REVIEW

Engineering photosynthesis: progress and perspectives

[version 1; peer review: 2 approved]

Douglas J. Orr1, Auderlan M. Pereira2,3, Paula da Fonseca Pereira2,3, Ítalo A. Pereira-Lima2,3, Agustin Zsögön3, Wagner L. Araújo1,2,3

1Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK
2Max-Planck Partner Group at the Departamento de Biologia Vegetal, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil
3Departamento de Biologia Vegetal, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil

First published: 26 Oct 2017, 6(F1000 Faculty Rev):1891
https://doi.org/10.12688/f1000research.12181.1

Abstract
Photosynthesis is the basis of primary productivity on the planet. Crop breeding has sustained steady improvements in yield to keep pace with population growth increases. Yet these advances have not resulted from improving the photosynthetic process per se but rather of altering the way carbon is partitioned within the plant. Mounting evidence suggests that the rate at which crop yields can be boosted by traditional plant breeding approaches is wavering, and they may reach a "yield ceiling" in the foreseeable future. Further increases in yield will likely depend on the targeted manipulation of plant metabolism. Improving photosynthesis poses one such route, with simulations indicating it could have a significant transformative influence on enhancing crop productivity. Here, we summarize recent advances of alternative approaches for the manipulation and enhancement of photosynthesis and their possible application for crop improvement.

Keywords
photosynthesis, crop improvement, Rubisco, Calvin-Benson cycle, CCM, light-use efficiency

Any comments on the article can be found at the end of the article.
Introduction

Photosynthesis consists of a series of biochemical reactions whereby plants use sunlight to reduce atmospheric CO$_2$ into carbohydrates, releasing O$_2$ as a byproduct. The first photosynthetic organisms appeared at least 2.5 billion years ago (Archean Eon) and were single-celled ocean-dwelling prokaryotes. Thus, photosynthesis was originally an aquatic-based process occurring in a strongly reducing atmosphere. The transition to a terrestrial environment and to an oxidizing atmosphere subsequently shaped the photosynthetic pathway into its current form. Plant cells contain chloroplasts, which are organelles that originated from endosymbiosis of a cyanobacteria-like organism. Chloroplasts harbor the photosynthetic machinery and confer upon plants their characteristic green color. Sunlight within the visible spectrum is captured by chlorophyll and other accessory pigments and used to energize electrons derived from a water molecule in the thylakoid membrane of the chloroplasts. High-energy electrons are then transferred to carrier molecules, which can donate them for the reduction of gaseous CO$_2$ to triose-phosphates in the chloroplast stroma. The enzyme responsible for the first step in CO$_2$ fixation is ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). The Calvin-Benson cycle allows for the regeneration of the ribulose-1,5-bisphosphate molecule (RuBP), whereas the fixed CO$_2$ molecule moves on to anabolic pathways for sucrose and starch biosynthesis.

The high energetic value of sucrose and starch drove the domestication of plants to create crops, spawning the agricultural revolution and the transition from a hunter-gatherer to the current agricultural-industrial society. It is thus clear that photosynthesis is a cornerstone of human civilization and, as such, the object of intense basic and applied research in the face of mounting pressure to feed an increasing population. Decades of research have provided a detailed picture of the intricacies of the photosynthetic process and suggested potential avenues for its improvement. A broad range of opportunities have been identified to improve photosynthetic efficiency; for recent detailed reviews, see 7,9–11. We now know, for instance, that owing to the complex interaction between physiological and environmental parameters photosynthetic rate does not directly extrapolate to whole plant growth rate. Breeders have managed to increase yields via processes that alter carbon partitioning rather than improving photosynthesis. Breeding better crops through improved photosynthesis is a long-sought goal but so far has remained unrealized because of the multiplicity of challenges involved. Here, we briefly review the current state of the ongoing efforts in molecular engineering to improve photosynthesis, plant growth, and yield (Figure 1).

We start by summarizing recent efforts to optimize Rubisco performance. Rubisco is an ancient enzyme that evolved in a CO$_2$-rich atmosphere devoid of O$_2$. It is a slow (turnover rate of ~3–5 s$^{-1}$ compared to around >100 s$^{-1}$ for most enzymes) and error-prone enzyme (fixing O$_2$ instead of CO$_2$ in up to one-third of reactions). The unavoidable side reaction with O$_2$, oxygenation of RuBP, leads to the photorespiratory cycle, which “recycles” unproductive reaction products. However, this recycling comes at the cost of previously fixed carbon and a further loss of chemical energy. To make up for such shortcomings, plants...
generally contain large amounts of Rubisco (up to 50% of leaf total protein), which entails a large N-investment\(^7\). Despite the significant natural variation in Rubisco catalysis and structure, it maintains a conserved, complex, catalytic mechanism that intrinsically imparts a trade-off between an enzyme specificity for CO\(_2\) over O\(_2\), and its catalytic speed. Next, we synthesize recent work aimed at optimizing other enzymes of the Calvin-Benson cycle. Theoretical and experimental data suggest that under non-Rubisco-limiting conditions other enzymes in the cycle begin to limit photosynthetic rate\(^11\). We summarize recent progress on the manipulation of carbon concentrating mechanisms (CCMs), which are evolutionary solutions to counter Rubisco inefficiency. Well-known examples in plants include C\(_4\) photosynthesis and crassulacean acid metabolism (CAM)\(^5\)\(^\text{-}^7\). C\(_4\) and CAM photosynthesis are highly efficient processes\(^3\), however, plants using these processes are relatively restricted in number within the plant kingdom\(^8\)\(^\text{-}^10\). Exciting recent developments in efforts to introduce CCMs from non-plants are also discussed and summarized in Figure 1. We additionally emphasize the challenges and opportunities to further understand the complex interplay between photosynthesis and related metabolic processes that has limited success in the manipulation and improvement of photosynthesis.

