LETTER TO THE EDITOR

Light regulation of photosynthetic light harvesting doubles the biomass yield in the green alga *Chlamydomonas*

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Due to the overall low thermodynamic efficiency (1-4%)of photosynthesis (Ort et al. 2011, Subramanian et al. 2013) and its impact on crop productivity, substantial efforts are being made to engineer photosynthesis to improve its light use and carbon capture efficiency to increase crop yields (Polle et al. 2003, Mussgnug et al. 2007, Beckman et al. 2009, Kirst et al. 2012, Mitra et al. 2012, Perrine et al. 2012, Cazznigga et al. 2014, Friedland et al. 2019). The greatest potential for increasing photosynthetic efficiency may still be realized, however, by improving its light-use efficiency (Zhu et al. 2008, Ort et al. 2011, Perrine et al. 2012). In plants and algae, light saturates photosynthesis at approximately one fourth of full sunlight intensity. (For a background on all aspects of photosynthesis, see Blankenship 2014 and Shevela et al. 2019.) The excess light energy must then be dissipated through nonproductive energy emission pathways often leading to substantial damage to the photosynthetic apparatus further reducing crop yields (Ohad et al. 1992, Niyogi 1999, Ruffle et al. 2001, Polle et al. 2003, Subramanian et al. 2013, Demmig-Adams et al. 2014, Berman et al. 2015, Wu et al. 2020). Earlier studies have shown that by reducing the optical cross section of the light-harvesting antenna complex, it is possible to increase photosynthetic efficiency and biomass yield in crops and algae by up to 40% when grown continuously in high light or in the field (Perrine et al. 2012, Friedland et al. 2019). In nature, however, light intensity varies substantially over the course of the day, with depth in the plant architecture or algal pond, and even seasonally (Mircovic et al. 2017). Theoretically, a lightharvesting apparatus that could be continuously adjusted in size for differing light regimes could lead to further improvements in photosynthetic efficiency (Negi et al. 2020).

Negi *et al.* (2020) have indeed described a strategy for the continuous light-mediated regulation of the lightharvesting antenna size in a green alga *Chlamydomonas reinhardtii*. This system is based on the post transcriptional regulation of chlorophyllide *a* oxygenase (CAO) protein levels and activity that catalyzes the synthesis of chlorophyll (Chl) b. Chl b is found only in the peripheral, nuclearencoded light-harvesting complexes and its selective reduction was shown to result in a corresponding decrease in the antenna size. Using the light-regulated nucleic acid-binding protein 1 (NAB1) translational repressor to control the expression of a gene fusion product between the 5' NAB1 - binding element (LRE) and the CAO gene (Mussgnug et al. 2005), Negi et al. (2020) demonstrated that Chlamydomonas LRE-CAO transformants lacking the wild-type CAO gene were able to continuously and reversibly alter the size of their light-harvesting complexes throughout the algal life cycle (see Fig. 1). In collaboration with Dr. Jun Minagawa's laboratory (in Japan), they demonstrated that LRE-CAO transgenics having the highest photosynthetic efficiencies also had reduced levels of photoinhibition under high light and greater activity of nonphotochemical quenching of the excited state of Chl a. Further, they observed that the thylakoid membrane architecture was altered in structure such that the membrane thickness and lumen space were much more favorable for enhanced electron transport activity. These results demonstrate that reduction in Chl b and light-harvesting antenna structure has pleiotropic effects on the photosynthetic apparatus. Significantly, when the LRE-CAO transgenics were grown as monocultures under conditions mimicking those of a commercial algal production pond, the transgenics had biomass yields that were more than two-fold higher than their wild-type parental strains. These are the greatest increases in biomass yield observed to date for algae engineered for improved photosynthetic efficiency.

An obvious concern is whether LRE-CAO transgenics would have an increased fitness advantage relative to wildtype algae in the wild. Early studies indicate that this is not likely to be the case. Thus, we have not engineered a 'monster' strain. Chlamydomonas strains engineered to have fixed but optimal light-harvesting antenna sizes for biomass yield were less competitive than wild-type algae in mixed cultures due to the shading effect of the wildtype algae on transgenics with smaller but more efficient

Received 2 June 2020, accepted 4 June 2020.

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Acknowledgment: We thank Győző Garab for reviewing this letter to the editor.

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Fig. 1. Light regulated translational control of chlorophyll *b* synthesis by the NAB1 translational repressor (Negi *et al.* 2020).

light-harvesting antenna complexes (Henley *et al.* 2013). These results have clear implications for addressing global challenges for food and biomass production as well as carbon capture.

For other ideas on engineering plants to use far-red light, *see* Blankenship *et al.* (2011).

