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# Optimising photosynthesis for environmental fitness

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**Abstract.** Optimisation of photosynthesis for environmental fitness is one of the most important approaches to increase productivity and acclimate plants to unfavourable environmental conditions. In this paper, the pathways of optimisation of photosynthesis are considered using novel tools both at the level of an individual plant and plant communities. Fast acclimation of photosynthetic apparatus to the environmental stresses and fluctuations of light intensity and light quality plays an important role in supporting effective photosynthesis. The bioengineered photosynthetic systems responsible for energy dissipation (non-photochemical quenching) and stomatal functioning, as well as some enzymes of  $CO_2$  fixation system alongside with introduction of effective mechanisms found in algae or cyanobacteria into chloroplasts, can be used for conservation of effective photosynthesis during such fluctuations. The conversion of some C3 crops grown in hot and arid climates into C4 plants may be a goal for the future. Special focus has been directed towards the detailed description of the photosynthetic optimisation under stress conditions taking into account the specifics of the most common stress factors.

**Keywords:** adaptation, ascorbate peroxidase, drought, hydrogen peroxide, plastoquinone pool, photosynthetic antenna, photosynthesis, photosystem II, salinity, stresses, reactive oxygen species.

Photosynthesis is the main driving force for plant growth, development, and obtaining products consumed by the population of the Earth. Photosynthesis also provides the main supply of energy and key metabolites necessary to support the growth and development of plants, thus driving plant productivity. Various environmental factors such as low and high light intensity, extreme temperature conditions, salinisation, lack of some mineral nutrition, water supply, poor soil quality, drought, and different pollutions may significantly impact plant photosynthetic function. Understanding the mechanisms involved in the protection of photosynthetic (PS) machinery against negative action of the environmental factors under extreme conditions are, therefore, of the critical importance for sustainable agricultural development.

In most cases, photosynthesis produces oxygen  $(O_2)$  as a by-product. However, this is not always the case because there are several different photosynthetic pathways. In a case of the oxygen evolution, water is the source of electrons and protons that are split off for the needs of photosynthesis. In contrast, other electron donors such as hydrogen sulfide may also be used (Allakhverdiev 2008). However, there are still many questions concerning photochemical reactions and the photosynthetic apparatus of various organisms that need to be answered. Photosynthesis is influenced by multiple environmental factors including salinity, temperature, light intensity, and carbon dioxide (CO<sub>2</sub>) concentration. The question of how plants grow under changes in these environmental conditions and how photosynthesis optimisation occurs are some of the most important and

interesting questions in studying plant growth, for if we are able to quantify the optimal environmental conditions that maximise photosynthesis, it can be employed in controlled environments to increase crop productivity. Hence, this special issue of *Functional Plant Biology* contains a selection of the best six papers dealing with these issues.

### Optimisation of photosynthesis during light dynamics

Flexibility of plant metabolism can provide acclimation to environmental conditions, especially to saline environments. A good example is a night respiration that may provide wateruse efficiency and the maintenance of plant growth (Fricke 2020).

Two key metabolic factors regulate photosynthesis in green cells. The first one is the redox state of chloroplast key components, including the redox state of plastoquinone pool, glutathione and thioredoxin systems. The second is the system for the utilisation of triose phosphates as the final product of synthesis light-dependent photosynthetic reactions (Paul and Foyer 2001). Rapid and significant fluctuations of incident light have been observed in the field (Kaiser *et al.* 2018), so a comprehensive understanding of photosynthetic responses to such light fluctuations will help to develop a strategy to improve photosynthetic efficiency and plant productivity. To improve the dynamics of photosynthesis, three main strategies have been considered (Kaiser *et al.* 2018, 2019):

 a model of canopy photosynthesis suggesting that slow non-photochemical quenching (NPQ) relaxation kinetics constrain crop photosynthesis by decreasing the quantum efficiency of photosynthesis in low-light periods (Zhu *et al.* 2004), prompting a need to accelerate NPQ relaxation after transition from strong to low light;

- (2) acceleration of key photosynthetic enzyme activation/ deactivation and, specifically enzymes of Calvin-Benson-Bassham (CBB) cycle; and
- (3) acceleration of stomatal responses to light fluctuations because although the acceleration of NPQ relaxation is expected to improve dynamic photosynthesis of both C3 and C4 plants, alterations in CBB enzyme activation and stomatal conductance mainly apply for improving C3 photosynthesis.

