CYANOBACTERIA- AN UNUSUAL PROKARYOTE

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Abstract: *Cyanobacteria, once popularly known as blue-green algae, are prokaryotes which exhibit very unusual characteristics unlike other prokaryotes. With very simple undifferentiated internal cellular organization without any membrane-bound organelles, they carry out three important physiological functions viz., oxygenic photosynthesis using chl* $_a$ *and other accessory pigments unlike photosynthetic bacteria which use bacteriochlorophyll,* N_2 *fixation by oxygen-sensitive nitrogenase as free-living N fixers and in symbiotic association and inorganic N reduction pathway, all three features which are not found together in any other prokaryote or eukaryote. a small number of strains can also use hydrogen sulfide (H2S) and convert it to elemental sulfur. This review is restricted only to special features of Cyanobacteria*

Key words: *Heterocysts, nitrogenase, phycobilins*

CYANOBACTERIA

Cyanobacteria, also known as **Cyanophyta**, is a phylum of bacteria that obtain their energy through photosynthesis. The name "cyanobacteria" comes from the color of the bacteria.They are often called **blue-green algae**, although the name is sometimes considered a misnomer because cyanobacteria are prokaryotes and the term "algae" is often reserved for eukaryotes.

Like other prokaryotes, cyanobacteria have no internal membrane bound organelles. They perform photosynthesis in distinctive folds in the outer membrane, unlike green plants which use organelles called chloroplasts. Symbiogenesis argues that the chloroplasts found in plants and eukaryotic algae evolved from cyanobacterial ancestors via endosymbiosis.

By producing oxygen as a byproduct of photosynthesis, cyanobacteria are thought to have converted the early reducing atmosphere into an oxidizing one, causing the "rusting of the Earth" (Schopf, 2012) and causing the Great Oxygenation Event, dramatically changing the composition of life forms on Earth by stimulating biodiversity and leading to the near-extinction of anaerobic organisms (that is, oxygen-intolerant).

Cyanobacteria are arguably the most successful group of microorganisms on earth. They are the most genetically diverse; they occupy a broad range of habitats across all latitudes, widespread in freshwater, marine, and terrestrial ecosystems, and they are found in the most extreme niches such as hot springs, salt works, and hypersaline bays. Photoautotrophic, oxygen-producing cyanobacteria created the conditions in the planet's early atmosphere that directed the evolution of aerobic metabolism and eukaryotic photosynthesis. Cyanobacteria fulfill vital ecological functions in the world's oceans, being important contributors to global carbon and nitrogen budgets.(Stewart and Falconer, 2008)

While contemporary cyanobacteria are linked to the plant kingdom as descendants of the endosymbiotic progenitor of the chloroplast, there are several features which are unique to this group.

Many filamentous cyanobacteria produce different cell types that play specific physiological, reproductive, or ecological roles. The most well known of these is the heterocyte (often called a heterocyst, although it is not a cyst). This thick-walled cell is formed by members of the Nostocales and Stigonematales and is the location of the enzyme nitrogenase for nitrogen fixation, the conversion of nitrogen gas into ammonium and then amino acids. This cell type is not a strict prerequisite for nitrogenase activity, however, because several nonheterocystous taxa in other orders are also known to fix nitrogen. Another specialized cell type is the akinete, a structurally reorganized cell that is formed under unfavorable conditions, and that allows cyanobacteria to overwinter in the sediments.

Some genera such as Nostoc produce hormogonia, a motile series of cells formed for reproduction. In one order of coccoid forms, the Pleurocapsales, reproduction is via the production of up to several hundred minute cells called baeocytes.

PHOTOSYNTHESIS

Cyanobacteria use the energy of sunlight to drive photosynthesis, a process where the energy of light is used to split water molecules into oxygen, protons, and electrons. Because they are aquatic organisms, they typically employ several strategies which are collectively known as a "carbon concentrating mechanism" to aid in the acquisition of inorganic carbon (CO_2 or bicarbonate). Among the more specific strategies is the widespread prevalence of the bacterial microcompartments known as carboxysomes (Kerfeld, et al.,2010). These icosahedral structures are composed of hexameric shell proteins that assemble into cage-like structures that can be several hundreds of nanometers in diameter. It is believed that these structures tether the CO_2-fixing enzyme, RuBisCO, to the interior of the shell, as well as the enzyme carbonic anhydrase, using the paradigm of metabolic channeling to enhance the local CO_2 concentrations and thus increase the efficiency of the RuBisCO enzyme (Long et al., 2007)

