

# Vertical adaptive radiation in ocean *Prochlorococcus*: Evolutionary implications of the Chl *b/a* ratio from molecular evidence

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## Abstract

*Prochlorococcus* is a marine cyanobacterium of global significance. Two ecotypes are adapted to either high-light (HL) or low-light (LL) conditions. The ratio between chlorophyll (Chl) *a* and *b* is a distinguishing characteristic of these two ecotypes. However, how this ratio evolved in *Prochlorococcus* during this ecotype differentiation remains unclear. Our analyses reveal that the ancestor of *Prochlorococcus* was typically low-light adapted. The LL ecotype showed a stagnant evolution, and the HL ecotype was recently diverged. There was an adaptive radiation after directional evolution in the Chl *b/a* ratio regulation. Recombination in chlorophyllide *a* oxygenase (CAO) and positive selection on Clp protease contributed to the directional evolution of *Prochlorococcus*. The recombinant fragments of CAO were correlated with a large group of shared coevolving sites. Evidence of positive selection was found in both subunits of Clp. Chl *b/a* ratio evolution, as annotated by molecular evidence, appears to be among the crucial reasons that explain how *Prochlorococcus* has become the dominant photosynthetic organism in the ocean.

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## 1. Introduction

Plants and algae can potentially use the reactions of the chlorophyll (Chl) cycle to adjust the Chl *b/a* ratio to their particular needs under various physiological and environmental conditions [1].

*Prochlorococcus* is a marine cyanobacterium of global significance and is the most abundant photosynthetic organism on earth. It inhabits the ocean within the 40° N to 40° S latitudinal bands, and its high density and phototropic metabolism make it accountable for an important part of the primary production of the world's oceans. Its vertical distribution spans from the surface to a depth of 200 m, where the light level can be as low as 0.1% of surface

irradiance. *Prochlorococcus* possesses a remarkable pigment complement, which includes divinyl derivatives of Chl *a* and Chl *b* [2]. Its contribution as a major component of the carbon cycle is at least partly due to its unique pigment systems. Divinyl Chl *b* is especially important for enabling *Prochlorococcus* to live and thrive within its specialized niche [3].

*Prochlorococcus* exhibits unusually large changes in Chl *b/a* ratio with depth [4]. There are at least two ecotypes of *Prochlorococcus* that coexist in the oceans; these are distinguished not only by their photophysiology but also by their molecular phylogeny [5]. One ecotype (LL) is adapted to the low light of the deep euphotic zone, while the other (HL) is adapted to the high light at the surface. The two ecotypes are characterized *in vivo* by high Chl *b/a* ratios (LL ecotype) and low Chl *b/a* ratios (HL ecotype). The ratio of Chl *b/a* increases as irradiance decreases, but at

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any particular growth irradiance, the HL isolates will always have significantly lower Chl *b/a* ratios than the LL isolates ( $P < 0.01$ ) [2,4].

The reduction of Chl *b* to Chl *a* (and its hydrolysis to chlorophyllide *a*) and the biosynthesis of Chl *b* from chlorophyllide *a* can be considered to operate as a cycle that starts and ends with chlorophyllide *a*. Biosynthesis of both Chls begins with chlorophyllide *a*. Completion of Chl *a* biosynthesis needs only the step of esterification catalyzed by Chl synthase, while Chl *b* biosynthesis includes a two-step reaction catalyzed by chlorophyllide *a* oxygenase (CAO) and a subsequent esterification step [1,6,7]. The pathway of *Prochlorococcus* chlorophyll synthesis is essentially the same as the known pathways in other algae and in higher plants. The pathway is illustrated in Fig. 1, which was revised from Kettler et al. [8] and generated by Pathway Tools [9]. It is reasonable to consider that the biosynthesis of chlorophyll *a* and *b* is tightly regulated [10].

Biochemical and genetic evidence has shown that CAO is the only enzyme necessary for the transition of *a*-type to *b*-type chlorophyll pigments [1]. The CAO gene is a unique gene in the synthesis of Chl *b* and has recently been identified in *Prochlorococcus* [3,11]. CAO protein levels correlate with changes in Chl *b* levels and with the Chl *b/a* ratio [12]. Regulation is thought to occur via interaction between Lhcb apoproteins and the CAO protein, as suggested by the enhanced Chl *b* synthesis that has been shown in cyanobacteria that coexpress both CAO and Lhcb [12,13].