The main contributor to plant NPQ is the energy-dependent quenching (qE), which requires the build-up of a proton gradient and subsequent relaxation within a timeframe of seconds to minutes (Müller *et al.* 2001). For example, the simultaneous overexpression of three key genetic components involved in qE (PsbS and two enzymes ZEP and VDE of xanthophyll cycle) increased the biomass production of tobacco plants grown in the field by 15–20% (Kromdijk *et al.* 2016).

Diurnal changes in a light quality and intensity influence stomatal activity (Matthews *et al.* 2018, 2020). Here, red light response is saturated at high red irradiance, whereas blue light response is saturated at low blue irradiance; stomatal conductance depends on red/blue light ratio, and although the photosynthetic response is quickly altered under dynamic light conditions, stomatal conductance changes more slowly. Therefore, there is a potential for the bioengineering of stomatal response to light quality in order to improve drought tolerance and plant productivity.

There is evidence that the extracellular enzyme invertase is the key link in the photosynthesis regulation at the leaf level (Chikov 2008). Through this enzyme, the stomata coordinate the functioning of photosynthetic processes with the flow of  $CO_2$ into the leaf and, accordingly, with the export of assimilates from the leaf to the economically important organs of the plant. It is also important to study the adaptation of this assimilate distribution apparatus to light fluctuations.

## C3 and C4 plants

Two major types of plant photosynthesis in nature are the C3 and C4 photosynthetic pathways. The maximum conversion efficiency of solar energy into biomass is 4.6% for C3 photosynthesis at 30°C and current 380 ppm in the atmosphere [CO<sub>2</sub>], but 6% for C4 photosynthesis (Zhu et al. 2008). It should be noted that, however, that net  $CO_2$ assimilation is determined by not only the rate of photosynthesis, but by processes of respiration and photorespiration. The bioenergy processes of photosynthesis, photorespiration and respiration are mutually beneficial. Their interaction is associated with the optimisation of photosynthesis. The interaction of these three pathways is facilitated by two main phenomena: the sharing of energy resources and metabolites, and the maintenance of optimal levels of reactive oxygen species (ROS) (Sunil et al. 2013). The distribution of resources between the various compartments of plant cells is based on the production and use of reducing equivalents (NADPH) and ATP, as well as the metabolite exchange. The efficiency of accumulation of organic substances depends on the ratio of these processes. Taking respiration into account, biomass accumulation for a certain period is considered as the difference between the biomass created in the light and the mass used up for respiration. As a rule, a loss of respiratory energy is ~15–25%, but if a crop is dense, then the lower and sometimes middle leaves may be consuming rather than synthesising, thus markedly altering the loss.

C4 photosynthesis is more effective than C3 photosynthesis in hot and arid climates (Zhu *et al.* 2008). Reduced photorespiration in C4 plants is one of the main reasons of this difference. Hence, cereals like rice or wheat grown under such conditions grow better by changing from C3 to C4 photosynthesis. By stepwise identification of all components needed for engineering, it may become possible to employ this powerful machinery to increase yields in the future (Schuler *et al.* 2016). Schuler *et al.* (2016) proposes a simplified rational engineering model for changing C3 plants into C4 plants built with known C4 metabolic components.

#### Photosynthetic productivity and efficiency

For photosynthesis optimisation, it is important to evaluate parameters such as photosynthesis productivity, that is, the amount of dry biomass created per unit area of the leaf surface. On average, this value typically ranges from 5 to 12 g of dry matter  $m^{-2}$  of leaf surface day<sup>-1</sup>, with variation depending on the species and conditions.

Another important parameter to evaluate is photosynthetic efficiency, characterising the percentage of energy storage in the photosynthetic products. Although photosynthesis ultimately supplies the entire biosphere with energy, the efficiency of this process in leaves is low. Indeed, real photosynthesis is a complex multi-stage process, where energy is lost at every stage of it (Hall and Rao 1999). Serious energy losses occur during both the primary photosynthetic processes as well as the process of CO<sub>2</sub> fixation in the tricarboxylic acid cycle. Only a few cultures under certain optimal conditions achieve highly efficient photosynthesis. One such example is sorghum grown for the production of biofuels, where efficiency of solar energy conversion into chemical energy is 6.6%. Further, an efficiency of 7-8% has been obtained in corn crops. This is much higher than that of many other common crops such as wheat and rice, which have an efficiency of ~4% (Slattery and Ort 2015).

