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Optimization of photosynthetic light energy utilization by microalgae

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ABSTRACT

Over 50% of the energy losses associated with the conversion of solar energy into chemical energy during photosynthesis are attributed to kinetic constraints between the fast rate of photon capture by the light harvesting apparatus and the slower downstream rate of photosynthetic electron transfer. At full sunlight intensities, energy flux from the light harvesting antennae to the reaction centers may be 100-folds greater than the overall linear electron flow resulting in the dissipation of up to 75% of the captured energy as heat or fluorescence. One possible means to couple energy capture and photosynthetic electron transfer more efficiently is to reduce the optical cross-section of the light harvesting antennae. We show that by partially reducing chlorophyll b levels in the green alga, Chlamydomonas reinhardtii, we can tune the peripheral light harvesting antennae size for increased photosynthetic efficiency resulting in more than a two-fold increase in photosynthetic rate at high light intensities and a 30% increase in growth rate at saturating light intensities. Unlike chlorophyll b-less mutants which lack the peripheral light harvesting antennae; transgenics with intermediate sized peripheral antennae have the advantage that they can carry out state transitions facilitating enhanced cyclic ATP synthesis and have robust zeaxanthin-violaxanthin cycles providing protection from high light levels. It is hypothesized that the large antennae size of wild-type algae and land plants offers a competitive advantage in mixed cultures due to the ability of photosynthetic organisms with large light harvesting antennae to shade competing species and to harvest light at low flux densities. Published by Elsevier B.V.

1. Introduction

Single celled microalgae are among the most productive autotrophic organisms in nature due to their high photosynthetic efficiencies and the lack of heterotrophic tissues [1–4]. Yet, photosynthetic efficiencies and areal productivities are 2 to 3-folds lower than their theoretical potential [5,6]. This inefficiency is attributed in large part to the poor kinetic coupling between light capture by the light harvesting apparatus and down-stream photochemical and electron transfer processes. During photosynthesis, light captured by the peripheral light-harvesting antenna complexes (LHC) is transferred at nearly 100% efficiency (via quantum coherence processes) to the proximal antenna complexes of the photosystem II (PSII) and photosystem I (PSI) reaction center (RC) complexes where the primary charge separation occurs [7]. Wild-type (WT) algae typically possess large PSII peripheral antennae complexes (LHCII), which maximize light capture at both high and limiting light intensities [2]. However, light harvesting antenna size is not optimized for achieving maximal

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apparent quantum efficiency in monocultures where competition for light between different species is absent. In nearly all photosynthetic organisms, photosynthesis light saturates at ~25% of the full sunlight intensity [8]. This is due to the fact that at saturating light intensities, the rate of photon capture substantially $(>100\times)$ exceeds the rate of linear photosynthetic electron transfer resulting in a large fraction of the captured light energy being dissipated as heat or fluorescence by non-photochemical quenching (NPQ) processes [9]. These dissipative energy losses account for the greatest inefficiencies (~50%) in the conversion of light into chemical energy during photosynthesis [5,6]. Since light is a resource for photosynthetic organisms, it is expected that competition for this resource drives the evolution of antennae size. Ironically, having large, inefficient antennae may increase evolutionary fitness since organisms that compete better for light effectively shade those that are less efficient at capturing light. In mixed species communities, being best at capturing light may be a selective advantage but in monocultures being more efficient at light utilization (energy conversion) may be the better fitness or growth strategy.

To date, the most effective strategy to increase photosynthetic light utilization efficiency is to reduce the size of the light-harvesting antenna per RC complex [5,8,10]. By reducing the effective optical cross section of the antennae complexes the probability of saturating electron transfer at full sunlight intensities is reduced. Significantly, a reduction



Abbreviations: Chl, chlorophyll; LHC, light harvesting complex; P_{MAX} , maximum light-saturated photosynthesis rate; PSI, photosystem I; PSII, photosystem II; WT, wild type.

