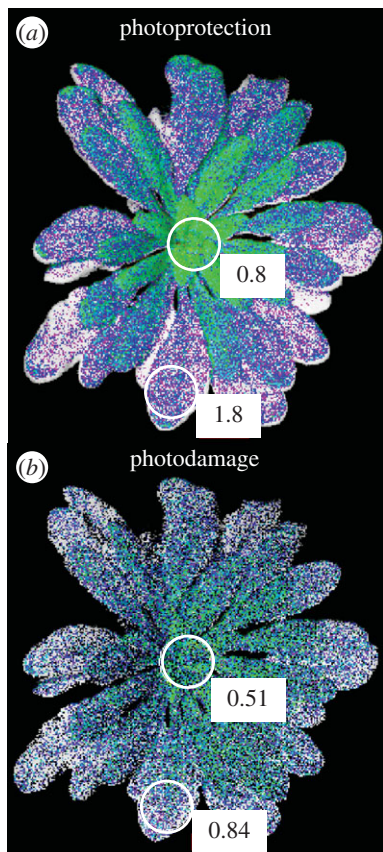
Figure 1. Images of protective NPQ (*a*) and the photodamage parameter qPd (*b*) in *Arabidopsis* plants (false colour scale), showing that young leaves in the centre of the rosette are less protected than the outer leaves (*a*, higher pNPQ) resulting in a higher rate of a photodamage (*b*, lower qPd).

Figure 2. The epidermis of an *Arabidopsis* leaf expressing redox-sensitive green fluorescent protein in the cytosol. The image shows a single stomata surrounded by epidermal cells.

general oxidation of the cytosol and nuclei as well as changes in nuclear gene expression.

developmental changes. The production of ROS and other redox-active mediators is a key to the signalling function of chloroplasts. Plant cells possess complex and elaborate mechanisms of redox sensing, signalling and regulation. One of the most well-characterized and widespread mechanisms that plant cells use to sense and transmit information about the redox state involves small proteins called thioredoxins (Trx). The Trx system of the chloroplasts coordinates the activities of the enzymes involved in CO_2 assimilation (Calvin–Benson cycle). Reduced Trx, produced via oxidation of the NADPH produced by the photosynthetic electron transport chain transfers reducing equivalents to the redox-sensitive cysteine residues of a number of Calvin–Benson cycle enzymes, only the reduced forms of which are active. In this way, the photosynthetic electron transport chain is able to switch on CO_2 assimilation in the light and avoid futile cycles. A broad overview of the role of thiol-based redox regulation is presented by Rintamaki and co-workers [18] covering functions such as the control of chloroplast biogenesis, the regulation of light harvesting and distribution of light energy between photosystems, as well as plant stress responses. Crucially, this paper evaluates the prospects for improvement of photosynthetic performance by modifying the Trx composition in plants. Foyer and co-workers [19] show how the application of widely used inhibitors of chloroplast and mitochondrial functions alter the redox status of root and leaf cells (figure 2). Using the *in vivo* redox reporter roGFP2, these authors show that the presence of inhibitors such as norflurazon, lincomycin, antimycin A and salicylhydroxamic acid enhance cellular oxidation. All these inhibitors caused a
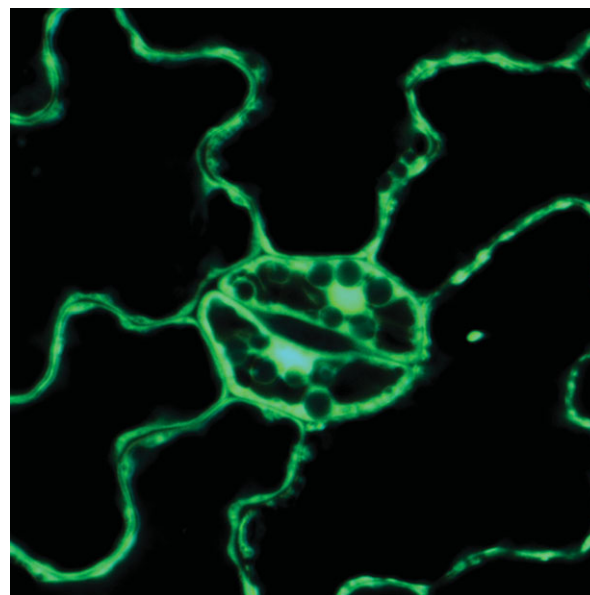
5. How to deliver increased photosynthesis in crop plants

