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Title
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Permalink
https://escholarship.org/uc/item/82g0g42k

Journal
Plant Physiology, 155(1)

ISSN
0032-0889

Authors
Ort, Donald R
Zhu, Xinguang
Melis, Anastasios

Publication Date
2011-01-03

DOI
10.1104/pp.110.165886

Peer reviewed

Optimizing Antenna Size to Maximize Photosynthetic Efficiency[W]

Donald R. Ort*, Xinguang Zhu (朱新广), and Anastasios Melis

Global Change and Photosynthesis Research Unit, United States Department of Agriculture Agricultural Research Service, Departments of Plant Biology and Crop Sciences, Institute of Genomic Biology, University of Illinois, Urbana, Illinois 61801 (D.R.O.); Chinese Academy of Sciences-German Max Planck Society Partner Institute for Computational Biology and Institute of Plant Physiology and Ecology, Shanghai Institutes for Biological Sciences, Shanghai, China 200032 (X.Z.); and Department of Plant and Microbial Biology, University of California, Berkeley, California 94720–3102 (A.M.)

The theoretical upper limit for the operational efficiency of plant photosynthesis has been estimated from a detailed stepwise analysis of the biophysical and biochemical subprocesses to be about 4.6% for C_3 and 6.0% C_4 plants (Zhu et al., 2008, 2010). (These estimates assume a leaf temperature of 30°C and an atmospheric $[CO_2]$ of 387 ppm and were calculated relative to the full solar spectrum at the earth's surface. These efficiencies would be slightly more than double if calculated relative to only the photosynthetically active radiation [i.e. 400–700 nm; Zhu et al., 2008].) While estimates of the theoretical upper limit of photosynthetic efficiency in microalgae have not been conducted as systematically, the same considerations apply as for plants, although microalgae may have a lower respiratory rate that would raise the upper limit for the efficiency of net photosynthesis accordingly (Melis, 2009). Microalgae expressing bicarbonate transporters will mimic the higher efficiency of C_4 plants due to suppression of photorespiration, while those that do not actively concentrate CO_2 would have upper efficiency limits similar to C_3 plants. The highest short-term efficiencies observed for plants in the field, assessed from maximum growth rates, are about 3.5% for C_3 and 4.3% for C_4 plants, and these drop further to 2.4% and 3.4% when calculated over a full growing season (Monteith, 1977; Piedade et al., 1991; Beale and Long, 1995). For crop plants, these highest full growing season efficiencies are those that define the yield potential (Fischer and Edmeades, 2010) or record yield of the crop and are at least twice greater than photosynthetic efficiencies observed under most commercial farming conditions.

The primary reason why the highest observed photosynthetic efficiencies are 30% or more lower than theoretical efficiencies is light saturation of photosynthesis. Photosynthesis responds nonlinearly to increases in insolation. For example, C_3 leaf photosynthesis is saturated by approximately 25% of maximum full sunlight, and light intercepted above this amount will lower photosynthetic efficiency in proportion to the excess light absorbed (Fig. 1). In plant canopies or microalgae mass cultures, this leads to a situation in which photosynthetic tissue directly exposed to bright sunlight is saturated and wastefully dissipates energy, while photosynthesis in shaded leaves or shaded microalgal cells in the culture interior are light limited. High radiation also engages photoprotective mechanisms (Li et al., 2009), which in dynamic light environments can further lower efficiency (Zhu et al., 2004a) or result in photodamage from which repair is required to restore efficiency (Melis, 1999). Greater light penetration beyond the top layers of photosynthetic tissue mitigates efficiency losses associated with light saturation. For example, canopy structure in which the upper leaves are vertically oriented enhances light distribution within the canopy and thereby improves the efficiency of photosynthetic carbon gain (Long et al., 2006), a strategy that has contributed to enhanced yield of super hybrid rice (*Oryza sativa*). Lowering the chlorophyll (Chl) content of photosynthetic tissue is another and potentially more robust strategy to improve light penetration into plant canopies and algal mass cultures. But hasn't evolution already optimized Chl content in plants and microalgae? No doubt it has for competitive natural habitats where a large assembly of antenna pigments confers a selective advantage. That is, even when photosynthesis is already saturated, intercepting more light deprives a potential competitor that may have otherwise received the light. However, evolution has not optimized Chl content for achieving maximum carbon gain in dense crop monocultures or microalgal mass cultures where competition for resources including light is not a benefit (Anten, 2005). Here, we discuss the theory and physiological factors that need to be considered in optimizing Chl content for improved photosynthetic efficiency and maximum carbon gain by crops and microalgae.