In contrast to chloroplast-containing eukaryotes, cyanobacteria lack compartmentalization of their thylakoid membranes, which are contiguous with the plasma membrane. Thus, the protein complexes involved in respiratory energy metabolism share several mobile energy carrier pools (e.g., the Quinone pool, cytochrome c, ferredoxins), so photosynthetic and respiratory metabolism interact with each other. Furthermore, there is a tremendous diversity among the respiratory components between species. Thus cyanobacteria can be said to have a "branched electron transport chain", analogous to the situation in purple bacteria. In general, photosynthesis in cyanobacteria uses water as an electron donor and produces oxygen as a byproduct, though some may also use hydrogen sulfide (Cohen et al., 1986), a process which occurs among other photosynthetic bacteria such as the purple sulfur bacteria. Here Cyanobacteria use hydrogen sulfide as electron donor instead water and produce elemental sulphur intead of O_2.

Cyanobacteria are photosynthetic prokaryotes that capture sunlight for energy using chlorophyll *a* and various accessory pigments. They are common in lakes, ponds, springs, wetlands, streams, and rivers, and they play a major role in the nitrogen, carbon, and oxygen dynamics of many aquatic environments.

Cyanobacteria were formerly classified as blue-green algae because of their algal-like appearance, their possession of chlorophyll rather than bacteriochlorophyll, and their photosynthetic production of oxygen by a two-photosystem process as in algae and higher plants.

Ultrastructural studies, however, clearly show that the Cyanobacteria are prokaryotic; that is, they lack nuclei and other organelles and they have a peptidoglycan cell wall that is typical of gram-negative Eubacteria

All cyanobacteria contain chlorophyll *a* and most contain the blue phycobiliproteins phycocyanin and allophycocyanin, giving the cells their characteristic blue-green color. Many taxa also contain the phycobiliprotein phycoerythrin, making the cells red, or sometimes black.

Although cyanobacteria lack membrane-bound organelles, they have a variety of cellular structures and inclusions that have specialized functions and that contribute to their ecological success. These include the photosynthetic thylakoid membranes containing the phycobilisomes, and the nucleoid region or centroplasm in the center of the cell, which contains the complex folded, circular DNA, often in multiple copies

N_2 FIXATION

Cyanobacteria can fix atmospheric nitrogen in anaerobic conditions by means of specialized cells called **heterocysts.** Heterocysts may also form under the appropriate environmental conditions (anoxic) when fixed nitrogen is scarce. Heterocyst-forming species are specialized for nitrogen fixation and are able to fix nitrogen gas into ammonia (NH_3),nitrites (NO− 2) or nitrates (NO− 3), which can be absorbed by plants and converted to protein and nucleic acids (atmospheric nitrogen is not bioavailable to plants, except for those having endosymbiotic nitrogen-fixing bacteria, especially the Fabaceae family, among others).

Within the wide biodiversity that is found in the bacterial world, Cyanobacteria represents a unique phylogenetic group that is responsible for a key metabolic process in the biosphere — oxygenic photosynthesis — and that includes representatives exhibiting complex morphologies. Many cyanobacteria are multicellular, growing as filaments of cells in which some cells can differentiate to carry out specialized functions. These differentiated cells include resistance and dispersal forms as well as a metabolically specialized form that is devoted to N_2 fixation, known as the heterocyst.

Heterocysts are specialized nitrogen-fixing cells formed during nitrogen starvation by some filamentous cyanobacteria, such as *Nostoc punctiforme*, *Cylindrospermum stagnale*, and *Anabaena sphaerica*. They fix nitrogen from dinitrogen (N_2) in the air using the enzyme nitrogenase, in order to provide the cells in the filament with nitrogen for biosynthesis (Wolk et al., 1994). Nitrogenase is inactivated by oxygen, so the heterocyst must create a microanaerobic environment. The heterocysts' unique structure and physiology require a global change in gene expression.