Enhanced photosynthetic efficiency has to be achieved alongside more efficient use of natural resources employing an integrated approach from multiple natural science disciplines. The prospects for enhancing photosynthesis by introducing novel genetic diversity in crop plants are comprehensively discussed by Leister and co-workers [20]. These authors discuss different possible sources of natural variation, and argue that a novel approach is required. These authors suggest that a synthetic bacterial platform may provide a solution to the enhancement of eukaryotic photosynthesis. Bate and co-workers [21] provide an overview of the industry perspective and consider how photosynthesis may be optimized for industrial agriculture, discussing the translation of basic and applied research into increased productivity from the development and application of novel gene discovery techniques to translation and evaluation of traits in the modern production environment. Two papers in this issue concern the potential for increasing the yield potential of wheat through increased photosynthesis. The first is by Long and co-workers [22], who report that over 20% of the productivity is lost in wheat by the slow induction of photosynthesis during shade to sun transitions. These authors show that the adjustment of shade-grown flag leaf photosynthesis to full sunlight required about 15 min and that the time taken to gain maximum photosynthetic efficiency was dictated for the most part by the activation of the primary carboxylase of C3 photosynthesis, ribulose-1 : 5-bisphosphate carboxylase/oxygenase (Rubisco). The second paper is by Raines and co-workers [23], who describe how increasing the level of another enzyme involved in the Calvin–Benson cycle of CO_2 assimilation, sedoheptulose-1,7-biphosphatase (SBPase) leads to enhanced photosynthesis, increased total biomass and dry seed yield. The review by

Hibberd & Reyna-Llorens [24] considers what can be learned from the evolution of C4 photosynthesis, a process that facilitates CO_2 concentration in the Rubisco environment leading not only to improved carbon capture but also to increasing water and nitrogen use efficiencies. This scholarly overview considers how the polyphyletic evolution of C4 photosynthesis is built upon pre-existing metabolic and genetic networks and considers how relatively changes in pre-existing genetic minor and metabolic networks underpin the recurrent evolution of this process. With this knowledge, the transfer of C4 traits into C3 crops becomes a more tractable problem.

6. Concluding remarks

Over the past 50 years, crop yield increases achieved by conventional plant breeding have remained steady at about 1% per year. After the considerable improvement in cereal crop yields achieved during the Green Revolution, the increase in genetic yield potential appears to have stalled. However, crop yields have to increase by 100% by 2050 to meet the predicted future food needs for a global population. This requires a year-on-year yield increase of 1.7%. One way in which such a large increase could be achieved is by improving the efficiency of photosynthesis [25]. The improvement of photosynthetic efficiency now appears to provide an exciting opportunity to address the challenge of sustainable yield increases needed to meet future food demand. Achieving higher photosynthesis rates for the same or decreased use of water and nitrogen resources could be the game-changer required to transform the agriculture of the twenty-first century. The development of more efficient photosynthesis alongside sustainable and climate-resilient cropping systems is required to improve both yields and crop nutritional value. Moreover, added value will accrue from an improved understanding of photosynthesis and the incorporation of new technologies.

References

1. Blankenship RE *et al.* 2011 Comparing photosynthetic and photovoltaic efficiencies and recognizing the potential for improvement. *Science* **332**, 805–809. (doi:10.1126/science.1200165)

2. Belgio E, Kapitonova E, Chimeliov J, Duffy CDP, Ungerer P, Valkrunas L, Ruban AV. 2014 Economic photo-protection in photosystem II that retains a complete light harvesting system with slow energy traps. *Nat. Commun.* **5**, 4433. (doi:10.1038/ncomms5433)

3. Lin MT, Occhialiana A, Andralojc PJ, Parry MA, Hanson MR. 2014 A faster Rubisco with potential to increase photosynthesis in crops. *Nature* **513**, 547–550. (doi:10.1038/nature13776)

4. Engineer CB, Ghassemain M, Anderson JC, Paek SC, Hu H, Schroeder JI. 2014 Carbonic anhydrases, EPF2 and a novel protease mediate CO_2 control of stomatal development. *Nature* **513**, 246–250. (doi:10.1038/nature13452)

5. Romero E *et al.* 2014 Quantum coherence in photosynthesis for efficient solar-energy conversion. *Nat. Phys.* **10**, 676–682. (doi:10.1038/nphys3017)

6. Woehle C, Dagan T, Landan G, Vardi A, Rosenwasser S. 2017 Expansion of the redox-sensitive proteome coincides with the plastid endosymbiosis. *Nat. Plants* **3**, 17066. (doi:10.1038/nplants.2017.66)

7. Martin WF, Sies H. 2017 Genomic redox footprints. *Nat. Plants* **3**, 17071. (doi:10.1038/nplants.2017.71)

8. Falkowski PG, Lin H, Gorbunov MY. 2017 What limits photosynthetic energy conversion efficiency in nature? Lessons from the oceans. *Phil. Trans. R. Soc. B* **372**, 20160376. (doi:10.1098/rstb.2016.0376)