LIGHT DEPENDENCE OF PHOTOSYNTHETIC CO_2 UPTAKE RATES—THEORY

The light response of the photosynthetic CO_2 uptake rate by a suspension of microalgae or a leaf per unit

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area (A) is well described by a nonrectangular hyperbola:

$$A = \frac{\Phi_{CO2}I + A_{sat} - \sqrt{(\Phi_{CO2}I + A_{sat})^2 - 4\theta\Phi_{CO2}IA_{sat}}}{2\theta} - R \quad (1)$$

where Φ_{CO2} is the maximal quantum efficiency of photosynthetic CO_2 fixation, θ is the convexity of the hyperbola, A_{sat} is the light-saturated rate of photosynthetic CO_2 uptake rate, I is the photosynthetic photon flux density (PPFD), and R is the rate CO_2 efflux from mitochondrial respiration. As Figure 1 depicts for a tobacco (*Nicotiana tabacum*) leaf, initially A increases nearly linearly with I and after an inflection A approaches a plateau. The initial slope of A versus PPFD represents the quantum yield of CO_2 uptake, i.e. the fractional number of CO_2 molecules that can be fixed with absorption of one photon.

The attenuation of PPFD with depth in a uniform suspension of microalgae can be inferred to a first approximation from the Beer-Lambert law:

$$a = e \times b \times c \quad (2)$$

where a is the absorbance of light from the surface to the particular depth; e is the molar absorbtivity of algal pigments with units of L mol^{-1} cm^{-1}; b is the path length of the sample, in this case, the depth into the microalgae suspension from the surface (cm); and c is the concentration of the microalgae pigments in each depth layer (mol L^{-1}). The absorbance at the ith depth (I_i) is calculated based on the difference of a between the ith depth and the $(i-1)^{th}$ depth:

$$I_i = I_0(a_i - a_{(i-1)}) \quad (3)$$

where a_i represents the absorbance by the ith layer and above and $a_{(i-1)}$ represents the absorbance by the $(i-1)^{th}$ layer and above. I_0 is the incident light level above the suspension. The daily integral gross CO_2 uptake of the microalgae suspension (A_{ta}) is then calculated as:

$$A_{ta} = \sum_{H=1}^{24} \sum_{i}^{L} A(H,i) \quad (4)$$

where $A(H, i)$ is the net CO_2 uptake for all algae cells at the ith depth at the Hth hour, calculated based on the light response curve of Equation 1 and a, and L is the total number of depth layers of the microalgae suspension.

In a crop canopy, gross photosynthesis (A_c) is the integral of photosynthetic CO_2 uptake rate of all leaves in the canopy, as shown in Equation 5.

$$A_c = \sum_{n=1}^{LN} A(n) \quad (5)$$

$$A_{tc} = \sum_{h=1}^{24} \sum_{n=1}^{LN} A(h,n) \quad (6)$$

Total canopy CO_2 uptake rate (A_{tc}) is correspondingly the integral of the leaf photosynthetic CO_2 up-take for all the leaves over the course of an entire day (Eq. 6).