**Engineering Rubisco**

The observed inefficiencies of Rubisco such as a slow CO\(_2\)-fixation rate and poor specificity for CO\(_2\) over O\(_2\) have made it a key engineering target to improve photosynthesis in crop plants (for reviews, see \(^8\)\(^\text{-}^17\)). Whilst there is a good understanding of the reaction mechanism\(^18\)\(^\text{-}^21\), engineering efforts have yet to produce the holy grail of a “super Rubisco”, as efforts to modify one aspect of its catalytic biochemistry typically come at a cost to another\(^22\)\(^\text{-}^27\). A notable discovery was that a single amino acid mutation acted as a catalytic “switch” to convert Rubisco from different *Flaveria* species from a “C\(_4\)” style enzyme to a “C\(_3\)” style and vice versa\(^27\). This clearly demonstrates the potential for manipulating the performance of Rubisco with targeted changes inferred from comparisons of natural diversity in enzyme sequence and catalysis. This has spurred a recent influx of data on the natural diversity of Rubisco in a bid to identify amino acid changes that can improve its catalysis in plants\(^28\)\(^\text{-}^30\). Insights into how Rubisco and other photosynthetic traits have co-evolved are critical to guiding kinetic characteristics for an improved crop Rubisco under differing environmental scenarios (e.g. \(^37\)\(^,\) \(^38\)). Rubisco screens extending outside of the plant realm have also proved highly informative. For example, the Rubisco from diatom and haptophyte microalgae has undergone differing selection pressures that see its kinetic properties diverge from the canonical trade-off between catalytic rate and affinity for CO\(_2\)\(^39\)\(^\text{-}^40\), providing possible new areas of exploration for improving Rubisco efficiency\(^40\).

A key challenge in engineering Rubisco in plants is that it is a hefty 550 kDa hexadecameric complex comprising eight large subunits (ca. 52 kDa each) and eight small subunits (ca. 13 to 15 kDa). It is produced through an exquisite synthesis and assembly process that is dependent on a number of nucleus- and chloroplast-encoded components\(^42\). Typically, research has focused on the chloroplast-encoded large subunits, which contain the catalytic sites and can be routinely manipulated in tobacco for functional genomic studies\(^24\)\(^,\) \(^41\). More recent reports have highlighted the impact on catalysis of manipulating the small subunit\(^46\)\(^\text{-}^47\). The nuclear-encoded small subunit gene family (RbcS) is therefore a growing target for engineering, as nuclear transformation is already established in many species compared to the relatively few species amenable to chloroplast transformation\(^42\)\(^\text{-}^48\). An alternative approach to altering the extant Rubisco in a crop species is to replace it with better-performing natural variants, although this is subject to similar technical limitations. Introduction of foreign Rubisco is typically hampered by the complicated assembly requirements of the enzyme in the chloroplast (see \(^45\)), though important advances have been made in co-engineering introduced Rubisco alongside assembly chaperones\(^20\). Besides efforts to introduce a cyanobacterial CCM into higher plants (see below), the Rubisco from *Synechococcus elongatus* has now been successfully introduced into tobacco\(^1\) and can support growth at elevated CO\(_2\)\(^5\). Whilst supporting much higher catalytic rates than higher plant Rubisco, the Rubisco from cyanobacteria has lower CO\(_2\) affinity and specificity for CO\(_2\) over O\(_2\). Thus, for cyanobacteria Rubisco to support plant growth at ambient CO\(_2\) levels, co-engineering of a functional CCM is required\(^9\).

**Calvin-Benson cycle optimization**

It has long been recognized that other enzymes in the Calvin-Benson cycle represent viable targets to accelerate carbon fixation in plants (reviewed in \(^9\)\(^,\) \(^18\)\(^\text{-}^56\)). Recently, efforts have built on prior success in overexpressing SSBpase (sedoheptulose-1,7-bisphosphatase) to improve growth in tobacco and rice\(^5\)\(^,\) \(^37\)\(^,\) \(^38\). These efforts have now expanded to include other Calvin-Benson enzymes in a combinatorial manner to avoid creating new bottlenecks in different parts of the cycle\(^59\)\(^,\) \(^60\). Increases in plant biomass have also been obtained by jointly manipulating genes in the Calvin-Benson cycle and the photosynthetic pathway\(^60\). An alternative approach has been to avert the CO\(_2\) and energy costs of photorespiration by introducing synthetic “photorespiratory bypass” pathways in the chloroplast that direct CO\(_2\) release in the proximity of Rubisco\(^51\)\(^\text{-}^64\). The potential benefits and caveats of the differing bypass strategies are reviewed in \(^65\)\(^\text{-}^66\).

