
Molecular mechanisms in the nitrogen-fixing *Nostoc*-Bryophyte symbiosis

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Introduction

The metabolic products of cyanobacteria are highly coveted by organisms in their immediate environment. A basis for this directional relationship is that cyanobacteria are amongst the most nutritionally independent organisms in the biosphere. Their unifying characteristic is an oxygen-evolving photosynthetic mechanism, leading to a CO₂ fixing autotrophic metabolic mode. Thus, they require only light, water, CO₂ and a few inorganic molecules or elements for growth; consequently, cyanobacteria are ubiquitous in illuminated habitats (Whitton and Potts 2000). Cyanobacteria and their evolutionary progeny, the chloroplasts of algae and plants (Douglas 1998; Raven and Allen 2003), are the overwhelmingly dominant producers of the reduced carbon that sustains growth of heterotrophic organisms in the biosphere via detrital and grazing food chains. A subset, distributed amongst all five taxonomic orders (subdivisions) of the cyanobacteria (Castenholz 2001), are also capable of nitrogen fixation (Rippka and Herdman 1992), thereby enhancing both their nutritional independence and the desirability of their metabolites.

However, oxygenic photosynthesis and nitrogen fixation are biochemically incompatible processes, due the oxygen liability of the nitrogenase enzyme complex. Cyanobacteria have evolved temporal behavioral and spatial morphological solutions to the oxygen incompatibility dilemma. The common behavioral solution is to photosynthesize during the day, accumulating reserves of photosynthate, and fix nitrogen at night when the cellular oxygen tension can be reduced by a lack of production, coupled with respiratory consumption, fueled by the stored photosynthate (Fay 1992; Gallon 1992). A spatial separation from concurrent oxygen production is provided by highly differentiated cells called heterocysts, which are specialized for nitrogen

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fixation. Heterocysts differ physiologically from vegetative cells by a loss of the oxygen-evolving photosynthetic mechanism, reflecting a transition to a heterotrophic metabolic mode, an increased rate of aerobic respiration, and the deposition of a solute and gas impermeable extra wall layer (this wall layer is interrupted at the junctions with adjacent vegetative cells), all of which contribute to a microoxic cytoplasm. Heterocyst formation occurs only in filamentous cyanobacteria in which they establish a reciprocal source-sink relationship. Vegetative cells provide heterocysts with reductant in the form of photosynthate, most likely as sucrose, to support nitrogen fixation and respiratory activities, and receive fixed nitrogen as glutamine in return (Wolk et al. 1994).

Similar to other bacteria, even superficial observations indicate that cyanobacteria rarely lead a solitary life in nature. They are found in nonspecific association with a wide range of organisms, especially in marine ecosystems (Carpenter and Foster 2002). A close association with an autotroph is highly beneficial to a heterotroph, be it a unicellular prokaryote or a multicellular, multitissue eukaryote, because it minimizes competition for the reduced carbon. Such a breadth of organismal associations with cyanobacteria has been documented (Adams 2000; Paerl 1992; Rai et al. 2002) and many more transient associations are predicted to occur. Nitrogen-fixing, heterocyst-forming, *Nostoc* species, and their close relatives, are also recruited into specific associations with representative nonphotosynthetic and photosynthetic eukaryotes that span the phylogenetic spectrum. The nonphotosynthetic eukaryotes include extracellular associations with lichenized fungi (Rikkinen 2002), as well as an intracellular association with the unique mycorrhizal fungus *Geosiphon pyriforme* (Mollenhauer et al. 1996). The photosynthetic eukaryotes range from aquatic unicellular forms, such as the marine diatoms *Rhizosolenium* sp. (Mague et al. 1974) and *Hemiaulus* spp. (Villareal 1991), to representatives of the major divisions of terrestrial plants. The plant representatives include the spore-producing non-vascular bryophytes, especially the hornworts (Ridgeway 1967), the spore-producing vascularized ferns, specifically the aquatic fern *Azolla* (Peters and Mayne 1974), seed-producing gymnosperms represented by cycads (Bergersen et al. 1965), and one family of angiosperms, the Gunneraceae (Silvester and McNamara 1976). The nitrogen-fixing cyanobacterial-plant associations have been more highly studied than any other cyanobacterial association and comprehensive reviews have recently been published (Adams 2000; Bergman et al. 1996; Meeks 1998, 2003; Rai et al. 2000, 2002).