In this equation, h represents time, while $A(n)$ represents the photosynthetic CO_2 uptake rate for leaf number n. Because it is experimentally challenging to measure all the relevant microclimatic parameters within a canopy, in practice numerous simplified models have been developed to simulate microclimatic conditions inside canopies to estimate canopy photosynthetic CO_2 uptake rates. These models include the big-leaf models, the sun-shade models, and multilayer models (Farquhar et al., 1980; Forseth and Norman, 1991; Humphries and Long, 1995). The big-leaf model assumes that the entire canopy can be effectively represented by a single leaf of specified leaf area index (LAI) and photosynthetic properties. The sunlit-shade model treats all leaves of a canopy as two dynamic populations, i.e. those that are directly sun exposed and those that are shaded. Following the formulations of Forseth and Norman (1991), the total canopy photosynthetic CO_2 uptake rate is computed as the integral of the photosynthetic CO_2 uptake rates of these two dynamic leaf populations. The multilayer model further paramaterizes the canopy by dividing it into multiple layers of leaves, each with different photosynthetic properties and microclimatic conditions. Using the sunlit-shaded model as implemented in the WIMOVAC (for Windows Intuitive MOdel of Vegetation response to Atmosphere and Climate change) model (Humphries and Long, 1995), we have simulated the response of A_c and A_{tc} to changes in light levels, photosynthetic properties, and canopy extinction coefficient (Fig. 2). The detailed equations used to predict the light environments inside the canopy in WIMOVAC are the same as in Zhu et al. (2004b) and for convenience are provided here in Supplemental Appendices S1 and S2. Over the course of a day, instantaneous A_c is described by a bell-shape curve that follows the diurnal changes in light level incident on the top of the canopy (Fig. 2A). The inability of the upper layer leaves in a canopy to utilize all the available light energy can be directly demonstrated by the increase of A_{tc} upon gradual increase of both V_{cmax} and J_{max} at the top of the canopy, i.e. in the sunlit leaves (Fig. 2B). We simulated the total available light and also A_{tc} for different days of a year, illustrating the relationship between the total available light and A_{tc} (Fig. 2C).

We further simulated decreases in leaf Chl content by decreased canopy extinction coefficient, which inherently incorporated higher transmittance through the canopy. With the decrease in Chl content, there is a concurrent decrease in the initial slope of the light response curve (Hikosaka and Terashima, 1995). Assuming a Chl content of 0.5 mmol m^{-2} (Evans, 1989), the initial slope of the light response curve was estimated based an empirical equation (Hikosaka and Terashima, 1995). We further assumed that with decreased Chl content, there was a proportional decrease in the canopy extinction coefficient and a proportional
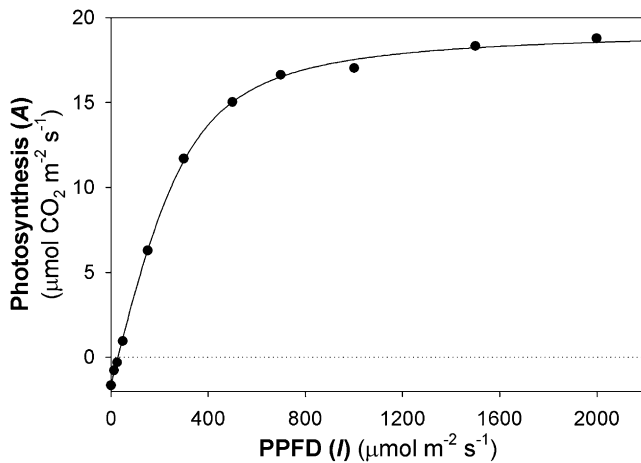
Figure 1. The light intensity dependence of net photosynthesis of a chamber-grown tobacco leaf. The measurement temperature was 25°C and the [CO_2] in the measurement chamber (LI-COR 6400-40) was 400 ppm. The data are fit to Equation 1, for which Φ_{CO2} = 0.059, A_{sat} = 21.03 μmol CO_2 m^{-2} s^{-1}, θ = 0.79, and R = 1.65 μmol CO_2 m^{-2} s^{-1}.