In addition to the overexpression of native enzymes (Figure 1), a number of studies have also shown effects through the expression of foreign membrane transporter proteins in both model\(^59\)\(^,\) \(^57\)\(^\text{-}^60\) and crop species such as soybean and rice\(^65\)\(^,\) \(^67\). These genes derived from cyanobacteria include the frequently studied but functionally-unknown membrane transporter protein IctB\(^7\). Introducing IctB has not always improved crop growth: for example, in one case changes were noted in photosynthetic rate without an increase in biomass\(^1\). In contrast, IctB expression improved growth in crop species such as wheat in the glasshouse\(^7\) and soybean in the field\(^7\). Importantly, extended field testing under future environmental scenarios through free-air CO\(_2\) enrichment (FACE) experiments enables validation of *in silico* and glasshouse-based predictions. For example, in soybean one such manipulation has been shown to counteract some of the negative impact of future climate on yield\(^6\). These inconsistent findings underscore the frequent discontinuity in crop yield predictions between glasshouse and field trials and the importance of FACE field studies for screening the suitability of natural and engineered crops for future climates.
Optimizing response to changes in light-use efficiency

Major losses of energy conversion during plant biomass formation occur during light absorption and the photochemical reactions. Dramatic increases in tobacco growth rate in the field were obtained recently by improving the rate of relaxation of photoprotection (non-photochemical quenching, NPQ). NPQ is the process by which plants dissipate excess light as heat when they receive more than they are capable of using. Modeling suggested this as an area where there is room for improvement. Combinations of genes involved in photoprotection were transformed into tobacco and those that accelerated the relaxation of NPQ increased the rate of biomass production by as much as 20% in greenhouse trials and around 15% in duplicated field trials. The modifications involved introducing multiple genes expressing key components of the xanthophyll cycle and the PsbS subunit of photosystem-II. This combination allowed the plants to more quickly adapt to fluctuating light, turning off photoprotection and using light for photosynthesis rather than continuing to dissipate it as heat after a decrease in light level. The conservation of NPQ across plants suggests this approach may also serve to improve the growth of other crops. However, the mechanisms allowing plant cells to cope with the excess energy, such as NPQ, tend to decrease the overall efficiency of energy storage, since surface cells exposed to the light dissipate much of the available energy whereas cells in the lower layers remain light limited. Thus, the temptation to increase the capacity to process the influx of energy by the photosynthetic apparatus is a challenge that must be pursued to ameliorate energy losses during plant photosynthesis (reviewed in 79). Increasing light energy capture might also be feasible by incorporating the bacteriochlorophylls found in many anoxygenic photosynthetic organisms into one of the photosystems in plants with the aim of extending the light absorption spectrum by plants to the far red region out to ~1,100 nm.

Changes in the antenna size of the photosystems have also been suggested as a route that could enhance solar conversion efficiency while reducing NPQ. This assumption is based on the fact that the antennae trap more light than can be used for photochemistry. Based on this, the theory is that in plants with a reduced number of light-harvesting pigments (e.g. chlorophyll and carotenoids) per photosystem, solar energy conversion efficiency could be significantly enhanced. Changes in the leaf optical properties would alleviate over-absorption and mitigate efficiency losses associated with wasteful dissipation of sunlight by the upper canopy. Furthermore, they could bring about enhancements of photosynthetic productivity due to greater transmittance of light to lower layers, thus improving canopy light distribution and canopy photosynthesis. This truncated light-harvesting antenna (TLA) concept has been successfully applied in microalgae and cyanobacteria. Recent work has shown that TLA enhances both photosynthesis and plant canopy biomass accumulation under high-density cultivation conditions in both tobacco and rice. This approach presents intrinsic practical limitations and challenges, but ongoing research suggests that expanded efforts could ultimately optimize this exciting biotechnological process.

Synthetic biology for CO₂ fixation in non-plants

Synthetic photosynthesis has made exciting progress recently via the incorporation of non-native Calvin-Benson-like carbon assimilation in Escherichia coli. The highlight was the production of a bacterium that is capable of making sugars and other life-preserving metabolites from atmospheric CO₂. Although at this stage both energy and reducing power are required through the oxidation of an external organic acid in an isolated metabolic module and thus no net carbon gain is achieved, this discovery clearly proves the potential of synthetic biology to optimize pathways of biotechnological significance and may even lead to new avenues for optimizing CO₂ fixation in plants. Along such lines is the successful development of a synthetic carbon fixation pathway that functions efficiently in vitro but faces significant challenges for it to be compatible in a biological context.

Introducing the C₄ cycle in C₃ crops

C₄ photosynthesis has evolved independently of C₃ photosynthesis in several angiosperm families during the last 25 million years in at least 66 independent events. Despite the frequency of these events, the evolution of C₄ photosynthesis is not distributed evenly in the plant kingdom. This multiple parallel evolution appears to have occurred as an adaptive response to low atmospheric CO₂ concentrations and high temperature. The transition from C₃ to C₄ plants requires the evolution of both morphological and physiological traits. Among these, the differentiation of photosynthetically active vascular bundle sheath cells, modification in the biochemistry of several enzymes, and increased intercellular and intracellular transport of metabolites are of pivotal significance. This makes the evolution of such a complex trait system in one single step highly unlikely. The first evidence of evolutionary intermediate C₃–C₄ forms was reported in the 1970s, and this spurred intensive efforts to understand the mechanistic bases of the transition from C₃ to C₄.

A better understanding of the initial events that occurred during the C₃ evolution to C₃–C₄ intermediates and then to C₄ plants can contribute to increasing photosynthetic efficiency in C₃ plants. Whilst C₄ photosynthesis requires considerable additional ATP, the plants benefit from enhanced biomass production and improvements in nitrogen and water use efficiencies. Using complementary approaches, including genome and transcriptome analyses, the international C₄ rice consortium is working toward introducing the C₄ mechanism into rice. This research initiative has already produced exciting results, including the identification of metabolite transporters and transcription factors. Although the genes identified are potentially useful for engineering C₃ rice, clearly further investigation is required. Additional examination of temporal, spatial, and environmental dynamics spanning C₃ through C₃–C₄ intermediacy and true C₄ species will no doubt be highly informative for identifying useful genes and regulatory components.