#### Optimisation of photosynthesis under the stress

One of the key issues in the optimisation of photosynthesis for environmental fitness is a plant's ability to maintain photosynthesis under unfavourable environments conditions (i.e. under stress). Drought and salinity are the most important stress factors observed in the field. Studies on model systems can contribute to our understanding of the photosynthetic optimisation mechanisms under such conditions. In *Arabidopsis*, the adaptation responses of photosynthetic apparatus to drought and salinity conditions were examined in the study of Borisova-Mubarakshina *et al.* (2020). A decrease in the content of PSII antenna proteins affected by changes in gene expression levels were detected under stress whereas no changes in PSII photochemistry were observed. In addition, under drought and salinity, hydrogen peroxide content ( $H_2O_2$ ) in sample leaves was higher than in the control. The authors proposed that a decrease in the PSII antenna size is one of the key mechanisms through which higher plants acclimate to environmental stresses, and such downregulation begins to function under mild stress conditions. In addition, redox state of the plastoquinone (PQ) pool and  $H_2O_2$  content is required for the photosynthetic apparatus adjustment to stress.

Another mechanism that enables plants to tolerate environmental stress is the regulation of pro-/antioxidant balance. This involves enhancing the activity of antioxidant enzymes and changing the contents of low-molecular antioxidants, especially components of the ascorbateglutathione (AsA-GSH) cycle, which is one of the key pathways in H<sub>2</sub>O<sub>2</sub> scavenging (Asada 2006). An increase in the content of H<sub>2</sub>O<sub>2</sub> and malondialdehyde (MDA), as well as alterations in the activities of AsA-GSH cycle enzymes and quantitative changes in AsA and GSH content during the day was observed in leaves of durum (Triticum durum Desf.) and bread (Triticum aestivum L.) wheat genotypes exposed to drought (Aliyeva et al. 2020a). Although PSII efficiency was significantly lower in the control and drought exposed leaves at the highest temperature in the afternoon, and the authors observed the increase in activity of ascorbate peroxidase, glutathione reductase and glutathione content at the expense of regeneration of oxidised glutathione. Results revealed that wheat can tolerate drought stress by enhancing antioxidant enzyme activity and altering the concentration of ascorbate and glutathione.

There are many factors that limit the growth and photosynthetic rate. Among them there is a high irradiance, in particular, high-intensity midday light, which leads to a lowered photosynthetic rate. In this case, the rate of photosynthesis depends mainly on the rate of the carboxylation enzyme Rubisco (Murchie and Niyogi 2011). However, it can also be influenced by the state of stomata, the rate of triose phosphates utilisation in the Calvin cycle, and inner CO<sub>2</sub> resistance of leaf tissue (A.A. Kosobryukhov pers. comm.). Limitations created by Rubisco can be overcome by improving the light distribution within a crop canopy, activation of Rubisco carboxylation function, or enhancement of  $CO_2$  input to Rubisco active sites (Ort *et al.* 2015).

The structure of the leaf its position has to be optimal for effective absorption and use of the solar radiation. The bulk of photosynthesis occurs in the leaves, so aiming for optimal leaf area is important when considering sowing options. If the leaf area is insufficient or too great, the efficiency of sunlight use will be reduced. Many studies have shown that having a large leaf area is not, on its own enough for optimal absorption: the leaf surface needs to be formed quickly. Therefore, the cultivation of varieties with a large, quickly formed leaves possessing mechanisms allowing long-term photosynthesis and high productivity is an important task.

Transport and harvest index are also important for creating an economically valuable crop. For example, in plants under shading, photosynthesis is limited more by the loading of assimilates into the phloem than by their formation in chloroplasts (Chikov 2008). The distribution and accumulation of photosynthetic products depend significantly on plant species. The impact of interstocks on growth and photosynthetic characteristic of Yuanxiaochun' Citrus seedling was studied by Wang et al. (2020). Using a comparative analysis of five interstocks, differences in photosynthetic parameters was detected under various treatments. For example, 'Ponkan' and 'Kumquat' as the interstock of Yuanxiaochun accumulated photosynthetic products most rapidly for normal plant growth. However, the yield of plants with improved photosynthesis can even be lower than that of the original plants if the conditions for improved photosynthesis functioning are not taken into account.