References

- Beckmann J., Lehr F., Finazzi G. *et al.*: Improvement of light to biomass conversion by de-regulation of light-harvesting protein translation in *Chlamydomonas reinhardtii*. – J. Biotechnol. **142**: 70-77, 2009.
- Berman G.P., Nesterov A.I., López G.V., Sayre R.T.: Superradiance transition and nonphotochemical quenching in photosynthetic complexes. – J. Phys. Chem C 119: 22289-22296, 2015.
- Blankenship R.E.: Molecular Mechanisms of Photosynthesis. 2nd Edition. Pp. 312. Wiley-Blackwell, Hoboken 2014.
- Blankenship R.E., Tiede D.M., Barber J. *et al.*: Comparing photosynthetic and photovoltaic efficiencies and recognizing the potential for improvement. – Science **332**: 805-809, 2011.
- Cazzaniga S., Dall'Osto L., Szaub J. *et al.*: Domestication of the green alga *Chlorella sorokiniana*: reduction of antenna size improves light-use efficiency in a photobioreactor. – Biotechnol. Biofuels 7: 157, 2014.
- Demmig-Adams B., Garab G., Adams III W.W., Govindjee (ed.): Non-Photochemical Quenching and Energy Dissipation in Plants, Algae and Cyanobacteria. Advances in Photosynthesis

and Respiration. Vol. 40. Pp. 649. Springer, Dordrecht 2014.

- Friedland N., Negi S., Vinogradova-Shah T. *et al.*: Fine-tuning the photosynthetic light harvesting apparatus for improved efficiency and biomass yield. – Sci. Rep.-UK 9: 13028, 2019.
- Henley W., Litaker W., Novoveská L. *et al.*: Initial risk assessment of genetically modified (GM) algae for commodity-scale cultivation. – Algal Res. 2: 66-77, 2013.
- Kirst H., Garcia-Cerdan J.G., Zurbriggen A. *et al.*: Truncated photosystem chlorophyll antenna size in the green microalga *Chlamydomonas reinhardti*i upon deletion of the TLA3-CpSRP43 gene. – Plant Physiol. **160**: 2251-2260, 2012.
- Mircovic T., Ostrumov E.E., Anna J.M. *et al.*: Light absorption and energy transfer in the antenna complexes of photosynthetic organisms. – Chem. Rev. **117**: 249-293, 2017.
- Mitra M., Kirst H., Dewez D., Melis A.: Modulation of the light-harvesting chlorophyll antenna size in *Chlamydomonas reinhardtii* by *TLA1* gene over-expression and RNA interference. – Philos. T. Roy. Soc. B **367**: 3430-3443, 2012.
- Mussgnug J.H., Thomas-Hall S., Rupprecht J. et al.: Engineering photosynthetic light capture: Impacts on improved solar energy to biomass conversion. – Plant Biotechnol. J. 5: 802-814, 2007.
- Mussgnug J.H., Wobbe L., Elles I. *et al.*: NAB1 is an RNA binding protein involved in the light-regulated differential expression of the light-harvesting antenna of *Chlamydomonas reinhardtii*. Plant Cell **17**: 3409-3421, 2005.
- Negi S., Perrine Z., Friedland N. *et al.*: Light regulation of light harvesting antenna size substantially enhances photosynthetic efficiency and biomass yield in algae. – Plant J.: https://doi. org/10.1111/tpj.14751, 2020. (In press)
- Niyogi K.K.: Photoprotection revisited: Genetic and Molecular Approaches. – Annu. Rev. Plant Phys. **50**: 333-359, 1999.
- Ohad I., Prášil O., Adir N.: Dynamics of photosystem II: mechanism of photoinhibition and recovery processes. – In: Barber J. (ed.): The Photosystems: Structure, Function and Molecular Biology. Pp. 295-348. Elsevier, Amsterdam 1992.
- Ort D.R., Zhu X.G., Melis A.: Optimizing antenna size to maximize photosynthetic efficiency. – Plant Physiol. 155: 79-85, 2011.
- Perrine Z., Negi S., Sayre R.T.: Optimization of photosynthetic light energy utilization by microalgae. – Algal Res. 1:134-142, 2012.
- Polle J.E.W., Kanakagiri S.-D., Melis A.: *tla1*, a DNA insertional transformant of the green alga *Chlamydomonas reinhardtii* with a truncated light-harvesting chlorophyll antenna size. – Planta 217: 49-59, 2003.
- Ruffle S.V., Wang J., Johnston H.G. *et al.*: Photosystem II peripheral accessory chlorophyll mutants in *Chlamydomonas reinhardtii*. Biochemical characterization and sensitivity to photo-inhibition. Plant Physiol. **127**: 633-644, 2001.
- Shevela D., Björn L.O., Govindjee G.: Photosynthesis: Solar Energy for Life. Pp. 204. World Scientific, Singapore 2019.
- Subramanian S., Barry A.N., Pieris S., Sayre R.T.: Comparative energetics and kinetics of autotrophic lipid and starch metabolism in chlorophytic microalgae: implications for biomass and biofuel production. – Biotechnol. Biofuels 6: 150, 2013.
- Wu G., Ma L., Sayre R.T., Lee C.-H.: Identification of the optimal light harvesting antenna size for high-light stress mitigation in plants. – Front. Plant Sci. 11: 505, 2020.
- Zhu X.-G., Long S.P., Ort D.R.: What is the maximum efficiency with which photosynthesis can convert solar energy into biomass? – Curr. Opin. Biotech. **19**: 153-159, 2008.

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