Recent efforts have expanded the number of genera studied beyond Flaveria species to include Cleome and Moricandia, two close relatives of the model C₄ Arabidopsis, which both contain intermediate as well as true C₄ species. This provides a
powerful opportunity to accelerate advances through comparison
with the large amount of data already available for Arabidopsis
in order to find the minimal genetic basis of C₄ photosynthesis.
This strategy has the growing potential to promote substantial
increments in the yield of C₄ crops usually cultivated in dry and
hot areas⁴⁵. Importantly, at least some of the technical difficulties
associated with separately isolating pure bundle sheath and
mesophyll cells from C₄ plants have been overcome in Arabidopsis⁴⁸. A very large-scale analysis of the bundle sheath
translatome in Arabidopsis demonstrated its high similarity with
the translatome in the root pericycle cells⁴⁹. This study not only
provides the foundation to enhance our understanding of the
evolutionary function of bundle sheath cells in C₄ plants but also
indicates that a highly similar and conserved regulatory net-
work might sustain bundle sheath and pericycle cell functionality
in Arabidopsis thaliana. Although several open questions remain,
it seems clear that these types of studies are likely to be key to
understanding the genetic triggers needed to re-organize the
anatomy, gene expression, and biochemistry within C₄ plants,
possibly paving the way toward producing C₄ rice.

Whilst perhaps less advanced than the efforts to understand and engineer C₄ photosynthesis, a number of groups are working to
better understand the key elements required for CAM
photosynthesis⁵⁰,⁵¹. CAM plants are typically highly effi-
cient in their use of water, and engineering of CAM into food or
bioenergy crops may prove most beneficial by improving crop
water use efficiency and expanding the land area capable of
supporting agriculture⁵². CAM species may also serve as a
suitable source of high-temperature-adapted enzymes of potential
application in photosynthetic engineering⁵³.

Introducing non-plant CCMs into C₄ plants
One approach to improving plant photosynthesis is using engi-
neering to implement CCMs from other photosynthetic organisms
such as cyanobacteria or algae. While components of the CCM
in cyanobacteria and algae can differ, both systems function to
create a high-CO₂ environment around Rubisco to maintain high CO₂
levels. In some instances, this association is contained within a protein micro-compartment to limit CO₂ escape and ensure high HCO₃⁻
levels can be sustained in the cytosol.

Cyanobacterial CCM
Amongst the CCMs currently being engineered into plants, the
cyanobacterial carboxysome-based system has made the most
striking progress in recent years. With a stronger—but still
incomplete—understanding of the construction of this bacterial
microcompartment (for in-depth reviews, see 72,105–109), sig-
nificant progress has been made in assembling partial carboxy-
somes in higher plants using tobacco as a model system⁴⁰. Lin
and colleagues¹¹ demonstrated the assembly of various complex
structures by expressing as few as three β-carboxysome proteins.
As mentioned above, parallel work on introducing a cyanobac-
terial Rubisco into tobacco was also successful⁴², with plants
expressing cyanobacteria Rubisco and either the chaperone
RbcX or the carboxyosomal CcmM35 protein viable at elevated
CO₂. These are key advances to build upon through the addition
of further components to assemble a fully functional carboxy-
some shell⁴³, and combining these to localize Rubisco inside the
carboxosome will be a critical next step toward functionality. The internal components such as CcmM35 are thought to be important
for the true icosahedral structure to be formed⁴⁴. The ability
to assemble bacterial microcompartments also has implications
beyond crop productivity⁴⁵.

An important consideration for introducing a full cyanobacte-
rial CCM into higher plants is creating a compatible HCO₃⁻/CO₂
environment by concentrating CO₂ inside the carboxosome shell, removing stromal carbonic anhydrase, and introducing
HCO₃⁻ pumps to increase the bicarbonate concentration in the
stroma⁴⁵,⁴⁶,⁴⁷. Progress has been made in attempting to intro-
duce transporters into tobacco⁴⁸,⁴⁹, and issues related to correct
localization are being targeted through a better understanding of
transit peptides (e.g. 115,116). Recent progress in other bacterial
microcompartments beyond the cyanobacterial carboxysome are
also providing key insights for targeting protein localization and
the assembly of these complex structures (reviewed in 110).

Pyrenoids
Although engineering an algal pyrenoid-based CCM into higher
plants is less developed than cyanobacteria CCMs⁴², there have
recently been a number of key discoveries related to pyrenoid
structure and function in the model Chlamydomonas reinhardtii
(see 105,109,115,116). Discoveries such as the highly disordered
linker protein essential pyrenoid component 1 (EPYC1) that
pulls Rubisco together⁵⁰ and that a loop structure on the Rubisco
small subunit is necessary for pyrenoid formation⁵¹ supply tar-
gets for engineering in plants. For example, mutagenesis of this
loop region has shown its modification has no effects on Rubisco
catalysis in Arabidopsis⁵². Recent advances in the availability of
a mutant Chlamydomonas library for functional studies⁵³ will
likely accelerate advances in understanding, and engineering,
algal pyrenoids. Increasing data on the CCM of other non-green
micro-algae may also help better understand pyrenoid function and
structural diversity⁵⁴,⁵⁵.

Future perspectives and directions
Conventional crop breeding has thus far been sufficient to avert
the dire Malthusian predictions of food shortage for a growing
human population. Most projections suggest that novel yield-
enhancing solutions are needed to avoid global crop produc-
tion reaching a plateau. Genetic manipulation has been used to
successfully engineer simple traits, such as insect and weed
resistance. More refined molecular tinkering holds the promise
of spectacular gains if fundamental pathways are targeted.
Photosynthesis is one such pathway.