Also, the distribution and accumulation of photosynthetic products may be substantially affected by light quality. For example, photosynthate distribution in potato plants depended on different light emitting diode (LED) treatments (i.e. white, red, blue and green regions of the visible spectrum (He et al. 2020)). Red (R)-treated plants had a higher proportion of large tubers (>20 g) than white (W)-plants, but they demonstrated a lower proportion of small-(2-20 g) and medium-sized (10-20 g) tubers. Conversely, blue (B)treated plants had more medium-sized and large tubers than W-plants, suggesting that R-plants distributed more assimilated photosynthate into the first tuber than the plants of other treatments. B-treated plants distributed more photosynthates into tubers rather than into other organs. Green light treatment showed the lowest allocation of photosynthates to organs and a lower tuber yield per plant than other treatments, leading to the conclusion that R treatment induced carbon assimilation and led to the formation of larger tubers than other treatments.

The current ideas for optimising photosynthesis to meet our energy and food demands include the following features (Kramer and Evans 2011; Ort et al. 2015; Dann and Leister 2017): (1) improving Rubisco performance; (2) reducing photorespiration by converting C3 plants to C4 plants, introducing of carbon concentration or other effective mechanisms found in algae or cyanobacteria into higher plant chloroplasts, or changing of the photorespiration metabolism structure; (3) increasing stability of PSII proteins, or changing the size of PSII light-harvesting complex or PQ-pool; and (4) the addition of new biosynthetic pathways to increase the intake of carbon in useful nutrients such as starch or oils. Although introducing or changing the paths for these processes will be an important step forward, it is important to note that these approaches can also significantly change energy requirements for photosynthesis.

In the work on optimising photosynthesis, particular emphasis has been directed towards improving Rubisco performance to enhance carboxylase function by inhibiting oxygenase function. The aim is to create varieties of stressresistant plants for growth under specific environmental conditions that exist in local geographical locations by means of various biologically active substances, thus creating conditions for efficient transport of photosynthate into the plant's storage organs. Photosynthesis optimisation under stress can be also achieved by treating plants with membrane stabilising agents. For example, the impact of  $\beta$ -1,3-glucan on the photosynthetic apparatus activity and lipid peroxidation was studied in tomato (*Lycopersicon esculentum* Mill., cv. Tamara) leaves under fusarium wilt (Kabashnikova *et al.* 2020). Artificial induction of wilt by the fungal pathogen *Fusarium oxysporum* led to the activation of the lipid peroxidation (LPO) processes in leaves and significant disturbances in the photosynthetic apparatus including a decrease in chlorophyll *a* and carotenoid contents, and also a worsening in the absorption and transformation of light energy in PSII. Thus,  $\beta$ -1,3-glucan decreases the intensity of lipid peroxidation and supports the level of a photosynthetic pigments and an efficiency of photochemical processes in the chloroplasts of infected leaves.

In response to stress conditions, the state of the photosynthetic apparatus in various tissues can vary. For example, the photosynthetic leaf tissue of C4 plants contains two types of distinct cell types: mesophyll and bundle sheath. In the work by Aliyeva *et al.* (2020*b*) it was demonstrated that the bundle sheath (BS) chloroplasts had 2-fold higher chlorophyll a/b ratio than mesophyll chloroplasts. In the same work, the PSII light-harvesting complex in chloroplasts of these tissues also had different contents of polypeptides in the region of 28–24 kDa. In BS chloroplasts, PSII photochemical activity was five times less than the activity of the mesophyll chloroplasts.

The final product of the photosynthesis is sugar. The effectiveness of solar conversion of  $CO_2$  and water into sugars is dependent not only on performance of the individual plant but also on the functioning of plant communities as a photosynthetic production system. The system includes many different components, and it constantly responding to changing external conditions. One of the main properties of a system is self-regulation, which is necessary to maintain plant community homeostasis.