Heterocysts:

- produce three additional cell walls, including one of glycolipid that forms a hydrophobic barrier to oxygen.
- produce nitrogenase and other proteins involved in nitrogen fixation.
- degrade photosystem II, which produces oxygen.
- up-regulate glycolytic enzymes.
- produce proteins that scavenge any remaining oxygen
- contain polar plugs composed of cyanophycin which slows down cell-to-cell diffusion

Cyanobacteria usually obtain a fixed carbon (carbohydrate) by photosynthesis. The lack of photosystem II prevents heterocysts from photosynthesizing, so the vegetative cells provide them with carbohydrates, which is thought to be sucrose. The fixed carbon and nitrogen sources are exchanged through channels between the cells in the filament. Heterocysts maintain photosystem I, allowing them to generate ATP by cyclic photophosphorylation.

Single heterocysts develop about every 9-15 cells, producing a one-dimensional pattern along the filament. The interval between heterocysts remains approximately constant even though the cells in the filament are dividing. The bacterial filament can be seen as a multicellular organism with two distinct yet interdependent cell types. Such behavior is highly unusual in prokaryotes and may have been the first example of multicellular patterning in evolution.

N_2 FIXATION IN NON-HETEROCYSTOUS CYANOBACTERIA

In the modern ocean, a significant amount of nitrogen fixation is attributed to filamentous, nonheterocystous cyanobacteria of the genus*Trichodesmium.* In these organisms, nitrogen fixation is confined to the photoperiod and occurs simultaneously with oxygenic photosynthesis. Nitrogenase, the enzyme responsible for biological N_2 fixation, is irreversibly inhibited by oxygen in vitro. How nitrogenase is protected from damage by photosynthetically produced O_2 was once an enigma. Using fast repetition rate fluorometry and fluorescence kinetic microscopy, it was shown that there is both temporal and spatial segregation of N_2 fixation and photosynthesis within the photoperiod. Linear photosynthetic electron transport protects nitrogenase by reducing photosynthetically evolved O_2 in photosystem I (PSI). It is postulated that in the early evolutionary phase of oxygenic photosynthesis, nitrogenase served as an electron acceptor for anaerobic heterotrophic metabolism and that PSI was favored by selection because it provided a micro-anaerobic environment for N_2 fixation in cyanobacteria (Ilana Berman-Frank et al., 2001).

The biological reduction of N_2 is catalyzed by nitrogenase, which is irreversibly inhibited by molecular oxygen. Cyanobacteria are the only diazotrophs (nitrogen-fixing organisms) that produce oxygen as a by-product of the photosynthetic process, and which must negotiate the inevitable presence of molecular oxygen with an essentially anaerobic enzyme.

Fixed nitrogen (N) often limits the growth of organisms in terrestrial and aquatic biomes, and N availability has been important in controlling the CO_2 balance of modern and ancient oceans. The fixation of atmospheric dinitrogen gas (N_2) to ammonia is catalysed by nitrogenase and provides a fixed N for N-limited environments. The filamentous cyanobacterium *Trichodesmium* has been assumed to be the predominant oceanic N_2-fixing microorganism since the discovery of N_2fixation in *Trichodesmium* in 1961. /Attention has recently focused on oceanic N_2 fixation because nitrogen availability is generally limiting in many oceans, and attempts to constrain the global atmosphere–ocean fluxes of CO_2 are based on basin-scale N balances[9]. Biogeochemical studies and models have suggested that total N_2-fixation rates may be substantially greater than previously believed but cannot be reconciled with observed *Trichodesmium* abundances (Sims and Dunigan, 1984). It is curious that there are so few known N_2-fixing microorganisms in oligotrophic oceans when it is clearly ecologically advantageous. Here we show that there are unicellular cyanobacteria in the open ocean that are expressing nitrogenase, and are abundant enough to potentially have a significant role in N dynamics.

NITROGEN FIXATION IN UNICELLULAR CYANOBACTERIA

Large colonial cyanobacteria in the genus *Trichodesmium* and the heterocystous endosymbiont *Richelia* have traditionally been considered the dominant marine N_2 fixers, but unicellular diazotrophic cyanobacteria and bacterioplankton have recently been found in the picoplankton and nanoplankton community of the North Pacific central gyre, and a variety of molecular and isotopic evidence suggests that these unicells could make a major contribution to the oceanic N budget· Rates of N_2fixation by these small, previously overlooked diazotrophs that, although spatially variable, can equal or exceed the rate of N_2fixation reported for larger, more obvious organisms.

(Joseph P. Montoya et al., 2004.). Direct measurements of $^{15}N_2$ fixation by small diazotrophs in various parts of the Pacific Ocean, including the waters off Hawaii where the unicellular diazotrophs were first characterized, show that N_2fixation by unicellular diazotrophs can support a significant fraction of total new production in oligotrophic waters.