Synthetic biology is making large steps in engineering alternate
CCM mechanisms into higher plants, in addition to
efforts in manipulating elements of the Calvin-Benson cycle
already present. Although mesophyll conductance to CO₂ had
been a relatively overlooked limiting factor until recently, it
is now considered a promising potential target for increasing
photosynthesis⁵⁶. It seems clear that expanded research efforts are
Currently required to build upon many of the technologies described above by, for example, enhancing our understanding of CAM metabolism and introducing alternative non-plant CCMs into C4 plants. Overcoming these challenges will require sustained investments in long-term research programs, with some of these research areas currently being advanced through large-scale, privately funded projects.

Ultimately, in the case of C3 rice, necessity for development in a C4 species as well as sufficiency for engineering C4 rice will need to be considered when determining gene function. Existing candidate regulators are currently being functionally validated, and this is ongoing: knockdown experiments in maize and setaria are examining necessity, while overexpression in rice is being used to scrutinize sufficiency. Future advances in engineering C4 rice will need to involve integrated analysis of these experiments together with further comprehension of the related gene regulatory networks. We posit that the successful integration of these different characteristics, as discussed above, coupled with the identification of the key regulators of C4 morphoanatomical pattern and the development of a strategy of how the C4 plant could be genetically altered allowing both the introduction and the establishment of the C4 pathway should be a significant breakthrough in the field of synthetic biology. Recent advances and ongoing incremental findings suggest that improved crop photosynthesis could assist towards feeding a growing population in the near future.

Competing interests
The authors declare that they have no competing interests.

Grant information
This work was made possible through financial support from the Max Planck Society, the National Council for Scientific and Technological Development (CNPq-Brazil grant no. 402511/2016-6), and the Foundation for Research Assistance of the Minas Gerais State (FAPEMIG-Brazil grant no. APQ 01078-15 and APQ 01357-14) to WLA. We also thank the scholarships granted by the Brazilian Federal Agency for Support and Evaluation of Graduate Education (CAPES-Brazil) to AMP and IAP-L. Research fellowship granted by CNPq-Brazil (grant no. 306281/2016-3) to WLA is also gratefully acknowledged.

The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Acknowledgements
DJO acknowledges support through a sub-contract from the University of Illinois as part of the Bill and Melinda Gates Foundation award “RIPE: Realizing Increased Photosynthetic Efficiency”. We also thank the reviewers for their suggestions and comments which helped improve the manuscript and apologize to our colleagues whose work could not be cited due to space limitations.

References
1. Niklas KJ. Plant Evolution. 1st ed. Chicago, USA: University of Chicago Press, 2016; 560. Reference Source
2. Hohmann-Marriott MF, Blankenship RE. Evolution of photosynthesis. Annu Rev Plant Biol. 2011; 62: 515–48. Published Abstract | Publisher Full Text
3. Nelson N, Ben-Shem A. The complex architecture of oxygenic photosynthesis. Nat Rev Mol Cell Biol. 2004; 5(12): 971–82. Published Abstract | Publisher Full Text
4. Martin W, Schiebel R, Schnarrenberger C. The Calvin Cycle and its regulation. in Springer Netherlands 2000; 9–51. Published Full Text
5. Harlan JR. Crops and man. American Society of Agronomy. 1975. Reference Source
6. Evans LT. Feeding the one billion: plants and population growth. Cambridge, UK: Cambridge University Press, 1998. Reference Source
7. Ort DR, Merchant SS, Alric J, et al. Redesigning photosynthesis to sustainably meet global food and bioenergy demand. Proc Natl Acad Sci U S A. 2015; 112(28): 8529–36. Published Abstract | Publisher Full Text | Free Full Text | F1000 Recommendation
8. Whitney SM, Houzat RL, Alonso H. Advancing our understanding and capacity to engineer nature’s CO2-sequestering enzyme, Rubisco. Plant Physiol. 2011; 155(1): 27–35. Published Abstract | Publisher Full Text | Free Full Text
9. Raines CA. Increasing photosynthetic carbon assimilation in C3 plants to improve crop yield: current and future strategies. Plant Physiol. 2011; 155(1): 36–42. Published Abstract | Publisher Full Text | Free Full Text
10. Maurino VG, Weber AP. Engineering photosynthesis in plants and synthetic microorganisms. J Exp Bot. 2013; 64(3): 743–51. Published Abstract | Publisher Full Text
11. Long SP, Marshall-Colon A, Zhu X. Meeting the global food demand of the future by engineering crop photosynthesis and yield potential. Cell. 2015; 161(1): 56–66. Published Abstract | Publisher Full Text | F1000 Recommendation
12. Evans JR. Improving photosynthesis. Plant Physiol. 2013; 162(4): 1780–93. Published Abstract | Publisher Full Text | Free Full Text
13. Fischer A, Byerlee D, Edmeades G. Crop yields and global food security: will yield increase continue to feed the world? Canberra, Australia: Australian Centre for International Agricultural Research, 2014; 634. Reference Source
14. Tcherkez GG, Farquhar GD, Andrews TJ. Despite slow catalysis and confused substrate specificity, all ribulose bisphosphate carboxylases may be nearly perfectly optimized. Proc Natl Acad Sci U S A. 2006; 103(19): 7246–51. Published Abstract | Publisher Full Text | Free Full Text | F1000 Recommendation
15. Timm S, Florian A, Fernie AR, et al. The regulatory interplay between photorespiration and photosynthesis. J Exp Bot. 2016; 67(10): 2923–9. Published Abstract | Publisher Full Text
16. Betti M, Bauwe H, Busch FA, et al. Manipulating photorespiration to increase plant productivity: recent advances and perspectives for crop improvement. J Exp Bot. 2016; 67(10): 2977–88. Published Abstract | Publisher Full Text | Free Full Text
17. Camo-Silva E, Scales JC, Maitiwick PJ, et al. Optimizing Rubisco and its regulation for greater resource use efficiency. Plant Cell Environ. 2010; 33(9): 1817–32. Published Abstract | Publisher Full Text | F1000 Recommendation
18. Raines CA. The Calvin cycle revisited. Photosynth Res. 2003; 75(1): 1–10. Published Abstract | Publisher Full Text

