



Exploring the potential of algae/bacteria interactions

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Algae are primary producers in aquatic ecosystems, where heterotrophic bacteria grow on organics produced by algae and recycle nutrients. Ecological studies have identified the co-occurrence of particular species of algae and bacteria, suggesting the presence of their specific interactions. Algae/bacteria interactions are categorized into nutrient exchange, signal transduction and gene transfer. Studies have examined how these interactions shape aquatic communities and influence geochemical cycles in the natural environment. In parallel, efforts have been made to exploit algae for biotechnology processes, such as water treatment and bioenergy production, where bacteria influence algal activities in various ways. We suggest that better understanding of mechanisms underlying algae/bacteria interactions will facilitate the development of more efficient and/or as-yet-unexploited biotechnology processes.

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Introduction

Algae are phototrophs that occur in freshwater and marine environments. They vary from small unicellular microalgae, such as cyanobacteria and diatoms, to large multicellular macroalgae, such as giant kelp. They are primary producers that synthesize organic compounds from carbon dioxide, thereby supporting heterotrophic organisms (consumers) that decompose organics and recycle elements. Ecological studies have identified specific phylogenetic groups of heterotrophic bacteria to occur in close association with specific algae [1]. For instance, Lachnit *et al.* analyzed biofilm communities attaching onto three different species of macroalgae in different seasons, suggesting that marine macroalgae harbor species-specific and temporally adapted epiphytic bacterial biofilms on their surfaces [2]. In addition to biofilm bacteria, algal

exudates may also influence planktonic organisms (e.g., heterotrophic bacteria) in the vicinity of algae, and the term ‘phycosphere’ has been coined to describe a region where algal exudates are influential upon co-occurring organisms [3]. A number of studies have demonstrated specific combinations of algae and bacteria to occur in phycospheres, suggesting the presence of their specific interactions. To cite an instance, two heterotrophic bacterial phyla, *Proteobacteria* (e.g., *Roseobacter* and *Sulfitobacter*) and *Bacteroidetes* (e.g., *Cytophaga* and *Flavobacterium*), appear to be consistently associated with diatoms [1,4]. On the other hand, it has also been shown that heterotrophic bacteria influence algal behaviors in various ways, including the stimulation of growth, morphogenesis, spore germination, and colonization [5]. These interactions are of ecological and biogeochemical importance, since they are considered to be fundamental factors in shaping aquatic communities.

Algae are also the focus of research for their application to biotechnology processes, such as water treatment and bioenergy production [6]. Bacteria may co-occur in these processes and affect biotechnological outcomes in various ways [7]. Moreover, studies have attempted to exploit algae/bacteria interactions in designed consortia, such as those for microbial solar cells (MSCs) [8**]. The design of microbial consortia is a recently proposed direction in biotechnology; for instance, an article has suggested that a synthesis of knowledge from studies of sophisticated natural interactions is expected to create an exciting tool for synthetic biology in which the assembled parts are not just genes, but organisms and communities [9]. Although such examples are currently very limited, complex algae/bacteria interactions are considered to provide attractive opportunities for synthetic biotechnology.

In the present article, we first review algae/bacteria interactions in the natural environment that are potentially relevant to biotechnology processes. We next summarize biotechnology processes that exploit consortia of algae and bacteria with a particular focus on designed consortia for MSCs. On the basis of these instances, this article suggests that a better understanding of mechanisms underlying algae/bacteria interactions will facilitate the development of more efficient and/or as-yet-unexploited biotechnology processes.

Algae/bacteria interactions in the natural environment

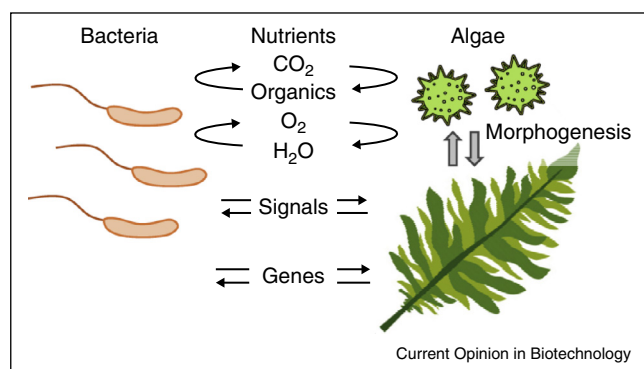
Extensive studies have been performed to elucidate algae/bacteria interactions in the natural environment. These studies have revealed different types of interactions to