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in antennae size/RC is also predicted to reduce cell shading and increase the penetration of photosynthetically active radiation to greater depths in the culture water column (Fig. 1A). In *Chlamydomonas reinhardtii*, it has been demonstrated that mutants with reduced antenna size can be generated by eliminating chlorophyll (Chl) *b* synthesis as well as by reducing expression of LHC genes [10,11]. Previous studies have shown that microalgae lacking the peripheral LHCII have increased photosynthetic rates; however, few studies have demonstrated an increase in growth rate with reduced peripheral antennae size under fully autotrophic growth conditions [8,11–15]. To date, nearly all growth studies with algae having altered antennae sizes have been done under mixotrophic (plus acetate) growth conditions.

In addition to harvesting light members of the LHCII gene/protein family also play important roles in; 1) balancing energy distribution between the photosystems (state transitions), 2) regulating cyclic photophosphorylation or ATP synthesis, and 3) mediating the dissipation of excess captured energy as heat through NPQ [9,16,17]. Thus, while the complete elimination of LHCII reduces kinetic constraints between light capture and energy conversion, elimination of all of the peripheral LHCII would be expected to impair the distribution of energy between the two photosystems, reduce the ability to modulate ATP/NADPH ratios, and increase susceptibility to photodamage. Hence, the complete lack of a peripheral antenna may not be the optimal solution for enhancing energy conversion efficiency and growth of algal monocultures.

To determine if there are more optimal antenna sizes for more efficient net photosynthesis, we generated transgenic *C. reinhardtii* strains having a range of LHCII antenna sizes that were intermediate between WT and a Chl *b* less strain which entirely lacks LHCII. We hypothesized that reducing but not eliminating the Chl *b* content would result in algal transgenics with intermediate LHCII levels. We demonstrate that transgenic algae having intermediate LHCII content are capable of state transitions as well as non-photochemical quenching of excess energy via the violaxanthin–zeaxanthin cycle. Algae with intermediate antennae sizes also have substantially higher growth rates than WT or Chl *b* lacking algal strains when grown autotrophically at saturating (in WT) light intensities while having growth rates similar to WT at low light intensities. We propose that these observations also have implications for improving the light harvesting efficiency of photosynthesis in the canopies of terrestrial plants. Leaves having smaller antennae in the upper canopy and larger antennae in the lower canopy may also have increased the apparent photosynthesis efficiency and improved productivity when grown in monocultures.

2. Materials and methods

2.1. Vector construction

The plasmid for inducing RNAi-mediated silencing of the chlorophyllide *a* oxygenase (*CAO*) gene in *C. reinhardtii* strain CC-424 (arg2 cw15 sr-u-2-60 mt –, *Chlamydomonas* Genetic Center) was constructed using a genomic-sense/cDNA-antisense strategy. The first two exons and introns of the *CAO* gene were amplified by PCR using GCTTTCGTCATATGCTTCCTGCGTCGCTTC and CTC TGGATCCGTCTGTGTAAATGTGATGAAGC as forward and reverse primers respectively and the resulting product was digested with

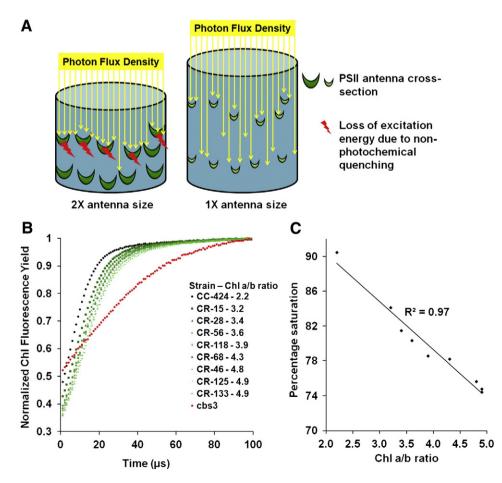


Fig. 1. Algae with truncated LHCII. (A) Model for light absorption and utilization by algae with large and truncated antennae at saturating light intensities. (B) Chl fluorescence rise kinetics in parental (CC-424), Chl *b* reduced transgenics (CR) and Chl *b* less mutant (*cbs3*). Chl fluorescence levels were measured under continuous, non-saturating illumination every 1 µs. (C) Correlation between Chl *a/b* ratio and percent closure of PSII RCs.

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