Page 7 of 11
39. Prins A, Schlüter U, Eisenhut M, et al.: On the Evolutionary Origin of CAM Photosynthesis. Plant Physiol. 2015; 174(2): 473–7.
Published Abstract | Publisher Full Text | Free Full Text

20. Winter K, Holton JA, Smith JA: Crassulacean acid metabolism: a continuous or discrete trait? New Phytol. 2015; 206(1): 73–8.
Published Abstract | Publisher Full Text | Free Full Text

19. Zhu X, Long SP, Ort DR: What is the maximum efficiency with which photosynthesis can convert solar energy into biomass? Curri Opin Biotechnol. 2008; 19(2): 153–61.
Published Abstract | Publisher Full Text | F1000 Recommendation

18. Sage RF: A portrait of the C4 photosynthetic family on the 50th anniversary of its discovery: species number, evolutionary lineages, and Hall of Fame. J Exp Bot. 2017; 68(2): 4039–56.
Published Abstract | Publisher Full Text | Free Full Text

17. Huang P, Studer AJ, Schnable JC, et al.: Catalysis and regulation in Rubisco. Photosynth Res. 2013; 116(3): 1621–36.
Published Abstract | Publisher Full Text | Free Full Text

16. Andersson I: Rubisco Catalytic Properties and Temperature Response to Improve Crop Photosynthetic Efficiency. Plant Physiol. 2016; 172(2): 707–17.
Published Abstract | Publisher Full Text | Free Full Text

15. Galmés J, Kapralov MV, Andralojc PJ, et al.: Temperature responses of Rubisco from Paniceae grasses provide opportunities for improving C3 photosynthesis. Nat Plants. 2016; 2: 16186.
Published Abstract | Publisher Full Text | F1000 Recommendation

14. Whitney SM, Sharwood RE, Or D, et al.: Isoenzyme 309 acts as a C4 catalytic switch that increases ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco) carboxylation rate in Flaviera. Proc Natl Acad Sci USA. 2011; 108(35): 14688–93.
Published Abstract | Publisher Full Text | Free Full Text

13. Tcherkez G: Modelling the reaction mechanism of ribulose-1,5-bisphosphate carboxylase/oxygenase and consequences for kinetic parameters. Plant Cell Environ. 2013; 36(9): 1586–96.
Published Abstract | Publisher Full Text | Free Full Text

12. Anderson I: C4 photosynthesis and growth by coexpressing its ancillary RA71 chaperone. Proc Natl Acad Sci USA. 2015; 112(11): 3564–9.
Published Abstract | Publisher Full Text | Free Full Text

11. Chen X, Yang J, Yu Z, et al.: Photosynthetic Trichomes Contain a Specific Rubisco with a Modified pH-Dependent Activity. Plant Physiol. 2017; 174(2): 2110–20.
Published Abstract | Publisher Full Text | Free Full Text | F1000 Recommendation

10. Bröcker A, Whitney SM, Hartl FU, et al.: Biogenesis and Metabolic Maintenance of Rubisco. Plant Physiol. 2017; 168: 29–60.
Published Abstract | Publisher Full Text | Free Full Text

9. Whitmarsh SM, Birch R, Kelso C, et al.: Improving recombinant Rubisco biogenesis, plant photosynthesis and growth by coexpressing its ancillary RA71 chaperone. Proc Natl Acad Sci USA. 2015; 112(11): 3564–9.
Published Abstract | Publisher Full Text | Free Full Text

8. Lin MT, Occhialini A, Andralojc PJ, et al.: A Faster Rubisco with potential to increase photosynthesis in crops. Nature. 2014; 513(7519): 547–50.
Published Abstract | Publisher Full Text | Free Full Text

7. Occhialini A, Lin MT, Andralojc PJ, et al.: Transgenic tobacco plants with improved cyanobacterialRubisco expression but no extra assembly factors grow at near wild-type rates if provided with elevated CO2. Plant J. 2016; 85(1): 148–60.
Published Abstract | Publisher Full Text | Free Full Text

6. Price GD, Howitt SM: Plant science: Towards turbocharged photosynthesis. Nature. 2014; 513(7519): 497–8.
Published Abstract | Publisher Full Text | Free Full Text

5. Bröcker A, Whitney SM, Hartl FU, et al.: Biogenesis and Metabolic Maintenance of Rubisco. Plant Physiol. 2017; 168: 29–60.
Published Abstract | Publisher Full Text | Free Full Text

4. Whitmarsh SM, Birch R, Kelso C, et al.: Improving recombinant Rubisco biogenesis, plant photosynthesis and growth by coexpressing its ancillary RA71 chaperone. Proc Natl Acad Sci USA. 2015; 112(11): 3564–9.
Published Abstract | Publisher Full Text | Free Full Text

3. Lin MT, Occhialini A, Andralojc PJ, et al.: A Faster Rubisco with potential to increase photosynthesis in crops. Nature. 2014; 513(7519): 547–50.
Published Abstract | Publisher Full Text | Free Full Text

2. Occhialini A, Lin MT, Andralojc PJ, et al.: Transgenic tobacco plants with improved cyanobacterialRubisco expression but no extra assembly factors grow at near wild-type rates if provided with elevated CO2. Plant J. 2016; 85(1): 148–60.
Published Abstract | Publisher Full Text | Free Full Text