increase in the leaf transmittance and reflectance. This assumed proportional changes between leaf Chl content and canopy extinction coefficient needs to be improved since the leaf absorbance and leaf Chl concentration has a strong nonlinear relationship (Evans, 1993). A more mechanistic model of canopy light environment is needed to better define the relationship between leaf Chl concentration and canopy extinction coefficient. The simulation results suggested that with increase in canopy extinction coefficient, i.e. increase in the leaf Chl concentration, the A_{tc} first increases and then gradually decreases (Fig. 2D). This gradual increase of A_{tc} with decrease of leaf Chl content arises from the fact that leaves at the top of canopies frequently receive more solar energy over the course of a day than they can efficiently utilize, while at the same time leaves in the lower layers of the canopy are light limited. As expected, when the Chl content is decreased below a certain threshold, then further decrease in leaf Chl content results in a decrease in A_{tc}. In principle, for a given LAI the canopy extinction coefficient could be manipulated and optimized for maximum A_{tc} by altering the leaf Chl content. However, to date, no systematic manipulation of Chl concentration to optimize A_{tc} has been undertaken in crop plants, possibly because low Chl mutations frequently carry agronomically undesirable pleiotropic effects (e.g. Pettigrew et al., 1989) and because Chl accumulation in Chl-deficient mutants is frequently dependent on developmental conditions and/or stage of growth (e.g. Droppa et al., 1988).

The optimal Chl concentration for maximal A_{tc} will depend on several factors. First, the optimal photosynthetic pigment concentration is influenced by the spatial and temporal heterogeneities of light inside a canopy (Zhu et al., 2004b) and correspondingly by the canopy architecture. For example, for a given LAI the

A_{tc} of canopies with more erect leaf orientation would be expected to benefit less with a given Chl reduction than canopies with horizontal leaf orientation. Similarly, due to differing solar angle, canopies at different latitudes will experience different ambient light levels and the optimal Chl concentrations would therefore be expected to differ with latitude. Different LAI will also influence the optimal leaf Chl content for maximal A_{tc}. Second, as transmittance of photosynthetically active radiation is increased, there will be an increase in amount of incident light that is reflected, potentially lowering the total PPFD absorbed by the canopy. In our simulation, we assumed that reflectance increased by the same amount that transmittance increased (Knipling, 1970). Had the reabsorption of a portion of the reflected light been included in our simulation, it would have had the effect of further reducing the Chl threshold at which reducing Chl will benefit A_{tc}. Third, the optimal Chl concentration will also depend on the rate of canopy development. The rate of canopy development determines how quickly self-shading develops and therefore how quickly into the growing season that reduced Chl levels become an asset versus a detriment to maximizing A_{tc}. Additionally, leaves at different layers within a canopy often acquire different physiological and photosynthetic properties, e.g. leaves adapted to shade environments showed increased light-harvesting complex compared to leaves adapted to high light (Evans, 1989; Hikosaka and Terashima, 1995) and leaves of different crops can have different physiological properties, such as longevity (Wright et al., 2004) and leaf optical properties (e.g. reflectance), all of which will influence the optimal Chl concentration. Fourth, the optimal Chl distribution may also depend on a number of other environmental factors that will influence the threshold between light limitation and light saturation. For example, many abiotic stresses lower photosynthetic capacity and therefore the irradiance at which photosynthesis becomes saturated (e.g. Ortiz-Lopez et al., 1990).

