Chapter 17

Adaptation, Acclimation and Regulation in Algal Photosynthesis

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Summary

Relating the photosynthetic processes of algae to their environments requires that the responses are considered over time-scales of seconds to minutes (regulation), hours to days (acclimation) and up to thousands of millions of years (adaptation). All of these responses are genetically determined, with so-called adaptations reflecting genetic changes which distinguish taxa from the strain (ecotype), i.e. infraspecific level, up to the Division (Phylum) level. Tempting as it is to assign the establishment of these genetic differences to natural selection, the genetic differences at the higher taxonomic levels should be related to the environments at the time at which they evolved. Genetic differences limit the responses that algal genotypes can make to their immediate environment (i.e. during a single generation). Using photosynthetic pigments as an example, the content per unit biomass of photosynthetic light-harvesting pigment-protein complexes, and, where they occur, of the energy-dissipating xanthophyll cycle pigments change with the photon flux density for growth; light-harvesting pigments decrease with increasing light, while xanthophyll cycle pigments increase. There are cost-benefit considerations not only in the extent of such acclimation, but also of the rate at which acclimation occurs. Regulation involves allosteric or covalent modification of pre-existing catalysts, e.g. ribulose bisphosphate carboxylase-oxygenase, xanthophyll cycle pigments, and the pigment-protein complexes involved in state transitions. Much remains to be done to not only understand adaptation, acclimation and regulation in algae, but also to understand how the three processes interact.

I. Introduction

Algal photosynthesis proceeds according to the (minimal) equation

\[ \text{catalysts} \quad \text{CO}_2 + 2\text{H}_2\text{O} + 8 \text{photons} \rightarrow (\text{CH}_2\text{O}) + \text{O}_2 + \text{H}_2\text{O} \]

The adaptation and acclimation of the photosynthetic machinery in algae concerns the responses of the organisms to variability in the availability of the substrates (CO₂, H₂O and photons), and variability in the build-up of the products (O₂ and (CH₂O)), of photosynthesis. It also concerns variability of the availability of the resources that are required to produce the catalysts used in the photosynthetic reactions. Among these requirements for producing the catalytic apparatus of photosynthesis are the carbohydrates produced by photosynthesis, and the nutrients obtained from the environment. These nutrients include N (immediately as NH₄⁺), P (as HPO₄²⁻), Mg²⁺, Cl⁻, Mn²⁺, Fe²⁺/Fe³⁺, Zn²⁺ and (often) Cu²⁺. The availability of these resources in algal habitats varies widely, in some cases by at least four orders of magnitude (Table 1).

At the outset we need to differentiate clearly amongst the terms adaptation, acclimation and regulation. Adaptation will be used to describe an outcome of evolution as recorded in the gene pool of a species. It also refers to changes in gene frequency within a gene pool as a result of selection with or without recombination. Acclimation will be used to describe changes of the macromolecular composition of an organism that occurs in response to variation of environmental conditions. According to this usage, photoacclimation occurs via synthesis or breakdown of specific components of the photosynthetic apparatus. Acclimation operates within constraints set by the genetic make-up of the species (or, more often, the clonal population) under investigation. Regulation

Abbreviations: CAM - Crassulacean acid metabolism; CF₁ - chloroplast or cyanobacterial ATP synthetase; dd-dt - diadinoxanthin-diatoxanthin cycle; I₁ - incident photon flux density; Iₚ - saturation function of photosynthesis; photon flux density at which the extrapolation of the initial slope of the photosynthesis incident photon flux density relationship intercepts the extrapolation of the light-saturated rate of photosynthesis; Kₘ - Michaelis-Menten constant; L₂-form II Rubisco with two large subunits; L₅S₅-form I Rubisco with eight large and eight small subunits; NADH - nicotinamide adenine dinucleotide (reduced form); NADPH - nicotinamide adenine dinucleotide phosphate (oxidized form); PQ - plastoquinone; PQ⁺ - plastoquinone; PQH₂ - plastoquinol; PSI - Photosystem I; PS II - Photosystem II; Ψₚ - pressure component of water potential; Ψₑ - osmotic component of water potential; Ψₚ - water potential; RCII - reaction center of Photosystem II; Rubisco - ribulose bisphosphate carboxylase-oxygenase; UQ - ubiquinone; UQ⁺ - ubisemiquinone; UQH₂ - ubiquinol; v-a-z - violaxanthin-antheraxanthin-zeaxanthin cycle

1 The term adaptation has been employed loosely in studies of algal photosynthesis and ecology to refer to genetic adaptation, physiological acclimation and physiological regulation. We feel that it is necessary to differentiate between these processes. The term behavior can be reserved for activities such as swimming or other movements/migrations.

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