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Research review paper

Algae–bacteria interactions: Evolution, ecology and emerging applications

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ABSTRACT

Algae and bacteria have coexisted ever since the early stages of evolution. This coevolution has revolutionized life on earth in many aspects. Algae and bacteria together influence ecosystems as varied as deep seas to lichens and represent all conceivable modes of interactions — from mutualism to parasitism. Several studies have shown that algae and bacteria synergistically affect each other's physiology and metabolism, a classic case being algae–roseobacter interaction. These interactions are ubiquitous and define the primary productivity in most ecosystems. In recent years, algae have received much attention for industrial exploitation but their interaction with bacteria is often considered a contamination during commercialization. A few recent studies have shown that bacteria not only enhance algal growth but also help in flocculation, both essential processes in algal biotechnology. Hence, there is a need to understand these interactions from an evolutionary and ecological standpoint, and integrate this understanding for industrial use. Here we reflect on the diversity of such relationships and their associated mechanisms, as well as the habitats that they mutually influence. This review also outlines the role of these interactions in key evolutionary events such as endosymbiosis, besides their ecological role in biogeochemical cycles. Finally, we focus on extending such studies on algal–bacterial interactions to various environmental and bio-technological applications.

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1. Introduction

Algae are the undisputed primary producers in the aquatic ecosystem and contribute approximately half of the global net primary productivity (Field et al., 1998). These photosynthetic organisms along with cyanobacteria live in the planktonic region of the aquatic habitat and are collectively called phytoplankton (Buchan et al., 2014). Phytoplankton and bacterioplankton numerically dominate the ocean and freshwater planktonic community (Sarmento and Gasol, 2012). These plankton communities together influence the global carbon cycle and ultimately the climate. Therefore, the interactions between these two groups of plankton and the influence of their interaction on each other and on a global scale are areas of recent research interest (Amin et al., 2015; Landa et al., 2015). Several studies show that heterotrophic bacteria play a ubiquitous role in algal growth and survival (Amin et al., 2015; Gonzalez and Bashan, 2000; Kim et al., 2014a; Seyedsayamdost et al., 2011). Thus, it opens the possibility for revisiting the global carbon cycle and other biogeochemical processes (Amin et al., 2012, 2015; Landa et al., 2015). Similarly, decades earlier in terrestrial ecosystem, it was proven that heterotrophic bacteria not only decompose plant and animal organic matter, but also promote plant growth by complex communication mechanisms and nutrient exchange (Philippot et al., 2013). In this context, evidence of prominent rhizosphere bacteria associated with algae casts light on the possibility of coevolution (Cooper and Smith, 2015; Goecke et al., 2013; Kim et al., 2014a; Ramanan et al., 2015). Therefore, mass cultivation in algal biotechnology should integrate the essence of evolutionary and ecologically relevant relationship between algae and bacteria. Together they not only influence ecosystems but also could potentially influence the growth of future biotechnology industry (Subashchandrabose et al., 2011; Wang et al., 2015). Thus, this review attempts to articulate algal–bacterial interactions in totality, from ecology and evolution, to the use of this knowledge to invigorate their combined biotechnological potential.

Evolution of life was transitionary where self-replicating molecules and chemicals formed the basis of prokaryotes. Subsequently, aggregation of prokaryotes let to eukaryotes. Cyanobacteria, a prokaryote, and their association with eukaryotes evolved into algae. A group of single-celled algae and other ancestors led to multicellular organisms (Herron and Michod, 2008). In this evolutionary hierarchy of life, a significant step is that of association of algae and bacteria. To completely understand the ecophysiology and symbiosis between algae and bacteria, thousands of years of time scale needs to be breached to reach their evolution. This evolutionary journey of algae and bacteria and their symbiosis taken together shall be a fair opening deliberation in this review.

2. Evolution of bacteria and algae

The evolution of life is one of the most intriguing research questions that is still in shade. But a prominent bright spot in the overarching shade is a general agreement on the role played by algae and bacteria in earth's evolution. One of the most potential reasons for existence of human or multicellular organisms on earth is due to the presence of archaea, bacteria, cyanobacteria and subsequently eukaryotic algae. These prokaryotic organisms (bacteria and cyanobacteria), which are the linchpin in the formation of eukaryotic algae and their subsequent interaction with each other, are discussed vividly in the subsequent sections.

2.1. Bacterial evolution benefitted algae

Earth is 4500 million years old and Earth's atmosphere was devoid of oxygen at origin. Oxygenic photosynthesis is the main reason for the present day atmosphere (Blankenship and Hartman, 1998). According to Earth scientists, life would have originated approximately 3800 million years ago (mya) in a hyperthermal environment as Earth and its oceans were boiling at about 100 °C. But whether life originated in oceans (Nisbet and Sleep, 2001), hydrothermal vents (Martin et al., 2008), rock environment or anoxic terrestrial geothermal fields (Mulkidjanian et al., 2012) is a question under serious debate. Nonetheless, it is clear that first organisms in Earth were perhaps prokaryotic thermophiles capable of living in a methane and sulfur atmosphere, crucially a life without oxygen (Gribaldo and Brochier-Armanet, 2006; Sleep, 2010). By 3500 mya, Earth has stabilized considerably from multiple explosions and bombardment resulting in photosynthesis, first anoxygenic and much later, oxygenic (Arndt and Nisbet, 2012; Sleep, 2010; Zahnle et al., 2010). This early phase in evolution could be understood from tracking the availability of atmospheric oxygen. Geological features suggestive of oxygen, such as red beds, lateritic paleosols, and sedimentary sulfate deposits, indirectly provide ample proof for atmospheric oxygen (Kopp et al., 2005; Rasmussen et al., 2008; Tomitani et al., 2006). The accumulation of oxygen occurred in two phases. Atmospheric oxygen increased gradually from void to 1–2% around 2400–2000 mya (Rasmussen et al., 2008). Scrutiny of oldest morphological fossils suggests that cyanobacteria originated around 2150 mya coinciding with the great oxygenation event (GOE). Although eukaryotes are known to have emerged 1780–1680 mya ago, levels of oxygen were stable perhaps due to trapping of oxygen by ferrous forming magnetite and other formations even by 850 mya (Holland, 2006). The second subsequent rise in oxygen to ~20% observed in today's atmosphere is credited to the emergence of photosynthetic eukaryotes such as algae and increased photosynthetic productivity by lichens colonizing land masses. This eventually accelerated the degradation of rocks, thereby releasing fertilizing minerals around 800 mya which increased oxygen concentration in the Carboniferous era (360–300 mya) coinciding with the existence of vascular plants and increased carbon sink (Holland, 2006; Rasmussen et al., 2008). It is also widely accepted that cyanobacteria have played a major role in evolution of eukaryotic algae through the primary endosymbiosis (PE) event, in addition to their contribution to GOE. In PE, a heterotrophic eukaryotic ancestor engulfed a cyanobacterium and retained it as an organelle thereby enabling photosynthesis in eukaryotes (Curtis et al., 2012; Yoon et al., 2004). The host cell which received the cyanobacterium was earlier thought to have originated from bacteria, but increasing evidence suggests that, it was indeed an archaea