Optimisation of photosynthesis in crops is one of the biggest problems in agriculture across the world. In crops with optimal photosynthesis, leaf area should be  $4-5 \text{ m}^2 \text{ m}^{-2}$ . The selection of the optimum optical density of crops is important, that is, it is necessary to introduce a crop density that allows the best use of available light, and new types of crops with increased plant productivity due to a higher photosynthetic activity such as strip crops.

The work of Konôpková *et al.* (2020) focussed on the forest ecosystems conservation, in particular, understanding how the intraspecific variation in the physiological stress response of trees can mitigate the expected negative effects of climate changes on forest ecosystems. These authors concluded that tree species originating from high altitudes corresponding to more humid and cold conditions in Central Europe demonstrated the most effective photosynthesis, and were less sensitive to moderate stresses such as heat and drought.

#### Conclusion

Photosynthesis is a process of a tremendous importance for the existence of the life on Earth. However, the process is not highly efficient. The highest short-term conversion efficiency, which is observed for brief periods during the life of a crop, can reach 3.5% for C3 and 4.3% for C4 plants. Throughout the course of evolution, terrestrial plants have repeatedly experienced various stressful situations, meaning that photosynthesis developed not as the most efficient process, but rather one that is stable, even under various unfavourable conditions (Dann and Leister 2017). During the evolution of plants, the main driver for selection can be assumed to be the sustainability of the photosynthesis process in terms of optimised plant suitability, so it should be possible to increase the photosynthetic productivity and use the available genetic diversity for further improvements in photosynthesis efficiency in agricultural plants.

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#### References

- Aliyeva NK, Aliyeva DR, Suleymanov SY, Rzayev FH, Gasimov EK, Irada M, Huseynova IM (2020*a*) Biochemical properties and ultrastructure of mesophyll and bundle sheath thylakoids from maize (*Zea mays*) chloroplasts. *Functional Plant Biology* **47**, 970–976. doi:10.1071/ FP20004
- Aliyeva DR, Aydinli LM, Zulfugarov IS, Huseynova IM (2020b) Diurnal changes of the ascorbate-glutathione cycle components in wheat genotypes exposed to drought. *Functional Plant Biology* 47, 998–1006. doi:10.1071/FP19375
- Allakhverdiev SI (2008) Resent perspectives of photosystem II: structure, function and dynamics. *Photosynthesis Research* 98, 1–5. doi:10.1007/ s11120-008-9390-2
- Asada K (2006) Production and scavenging of reactive oxygen species in chloroplast and their functions. *Plant Physiology* **141**, 391–396. doi:10.1104/pp.106.082040
- Borisova-Mubarakshina MM, Vetoshkina DV, Naydov IA, Rudenko NN, Elena M, Zhurikova EM, Balashov NV, Ignatova LK, Fedorchuk TP, Ivanov BN (2020) Regulation of the size of photosystem II light harvesting antenna represents a universal mechanism of higher plant acclimation to stress conditions. *Functional Plant Biology* 47, 959–969. doi:10.1071/FP19362
- Chikov VI (2008) Evolution of notions about relationships between photosynthesis and plant productivity. *Russian Journal of Plant Physiology: a Comprehensive Russian Journal on Modern Phytophysiology* 55, 130–143. doi:10.1134/S1021443708010160
- Dann M, Leister D (2017) Enhancing (crop) plant photosynthesis by novel genetic diversity. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 372, 20160380. doi:10.1098/ rstb.2016.0380
- Fricke W (2020) Energy costs of salinity tolerance in crop plants: nighttime transpiration and growth. *New Phytologist* 225, 1152–1165. doi:10.1111/nph.15773
- Hall DO, Rao KK (1999) 'Photosynthesis.' (6th edn) (Cambridge University Press: Cambridge, UK)
- He W, Li J, Pu M, Xu ZG, Lijun G (2020) Response of photosynthate distribution in potato plants to different LED spectra. *Functional Plant Biology* doi:10.1071/FP20131
- Kabashnikova L, Abramchik L, Domanskaya I, Savchenko G, Shpileuski S (2020) β-1,3-glucan effect on the photosynthetic apparatus and oxidative stress parameters of tomato leaves under fusarium wilt. *Functional Plant Biology* **47**, 988–997. doi:10.1071/FP19338