1. Price GD, Howitt SM: Plant science: Towards turbocharged photosynthesis. Nature. 2014; 513(7519): 497–8.
Published Abstract | Publisher Full Text | Free Full Text
a Glycolate Oxidative Cycle into A. thaliana Chloroplasts Leads to Growth Improvement. Plant Sci. 2012; 182: 21–30. PubMed Abstract | Publisher Full Text | Free Full Text

62. Kebesch R, Nissen M, Thunvethir K, et al.: Chloroplastic photoprotective bypass increases photosynthesis and biomass production in Arabidopsis thaliana. Nat. Biotechnol. 2007; 25(5): 593–9. PubMed Abstract | Publisher Full Text | F1000 Recommendation

63. Nöke G, Houdelet M, Kreuzaler F, et al.: The expression of a recombinant glycolate dehydrogenase polyprotein in potato (Solanum tuberosum) strongly enhances photosynthesis and tuber yield. Plant Biotechnol. J. 2014; 12(6): 734–42. PubMed Abstract | Publisher Full Text

64. South PF, Walker BJ, Canavan AP, et al.: Bile Acid Sodium Symporter BAS5 Can Transport Glucololate and Is Involved in Photopreservative Metabolism in Arabidopsis thaliana. Plant Cell. 2017; 29(4): 808–23. PubMed Abstract | Publisher Full Text | Free Full Text | F1000 Recommendation

65. Maurino VG, Peterhansel C: Thermal energy dissipation on transfer from high to low light may cause large improvement in crop productivity by accelerating recovery from photoprotection. Plant Physiol. 2011; 156(2): 574–85. PubMed Abstract | Publisher Full Text | Free Full Text

66. Kebesch R, Nissen M, Thunvethir K, et al.: Chloroplastic photoprotective bypass increases photosynthesis and biomass production in Arabidopsis thaliana. Nat. Biotechnol. 2007; 25(5): 593–9. PubMed Abstract | Publisher Full Text | F1000 Recommendation

67. Melis S: Solar energy conversion efficiencies in photosynthesis: Minimizing the chlorophyll antenna to maximize efficiency. Plant Sci. 2009; 177(4): 272–80. Publisher Full Text

68. Korch W, Hagl G, Ngoy KK, et al.: Photosynthetic antenna engineering to improve crop yields. Plant. 2017; 245(5): 1009–20. PubMed Abstract | Publisher Full Text | Free Full Text

69. Polle JE, Kanakagiri SD, Melis S: A titl, a DNA insertional transformant of the green alga Chlamydomonas reinhardtii with a truncated light-harvesting chlorophyll antenna size. Plant. 2003; 217(1): 49–59. PubMed Abstract

70. Nakajima Y, Tasukii M, Ueda R: Improved productivity by reduction of the content of light-harvesting pigment in Chlamydomonas reinigranulata. J. Appl. Phycol. 2001; 13(2): 99–101. PubMed Abstract | Publisher Full Text

71. Muşşugru JH, Thomas-Hall S, Rupprecht J, et al.: Engineering photosynthetic light capture: impacts on improved solar energy to biomass conversion. Plant Biotechnol. J. 2007; 5(6): 802–14. PubMed Abstract | Publisher Full Text | Free Full Text

72. Kast H, Formighieri C, Melis S: Maximizing photosynthetic efficiency and culture productivity in cyanobacteria upon minimizing the phycobilisome light-harvesting antenna size. Biochim Biophys Acta. 2014; 1837(10): 1653–64. PubMed Abstract | Publisher Full Text

73. Gu J, Zhou Z, Li Z, et al.: Rice (Oryza sativa L.) with reduced chlorophyll content exhibit higher photosynthetic rate and efficiency, improved canopy light distribution, and greater yields than normally pigmented plants. Field Crops Res. 2017; 200: 58–70. Publisher Full Text

74. Antonovský N, Gleizer S, Noor E, et al.: Sugar Synthesis from CO₂ in Escherichia coli. Cell. 2016; 166(11): 115–26. PubMed Abstract | Publisher Full Text | Free Full Text | F1000 Recommendation

75. Antónovský N, Gleizer S, Milo R: Engineering carbon fixation in E. coli: from heterologous Rubisco expression to the Calvin-Benson-Bassham cycle. Cur. Contrib Biotechnol. 2017; 51: 83–94. PubMed Abstract | Publisher Full Text | Free Full Text

76. Schorner T, Schada von Borzyszkowski L, Burgener S, et al.: A synthetic pathway for the fixation of carbon dioxide in vitro. Science. 2016; 354(6314): 900–4. PubMed Abstract | Publisher Full Text | Free Full Text | F1000 Recommendation

77. Dairy TF, Sage TL, Kocancin F: Photosynthesis and the evolution of C₄ photosynthesis. Annu Rev Plant Biol. 2012; 63: 19–47. PubMed Abstract | Publisher Full Text | Free Full Text

78. Schörner T, Weber AP: The Road to C₄ Photosynthesis: Evolution of a Complex Trait via Intermediary States. Plant Cell. 2016; 28(5): 881–9. PubMed Abstract | Publisher Full Text

79. Kennedy EA, Lastich VM: Plant species intermediate for c₃-c₄ photosynthesis. Science. 1974; 184(4141): 919–27. PubMed Abstract | Publisher Full Text

80. von Caemmerer S, Quick WP, Furbank RT: The development of C₄ rice: current progress and future challenges. Science. 2012; 336(6089): 1671–2. PubMed Abstract | Publisher Full Text