shape specific partnerships between algae and bacteria. According to previous studies [10], this article categorizes their interactions into three types, namely, nutrient exchange, signal transduction and gene transfer (Figure 1). Among them, nutrient exchange has been considered the most common type of interactions. Algae excrete a part of photosynthesized organics as dissolved organic carbon (DOC), and heterotrophic bacteria assimilate and decompose significant portions of algal DOC. DOC-decomposing bacteria in the phycosphere are selected according to their affinity to DOC and growth kinetics [11]. In addition, dead bodies of algae can also serve as nutrients of heterotrophs. Studies have estimated numbers of epiphytic bacteria that attached onto the surface of macroalgae, indicating that numbers of bacteria on diseased macroalgae were two orders of magnitude more than those (up to 5×10^6 bacteria per gram of algal fresh weight) on healthy individuals [12]. This observation suggests that heterotrophic bacteria also assimilate unprotected cells of algae. It is also noteworthy that healthy macroalgae are able to control bacterial colonization on their surfaces, and there may be mechanisms inhibiting excessive growth of bacteria that, in turn, reduces accessibility to nutrients and light. In addition, some groups of algae also produce particulate organic matter, for example, transparent exopolymer particles (TEPs), and it has been demonstrated that TEPs determine species and activities of heterotrophic bacteria to co-occur with algae [13]. Nitrogen is another important element, and nitrogen-fixing cyanobacteria (blue-green algae) are key organisms in nitrogen-mediated interactions in aquatic ecosystems. Some of them are endosymbionts inhabiting host eukaryotic algae, and they have adapted to symbiotic interactions with their hosts at the genomic level [14]. Nitrogen-mediated interactions are also found between microalgae and heterotrophic bacteria; screening of growth-promoting bacteria for the microalga *Dunaliella* has suggested a possibility that some bacteria facilitate nitrogen assimilation by microalgae [15]. In addition to these nutrients, interactions via particular vitamins have been elucidated; for instance, eukaryotic algae are auxotrophic for vitamin B₁₂ (cobalamin) that can only be

synthesized by prokaryotes, and studies have revealed mutualistic relationships between vitamin B₁₂-dependent algae and heterotrophic bacteria [16[•],17]. On the other hand, a metagenomic survey of alga-associated biofilms has revealed that genes involved in the biosynthesis of B vitamins and those for lipases and esterases are abundant and functional, suggesting their key roles in alga-associated bacteria [18^{••}]. We suggest that this approach is useful to find interactions via compounds that are difficult to be detected by chemical methods.

Signal transduction is another form of algae/bacteria interactions. In this case, chemicals used for their interactions do not serve as nutrients but activate or inhibit gene expression and/or physiological activities, thereby modifying their behaviors and growth. Signal transduction between algae and bacteria is categorized into ‘interkingdom signaling’ that has been found between eukaryotes and bacteria [19] and archaea and bacteria [20]. In algae/bacteria interactions, it has been known that bacteria secrete chemical signals that induce morphogenesis of algae [21]. Besides, as mentioned above, healthy macroalgae suppress the formation of excess biofilms (biofouling) on their surfaces, and studies have revealed that algae are able to excrete specific chemicals that inhibit bacterial quorum sensing, a mechanism essential for mature biofilm formation [22[•]]. Marine algae are also known to excrete volatile halogenated compounds [23] and fatty acids [24], some of which have antibacterial activities. On the other hand, bacterial quorum-sensing molecules (e.g., acyl homoserine lactones) have been reported to interfere with the germination and growth of *Ulva zoospores*, a macroalga causing biofouling of artificial constructs [25]. In addition, different taxa of bacteria, for example, *Shewanella* [26], *Streptomyces* [27], and *Bacillus* [28], are known to produce algicidal metabolites. These studies have manifested complex signaling interactions in phycospheres, which we expect to exploit for controlling algae and/or bacteria in the context of biotechnology.

Figure 1



Proposed three types of algae/bacteria interactions.

Gene transfer is an evolutionary process, in which genes are horizontally transferred between neighboring microbes, for example, algae and bacteria in phycospheres. Brembu *et al.* have found traces of horizontal gene transfer in the chloroplast genome of the diatom *Seminavis robusta* [29]. Moszczynski *et al.* have shown that the genome of Dinoflagellate *Minicircles* has genes that are closely related to those in *Algoriphagus* and/or *Cytophaga* bacteria belonging to the *Bacteroidetes* clade [30], suggesting the transfer of these genes to have occurred relatively recently. Some horizontally transferred genes confer key functions on algae to better survive in changing environments; for instance, diatom genes encoding enzymes in the ornithine-urea cycle (considered to have been transferred from bacteria) facilitate their metabolic response to episodic nitrogen availability [31[•]]. In addition,

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