A second key enzyme that responds to Chl *b/a* ratio regulation is Clp protease that consists of two subunits, ClpC1 and ClpP. This enzyme regulates the level of CAO through destabilization of the CAO protein in response to the accumulation of Chl *b* [10]. Clp is widely distributed in cyanobacteria and chloroplasts. The CAO in *Prochlorococcus* contains AB domains that are Clp signal sequences and that lead to CAO degradation by Clp [3,14,15].

The level of transcripts encoding Clp proteins and the chlorophyll fluorescence per cell both vary with the light intensity in *Prochlorococcus* [16] in conjunction with the changes in Chl *b/a* ratio [4]. These same phenomena are seen in *Arabidopsis thaliana* [10]. Clp protease has been shown to control chlorophyll *b* synthesis by regulating the level of CAO in *Arabidopsis thaliana* [10].

The reverse pathway, the transition of the *b*-type to *a*-type Chl pigments, seems to play a role in the degradation of Chl *b* and operates during acclimation of plants to different light regimes. However, this transition has so far been characterized only by activity tests, which point to two different enzymes for this transition, and this type of enzyme activity has not been detected in algae [1]. Therefore, chlorophyll *b* reductase was not examined in the present study.

Other pigments, such as phycoerythrin (PE) [17,18], also show different patterns of expression in HL and LL *Prochlorococcus*. In addition, the phycoerythrin content of *Prochlorococcus* is extremely low (PE/DV-Chl *b* ratio of about 1:330 while the typical phycobilin/Chl ratio is about 1:2 for a cyanobacterium). Thus, the capacity of

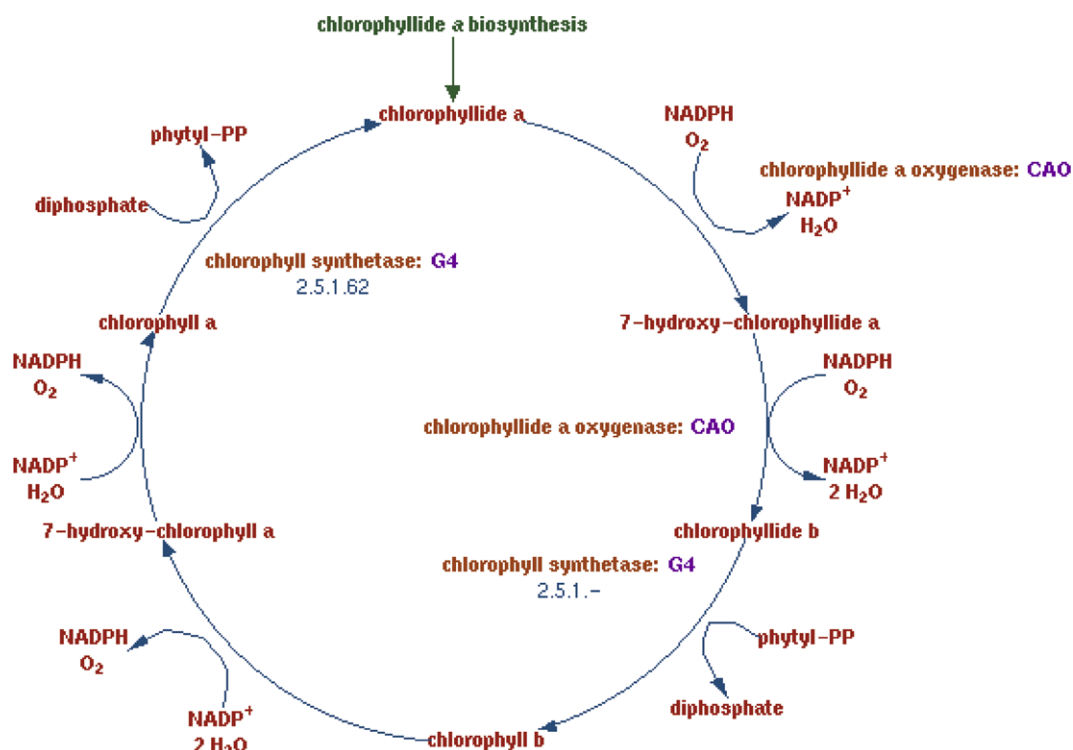


Fig. 1. The chlorophyll cycle of *Prochlorococcus*. If an enzyme name is shown in bold, there is experimental evidence for this enzymatic activity.

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