NITRATE METABOLISM IN CYANOBACTERIA

Nitrate uptake and reduction to nitrite and ammonium are driven in cyanobacteria by photosynthetically generated assimilatory power, i.e., ATP and reduced ferredoxin. High-affinity nitrate and nitrite uptake takes place in different cyanobacteria through either an ABC-type transporter or a permease from the major facilitator superfamily (MFS). Nitrate reductase and nitrite reductase are ferredoxin-dependent metalloenzymes that carry as prosthetic groups a [4Fe-4S] center and Mo-bis-molybdopterin guanine dinucleotide (nitrate reductase) and [4Fe-4S] and siroheme centers (nitrite reductase). Nitrate assimilation genes are commonly found forming an operon with the structure: nir (nitrite reductase)-permease gene(s)-narB (nitrate reductase). When the cells perceive a high C to N ratio, this operon is transcribed from a complex promoter that includes binding sites for NtcA, a global nitrogen-control regulator that belongs to the CAP family of bacterial transcription factors, and NtcB, a pathway-specific regulator that belongs to the LysR family of bacterial transcription factors. Transcription is also affected by other factors such as CnaT, a putative glycosyl transferase, and the signal transduction protein P(II). The latter is also a key factor for regulation of the activity of the ABC-type nitrate/nitrite transporter, which is inhibited when the cells are incubated in the presence of ammonium or in the absence of CO(2). Notwithstanding significant advance in understanding the regulation of nitrate assimilation in cyanobacteria, further post-transcriptional regulatory mechanisms are likely to be discovered (Flores et al., 2005).

CYANOBIONTS

Cyanobacteria form a wide variety of symbiotic associations with eukaryotic hosts including plants, fungi, sponges, and protists (Adams, 2000; Rai *et al.*, 2000, 2002; Adams *et al.*, 2006;Bergman *et al.*, 2007). Cyanobacteria have flexible photosynthetic apparatus that allows them to utilise light at very low levels, making them ideal symbionts for a wide range of organisms. Cyanobacteria are unique among the prokaryotes in their ability to form symbioses with a broad range of hosts (Usher, 2008). The cyanobacterial symbionts (cyanobionts) generally supply their hosts with fixed nitrogen, although they can also provide fixed carbon to non-photosynthetic hosts. The major plant hosts are bryophytes, cycads, the angiosperm *Gunnera*, the water-fern *Azolla*, and fungi (to form lichens). Although all cyanobacteria are photoautotrophs, many are also facultative heterotrophs and so are not restricted to the areas of the plant that receive light, and can be found in roots, stems, leaves, and thalli.

In the great majority of cases, plant cyanobionts are members of the genus *Nostoc*, which is commonly found free-living in nature; (Rai *et al.*, 2002). This is equally true of the liverworts and hornworts in which the major cyanobionts are *Nostoc* spp. (West and Adams, 1997; Costa *et al.*, 2001).

One of the most fascinating of all plant symbiosis involves a tiny aquatic water fern, *Azolla* and a microscopic filamentous cyanobvacterium *Anabaena azollae.* They grow together at the surface of quiet streams and ponds throughout tropical and temperate of the world. The most familiar symbiosis is the inhabitation of cyanobacteria in the corolloid roots of cycas, which have the ability to fix nitrogen. Nitrogen is an important component of many plant compounds and it is also one of the most limited nutrients. The complex physiological process of nitrogen fixation is a capability unique to prokaryotes and is a key feature of the relationship between Cycads and Cyanobacteria.

The symbiotic cyanobacteria living in marine environment, as opposed to the terrestrial symbioses, have received little attention. In fact, to date there are less than a dozen contemporary scientific investigations of these associations and a better understanding of cyanobionts is needed.

CONCLUSION

Thus Cyanobacteria, prokaryotic organisms, exhibit certain unique characteristics which no other organisms exhibit, such as oxygenic photosynthesis without a full fledged choloroplast, use of hydrogen sulphide as electron donor instead of water as a typical photosynthetic bacteria, nitrogen fixation in unicellular, heterocystous and non-heterocystous organisms and associated special devices to overcome O_2 inhibition of nitrogenase, nitrate reduction, the phenomenon of symbiosis, all these features put together in one group is unique to cyanobacteria.

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