81. Wang P, Vlad D, Langdale JA, et al.: Photosynthesis in C₃-C₄ Intermediate Moricandia species. J Exp Bot. 2017; 68(2): 191–206. PubMed Abstract | Publisher Full Text

82. Schörner T, Karki S, Biswal AK, et al.: Candidate regulators of Early Leaf Development in Maize Perturb Hormone Signalling and Secondary Cell Wall Formation When Constitutively Expressed in Rice. Sci Rep. 2017; 7(1): 4535. PubMed Abstract | Publisher Full Text

83. Lundgren MR, Christin PA: Despite phylogenetic effects, C₃-C₄ lineages bridge the ecological gap to C₄ photosynthesis. J Exp Bot. 2017; 68(2): 241–54. PubMed Abstract | Publisher Full Text

84. Marshall DM, Muhiadat R, Brown NJ, et al.: Closely related to Arabidopsis, contains species spanning a developmental progression from C₃ to C₄ photosynthesis. Plant J. 2007; 51(5): 886–96. PubMed Abstract | Publisher Full Text

85. Aubry S, Smith-Urna RD, Boursnell CM, et al.: Transcript residency on ribosomes reveals a key role for the Arabidopsis thaliana bundle sheath in sulfur and glucosinolate metabolism. Plant J. 2014; 78(4): 659–73. PubMed Abstract | Publisher Full Text

86. Boarland AM, Yang X: Informing the improvement and biodiesel of crassulacean acid metabolism via system dynamics modelling. New Phytol. 2013; 200(4): 946–59. PubMed Abstract | Publisher Full Text

87. Yang X, Cushman JC, Borland AM, et al.: A roadmap for research on crassulacean acid metabolism (CAM) to enhance sustainable food and bioenergy production in a hotter, drier world. New Phytol. 2015; 207(3): 491–504. PubMed Abstract | Publisher Full Text

88. Boarland AM, Hartwell J, Weston DJ, et al.: Engineering crassulacean acid metabolism to improve water-use efficiency. Trends Plant Sci. 2014; 19(3): 327–38. PubMed Abstract | Publisher Full Text | Free Full Text

89. Shivhare D, Mueller-Cajar O: In Vitro Characterization of Thermotolerant CAM Rubisco Active Reveals a Rubisco Interacting Surface Loop. Plant Physiol.
microcompartments as metabolic modules for plant synthetic biology. Plant J. 2016; 87(1): 69–75. PubMed Abstract | Publisher Full Text | F1000 Recommendation

114. McEachern JM, Long SP: Can the cyanobacterial carbon-concentrating mechanism increase photosynthesis in crop species? A theoretical analysis. Plant Physiol. 2014; 164(4): 2247–61. PubMed Abstract | Publisher Full Text | Free Full Text

115. Rolland V, Badger MR, Price GD: Redirecting the Cyanobacterial Bicarbonate Transporters BicA and SbtA to the Chloroplast Envelope: Soluble and Membrane Cargos Need Different Chloroplast Targeting Signals in Plants. Front Plant Sci. 2016; 7: 185. PubMed Abstract | Publisher Full Text | Free Full Text | F1000 Recommendation

116. Clayton H, Saladé M, Rolland V, et al.: Loss of the Chloroplast Transit Peptide from an Ancestral C2 Carbonic Anhydrase Is Associated with C2 Evolution in the Grass Genus Neurachne. Plant Physiol. 2017; 173(3): 1648–58. PubMed Abstract | Publisher Full Text | Free Full Text | F1000 Recommendation

117. Meyer MT, Genkov T, Skepper JN, et al.: Rubisco small-subunit α-helices control pyrenoid formation in Chlamydomonas. Proc Natl Acad Sci U S A. 2012; 109(47): 19474–9. PubMed Abstract | Publisher Full Text | Free Full Text

118. Li X, Zhang R, Patena W, et al.: An Indexed, Mapped Mutant Library Enables Reverse Genetics Studies of Biological Processes in Chlamydomonas reinhardtii. Plant Physiol. 2016; 173(3): 367–87. PubMed Abstract | Publisher Full Text | Free Full Text

119. Jin S, Sun J, Wunder T, et al.: Structural insights into the LCIB protein family reveals a new group of β-carboxylases. Proc Natl Acad Sci U S A. 2016; 113(51): 14716–21. PubMed Abstract | Publisher Full Text | Free Full Text

120. Flexas J, Ninemets U, Galé A, et al.: Diffusional conductances to CO₂ as a target for increasing photosynthesis and photosynthetic water-use efficiency. Photosynth Res. 2013; 117(1–3): 45–59. PubMed Abstract | Publisher Full Text

Publisher Full Text
Open Peer Review

Current Peer Review Status: ✅ ✅

Editorial Note on the Review Process

Faculty Reviews are review articles written by the prestigious Members of Faculty Opinions. The articles are commissioned and peer reviewed before publication to ensure that the final, published version is comprehensive and accessible. The reviewers who approved the final version are listed with their names and affiliations.

The reviewers who approved this article are:

1. Spencer Whitney
   ARC Centre of Excellence for Translational Photosynthesis, Research School of Biology, Australian National University, Acton, ACT, Australia
   Competing Interests: No competing interests were disclosed.

2. Xin-Guang Zhu
   Institute of Plant Physiology and Ecology, Chinese Academy of Sciences, Shanghai, 200032, China
   Competing Interests: No competing interests were disclosed.

The benefits of publishing with F1000Research:

- Your article is published within days, with no editorial bias
- You can publish traditional articles, null/negative results, case reports, data notes and more
- The peer review process is transparent and collaborative
- Your article is indexed in PubMed after passing peer review
- Dedicated customer support at every stage

For pre-submission enquiries, contact research@f1000.com