PROOF OF CONCEPT IN MICROALGAE MASS CULTURES

Current interest in the potential application of microalgae as feedstock for synthetic chemistry and biofuels (Dismukes et al., 2008; Melis, 2009; Sun et al., 2009; Radakovits et al., 2010; Stephens et al., 2010) has lead to significant public and private investment in improving the efficiency of mass culture technology and the photosynthetic efficiency of dense microalgal cultures for which the wasteful dissipation of light energy by cells on the surface is a dominating issue. Cyanobacteria (e.g. *Synechocystis*, *Synechococcus*, and *Arthrospira* spp.) and red algae (e.g. *Porphyridium* spp.) are especially subject to surface light saturation and attendant shading of cells lower in the water column as, in addition to their Chl pigment beds, these algae
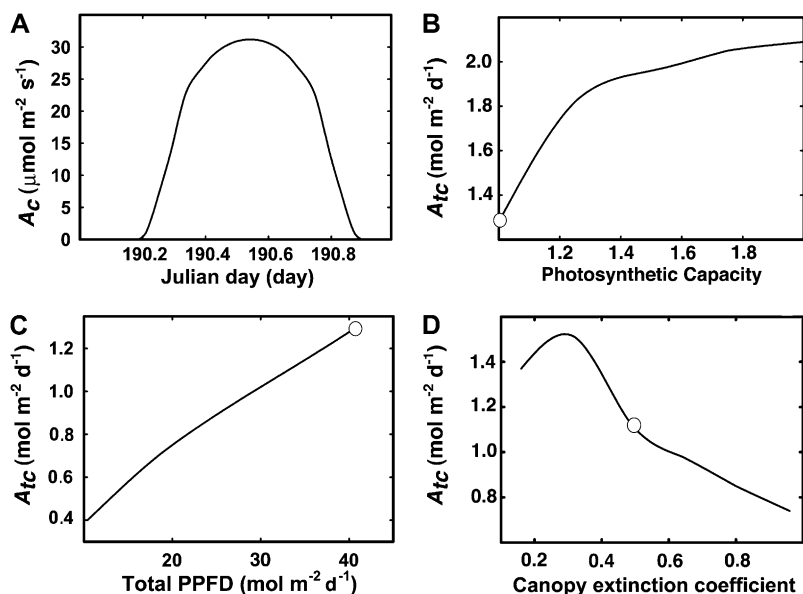
Figure 2. Simulations of the diurnal photosynthesis. Section A simulates a typical diurnal profile of the canopy photosynthetic CO_2 uptake rate (A_c) for day of year 190 at 52°N latitude for a LAI of 3. The changes of the photon flux density were achieved in WIMOVAC by changing the day of year used in the simulation. The modeled responses of the total daily integral gross canopy photosynthetic CO_2 uptake rate (A_{tc}) are shown for changes in the photosynthetic capacities (i.e. V_{cmx} and J_{max} relative to the default value; B), total PPFD (C), and canopy extinction coefficient (D). For A to C, the default LAI is 3, canopy extinction coefficient is 0.5, and total leaf reflectance and transmittance is 0.2 (Humphries and Long, 1995). For D, the assumed Chl concentration is 0.5 mmol Chl m^{-2}. The default values in B to D are shown by white circles. The canopy extinction coefficient was assumed to change proportionally with the changes in the leaf Chl concentration. We used the relationship between Chl concentration and the initial slope of the light response curve Φ from Hikosaka and Terashima (1995). The relationship between Chl concentration and leaf absorbance follows Evans (1993). In all these simulations, the light environments were predicted using WIMOVAC as done by Zhu et al. (2004b). In B and C, the daily total photosynthesis was calculated following Zhu et al. (2004b). In D, the daily total canopy photosynthesis was calculated based on Equations 1, 5, 6, and the predicted light environments using WIMOVC (with A_{max} 25 μmol m^{-2} s^{-1} and θ as 0.7). The detailed equations used in these WIMOVAC simulations are reproduced here in Supplemental Appendices S1 and S2.

possess phycobilisomes containing hundreds of light-harvesting bilin antenna pigments. Green microalgae (e.g. *Chlamydomonas*, *Dunaliella*, and *Haematococcus* spp.), and diatoms (*Cylindrotheca* and *Nitzschia* spp.), as well as brown algae (*Macrocystis pyrifera*), have smaller Chl antenna sizes that are comparable to those in C$_3$ plants (Melis, 1991).