9. Ma F, Swainsbury DJK, Jones MR, van Grondelle R. 2017 Photoprotection through ultrafast charge recombination in photochemical reaction centres under oxidizing conditions. *Phil. Trans. R. Soc. B* **372**, 20160378. (doi:10.1098/rstb.2016.0378)

10. Feilke K, Ajlani G, Krieger-Liszkay A. 2017 Overexpression of plastid terminal oxidase in *Synechocystis* sp. PCC 6803 alters cellular redox state. *Phil. Trans. R. Soc. B* **372**, 20160379. (doi:10.1098/rstb.2016.0379)

11. Becková M, Yu J, Krynická V, Kozlo A, Shao S, Koník P, Komenda J, Murray JW, Nixon PJ. 2017 Structure of Psb29/Thf1 and its association with the FtsH protease complex involved in photosystem II repair in cyanobacteria. *Phil. Trans. R. Soc. B* **372**, 20160394. (doi:10.1098/rstb.2016.0394)

12. Kerfeld CA. 2017 A bioarchitectonic approach to the modular engineering of metabolism. *Phil. Trans. R. Soc. B* **372**, 20160387. (doi:10.1098/rstb.2016.0387)

13. Ruban AV. 2017 Quantifying the efficiency of photoprotection. *Phil. Trans. R. Soc. B* **372**, 20160393. (doi:10.1098/rstb.2016.0393)

14. Ruban AV. 2016 Non-photochemical chlorophyll fluorescence quenching: mechanism and effectiveness in protecting plants against photodamage. *Plant Physiol.* **170**, 1903–1916. (doi:10.1104/pp.15.01935)

15. Ruban AV. 2017 Crops on fast track for light. *Nature* **541**, 36–37. (doi:10.1038/541036a)

16. Davis GA, Rutherford AW, Kramer DM. 2017 Hacking the thylakoid proton motive force for improved photosynthesis: modulating ion flux rates that control proton motive force partitioning into $\Delta\psi$ and ΔpH. *Phil. Trans. R. Soc. B* **372**, 20160381. (doi:10.1098/rstb.2016.0381)

17. Gollan PJ, Lima-Melo Y, Tiwari A, Tikkanen M, Aro E-M. 2017 Interaction between photosynthetic electron transport and chloroplast sinks triggers protection and signalling important for plant productivity. *Phil. Trans. R. Soc. B* **372**, 20160390. (doi:10.1098/rstb.2016.0390)

18. Nikkanen L, Toivola J, Diaz MG, Rintamäki E. 2017 Chloroplast thioredoxin systems: prospects for improving photosynthesis. *Phil. Trans. R. Soc. B* **372**, 20160474. (doi:10.1098/rstb.2016.0474)

19. Karpinska B, Alomrani SO, Foyer CH. 2017 Inhibitor-induced oxidation of the nucleus and cytosol in *Arabidopsis thaliana*: implications for organelle to nucleus retrograde signalling. *Phil. Trans. R. Soc. B* **372**, 20160392. (doi:10.1098/rstb.2016.0392)

20. Dann M, Leister D. 2017 Enhancing (crop) plant photosynthesis by introducing novel genetic diversity. *Phil. Trans. R. Soc. B* **372**, 20160380. (doi:10.1098/rstb.2016.0380)

21. Nuccio ML *et al.* 2017 Strategies and tools to improve crop productivity by targeting photosynthesis. *Phil. Trans. R. Soc. B* **372**, 20160377. (doi:10.1098/rstb.2016.0377)

22. Taylor SH, Long SP. 2017 Slow induction of photosynthesis on shade to sun transitions in wheat may cost at least 21% of productivity. *Phil. Trans. R. Soc. B* **372**, 20160543. (doi:10.1098/rstb.2016.0543)

23. Driever SM *et al.* 2017 Increased SBPase activity improves photosynthesis and grain yield in wheat grown in greenhouse conditions. *Phil. Trans. R. Soc. B* **372**, 20160384. (doi:10.1098/rstb.2016.0384)

24. Reyna-Llorens I, Hibberd JM. 2017 Recruitment of pre-existing networks during the evolution of C4 photosynthesis. *Phil. Trans. R. Soc. B* **372**, 20160386. (doi:10.1098/rstb.2016.0386)

25. Kromdijk J, Głowacka K, Leonelli L, Gabilly ST, Iwai M, Niyogi KK, Long SP. 2017 Improving photosynthesis and crop productivity by accelerating recovery from photoprotection. *Science* **354**, 857–860. (doi:10.1126/science.aai8878)