- Kaiser E, Morales A, Harbinson J (2018) Fluctuating light takes crop photosynthesis on a rollercoaster ride. *Plant Physiology* **176**, 977–989. doi:10.1104/pp.17.01250
- Kaiser E, Galvis VC, Armbruster U (2019) Efficient photosynthesis in dynamic light environments: a chloroplast's perspective. *The Biochemical Journal* 476, 2725–2741. doi:10.1042/BCJ20190134
- Konôpková A, Pšidová E, Kurjak D, Stojnić S, Petrík P, Fleischer P Jr, Kučerová J, Ježík M, Petek A, Gömöry D, Kmet J, Longauer R, Ditmarová L (2020) Photosynthetic performance of silver fir (*Abies alba*) of different origins under suboptimal growing conditions. *Functional Plant Biology* 47, 1007–1018. doi:10.1071/FP20040
- Kramer DM, Evans JR (2011) The importance of energy balance in improving photosynthetic productivity. *Plant Physiology* 155, 70–78. doi:10.1104/pp.110.166652
- Kromdijk J, Glowacka K, Leonelli L, Gabilly ST, Iwai M, Niyogi KK, Long SP (2016) Improving photosynthesis and crop productivity by accelerating recovery from photoprotection. *Science* 354, 857–861. doi:10.1126/science.aai8878
- Matthews JSA, Vialet-Chabrand S, Lawson T (2018) Acclimation to fluctuating light impacts the rapidity of response and diurnal rhythm of stomatal conductance. *Plant Physiology* **176**, 1939–1951. doi:10.1104/pp.17.01809
- Matthews JSA, Vialet-Chabrand S, Lawson T (2020) Role of blue and red light in stomatal dynamic behaviour. *Journal of Experimental Botany* 71, 2253–2269. doi:10.1093/jxb/erz563
- Müller P, Li XP, Niyogi KK (2001) Non-photochemical quenching. A response to excess light energy. *Plant Physiology* **125**, 1558–1566. doi:10.1104/pp.125.4.1558
- Murchie EH, Niyogi KK (2011) Manipulation of photoprotection to improve plant photosynthesis. *Plant Physiology* 155, 86–92. doi:10.1104/pp.110.168831

- Ort DR, Merchant SS, Alric J (2015) Redesigning photosynthesis to sustainably meet global food and bioenergy demand. *Proceedings* of the National Academy of Sciences of the United States of America 112, 8529–8536. doi:10.1073/pnas.1424031112
- Paul MJ, Foyer CH (2001) Sink regulation of photosynthesis. Journal of Experimental Botany 52, 1383–1400. doi:10.1093/jexbot/52.360.1383
- Schuler ML, Mantegazza O, Weber APM (2016) Engineering C4 photosynthesis into C3 chassis in the synthetic biology age. *The Plant Journal* 87, 51–65. doi:10.1111/tpj.13155
- Slattery RA, Ort DR (2015) Photosynthetic energy conversion efficiency: setting a baseline for gauging future improvements in important food and biofuel crops. *Plant Physiology* **168**, 383–392. doi:10.1104/ pp.15.00066
- Sunil B, Talla SK, Aswani V, Raghavendra AS (2013) Optimization of photosynthesis by multiple metabolic pathways involving interorganelle interactions: resource sharing and ROS maintenance as the bases. *Photosynthesis Research* **117**, 61–71. doi:10.1007/ s11120-013-9889-z
- Wang T, Xiong B, Tan L, Yang Y, Zhang Y, Ma M, Xu Y, Liao L, Sun G, Liang D, Xia H, Zhang X, Wang Z, Wang J (2020) Effects of interstocks on growth and photosynthetic characteristic in 'Yuanxiaochun' citrus seedling. *Functional Plant Biology* 47, 977–987. doi:10.1071/FP20079
- Zhu XG, Ort DR, Whitmarsh J, Long SP (2004) The slow reversibility of photosystem II thermal energy dissipation on transfer from high to low light may cause large losses in carbon gain by crop canopies: a theoretical analysis. *Journal of Experimental Botany* 55, 1167–1175. doi:10.1093/jxb/erh141
- Zhu X-G, Long SP, Ort DR (2008) What is the maximum efficiency with which photosynthesis can convert solar energy into biomass? *Current* Opinion in Biotechnology 19, 153–159. doi:10.1016/j.copbio.2008.02.004