Reducing the size of the light-harvesting pigment arrays in the photosynthetic apparatus has proven to be an effective strategy to mitigate photosynthetic inefficiency associated with the overabsorption of sunlight at the surface of microalgae mass cultures (Melis, 1999; Polle et al., 2003). Microalgae with truncated light-harvesting Chl antenna (abbreviated as Tla) have been shown to improve solar-to-biomass conversion efficiencies in mass cultures (Nakajima and Ueda, 1997, 1999; Mitra and Melis, 2008; Beckmann et al., 2009; Melis, 2009). Specifically, Tla microalgae required a higher light intensity for the saturation of photosynthesis and in mass culture showed overall greater productivity on a per Chl basis. Within the structural constrains permitted for Chl antenna size (Melis, 2009), productivity was found to be inversely proportional to the photosystem antenna size (Polle

et al., 2003). It was shown that Tla strains substantially reduced overabsorption and the consequent wasteful dissipation of excess incident sunlight, reduced photodamage and photoinhibition of photosynthesis, and minimized mutual cell shading that lowers productivity in cells deeper in the culture water column (Mitra and Melis, 2008).

A number of important criteria must be met to ensure that truncated antenna mutants are not photosynthetically handicapped in ways other than reduced Chl antenna size. To ensure that Tla strains will operate with improved solar energy conversion efficiency, the following analytical tests are useful: (1) the functional PSII and PSI Chl antenna size should be determined to assess the extent of reduction in antenna size, (2) the titer of functional PSII and PSI reaction centers per cell should be determined to ensure that the density of the photosynthetic electron-transport chains remains unaffected, (3) the quantum yield of photosynthesis must remain high to ensure that the efficiency of photosynthesis under limiting light remains unchanged, and (4) the light-saturated rate of photosynthesis should be inversely proportional to the measured Chl antenna size. With these criteria met, Tla

strains will very likely operate with improved solar energy conversion efficiency and productivity under mass culture and bright sunlight conditions. The utility of this verification approach was demonstrated in the screening of 6,500 *Chlamydomonas reinhardtii* transformants from a DNA insertional mutagenesis library that initially resulted in the isolation of 129 putative Tla transformants. From this screen, only a single strain, *tla1* (Polle et al., 2003), proved to be a truly useful truncated antenna mutant.

FINE-TUNING ANTENNA SIZE OF CROP CANOPIES

Under clear skies, the daily integral of photosynthesis of dense crop canopies is limited by the amount of light that reaches the lower leaves. The optimum situation for a crop monoculture would seemingly be to have a minimum antenna size in upper canopy leaves with progressively larger antenna as light intensity decreases within the canopy. In theory, this should lead to increased photosynthetic efficiencies of crop canopies, but there are counteracting considerations. For example, early in the growing season, reduced antenna size would prolong the period in which canopy density is insufficient to absorb all of the photosynthetically active radiation. While incomplete interception of light would not reduce the efficiency of canopy photosynthesis, it could reduce early season canopy carbon gain compared to a canopy of normally green leaves due to lower overall absorption of the available photosynthetically active radiation.

The hypothesis that a constitutive smaller antenna size will improve canopy photosynthetic efficiency and season long carbon gain has yet to be rigorously tested in crops, but there are promising indications that this may be so. Mutants of soybean (*Glycine max*) cultivars Clark Y9 and Y11 contain about one-half the Chl of the wild type. These mutant isolines are Chl *b* deficient, and in consequence the antenna size of PSII is reduced from approximately 250 Chl in the wild type to approximately 150 and for PSI from approximately 210 Chl to approximately 160 in the mutants. Furthermore, these Chl *b*-deficient mutant isolines compensated for a disproportionately large decrease in the PSII absorption cross section by increasing the PSII/PSI ratio by approximately 40% (Ghirardi and Melis, 1988). Yet, even with these ad hoc alterations to the photosynthetic apparatus, mature canopies of these low Chl soybean mutants are capable of a substantially higher daily integral of photosynthesis than wild type. More sunlight penetrating to the lower leaves in these Chl-depleted canopies increased the amount of leaf area positively contributing to canopy, resulting in greater than 30% increases in the daily integral of photosynthesis in some cases (Pettigrew et al., 1989). A secondary potential benefit is that increased light penetration could alter the canopy temperature regime with cooler temperatures in the upper portion of the canopies and warmer temperatures near the soil; if so, lowering temperature in warmest part of the canopy would be predicted to militate for improved yield (Ainsworth and Ort, 2010).

The way in which the antenna is reduced may also be important to determining the extent to which photosynthetic efficiency is improved. In particular, decreasing the antenna size by dramatically reducing Chl *b* synthesis, as is the case for the Clark Y9 and Y11 soybean mutants, would imbalance the antenna size of PSI and PSII, resulting in the increase in PSII/PSI ratio mentioned above. In addition, since Chl *b* binding is required to stabilize the accessory pigment proteins (Flachmann and Kühlbrandt, 1995), these mutations might be expected to create a respiratory drag due to continuous synthesis and degradation of pigment proteins. Finally, the Chl *b*-containing light-harvesting pigment proteins are critical to excitation energy transfer among PSII centers (Melis and Homann, 1976), whose absence would comprise efficiency as the likelihood of excitation into a closed PSII center increases at higher irradiance levels. These potential nonbeneficial alterations to the photosynthetic apparatus along with other pleiotropic effects of the mutations (e.g. changes in time to maturity; Pettigrew et al., 1989) may underlie the variable yield response of these Chl-deficient soybean mutants, which in some years showed yield increases (Pettigrew et al., 1989) and other years not (Hesketh et al., 1981). Down-regulating Chl synthesis early in the pathway might avoid some of these issues and be a better option for optimizing antenna size. For example, suppressing the rate of 5-aminolevulinate synthesis, the first committed step in tetrapyrrole biosynthesis, can drastically reduce leaf Chl content (e.g. Härtel et al., 1997; Goslings et al., 2004), and at least in the case of reduced Glu 1-semialdehyde aminotransferase activity, the titer of PSI and PSII units decreased but without a change in antenna size (Härtel et al., 1997). Intervening further upstream in the pathway(s) that regulates light-harvesting antenna assembly (e.g. Huq et al., 2004; Waters et al., 2009) has the potential to coordinately down-regulate the entire process and thereby avoid undesirable imbalances in energy distribution discussed above. For example, changes in antenna size in *C. reinhardtii* due to a mutation affecting the expression of the *TLA1* gene down-regulates LHC protein expression in tandem with the reduction in Chl synthesis (Mitra and Melis, 2010), thereby avoiding the respiratory penalty associated with excessive LHC turnover.

PERSPECTIVES

For the purposes of agriculture and the commercial application of microalgae mass culture, implementing truncated antenna to mitigate surface saturation of photosynthesis and improve light penetration is among the most promising strategies to improve photosynthetic efficiency in the near term. Nevertheless, given

the complexity of factors influencing the determination of the optimal Chl concentration for maximizing A_{tc}, particularly for crop canopies, a primarily empirical approach to determining the optimum antenna size is impractical. The development of more sophisticated models than we have employed here will need to play a central role in dealing with the complexity and optimizing Chl content for different crops with differing canopy architectures, differing planting dates, and at different geographical locations.

Use of Tla genetically modified organisms, whether plants or algae, inevitably would raise issues about release and the potential environmental impact of these organisms. Experience in the field with crop plants, and in the laboratory with microalgae, has consistently demonstrated that, when left on their own, Tla strains cannot effectively compete with their wild-type counterparts. Accordingly, Tla isolines, when cultivated under controlled and protective conditions, can afford substantial productivity improvements under high-density conditions, with little environmental risk of escape. But these facts also represent a limitation of the truncated antenna approach, i.e. organisms with truncated antenna would unavoidably be less competitive than their full antenna counterparts. For crop plants this means mostly reduced competitiveness against weeds. Current advanced weed control may have to be intensified for truncated antenna crops particularly with the prospect of herbicide resistance. For microalgal mass cultures, competition is a more serious issue and may limit the use of truncated antenna organisms to closed bioreactors to prevent airborne contamination by full antenna organisms.

Supplemental Data

The following materials are available in the online version of this article.

Supplemental Appendix S1. Equations used to simulate leaf and canopy net photosynthetic carbon uptake.

Supplemental Appendix S2. Definition of symbols.

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