

Algae-Bacteria Symbiosis: A Review

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Abstract

Microalgae and bacteria have evolved together over billions of years and interact to regulate nutrient cycling, bloom dynamics, and productivity of aquatic ecosystems. In the past 20 years, these associations have been reincarnated as engineering platforms. Algal-bacterial consortia have been found to yield higher biomass, remove nutrients more efficiently, be easier to harvest, and be more resilient to environmental stress and contamination than axenic monocultures. This review brings together the underlying mechanisms of these improvements: gas exchange, exchange of vitamins, nitrogen, phosphorus and iron, phytohormone signaling, quorum sensing and chemotaxis, and antagonistic interactions including algicidal activity. It then reviews consortium design (natural versus synthetic, ratio, co-culture conditions) and reviews applications in wastewater treatment, biofuel and lipid production, bioflocculation, high-added-value compound synthesis, and CO₂ capture. Lastly, it reviews the challenges for commercialization: community stability, contamination, scale-up and regulation, and how these challenges can be overcome through omics, synthetic biology, and AI-driven modeling to enable rational consortium design.

Keywords: Microalgae, Bacterial consortia, Quorum sensing, Wastewater, Biofuels, Bioflocculation

1. Introduction

The main reason that makes microalgae as attractive production organism is that they can fix CO₂ at high areal productivity, grow on land which is not suitable for farming, and produce lipids, carbohydrates, proteins, and pigments of commercial value, which are commercially important [4]. But, monocultures of axenic or near-axenic culture remain the dominant industrial practice for cultivation, and they require expensive protection from contamination, and are often limited by nutrient availability, self-shading, and expensive harvest. Algae in nature is never found in isolation. The phycosphere is a microscale environment around each cell that is rich in exuded organic matter and populated by certain types of bacteria [3], [28]. The practical application of algal-bacterial partnerships is also no new development, since the mid-twentieth century [23] high-rate and facultative wastewater ponds have utilized algal O₂ production to promote bacterial oxidation of organic matter. Today, the empirical perspective has been superseded by a molecular perspective, revealing specific metabolites and signals that promote cooperation, and demonstrating that the same partners can cooperate in one situation and then compete in another [2], [27]. The case for consortia over monocultures rests on four arguments: Metabolic complementarity. Partners exchange compounds that each cannot make efficiently, such as vitamin B12, fixed nitrogen, or bioavailable iron. Process intensification. Algal photosynthesis supplies O₂ for heterotrophic degradation of pollutants, while bacterial respiration supplies CO₂, reducing

aeration and carbon-supply costs [22]. Downstream advantages. Bacteria can induce flocculation, lowering harvesting costs [17], Robustness. Diverse communities can buffer environmental fluctuations and resist invasion. Countering these advantages, consortia introduce complexity: interactions are context dependent, outcomes can shift from mutualism to parasitism, and community composition drifts. This review therefore treats mechanisms, design, applications, and limits together, with the aim of connecting molecular understanding to engineering practice. It has been over a century since it was recognised that bacteria have an impact on algal growth. In the early culture studies, it had been noted that the growth rates of "pure" algal isolates were often poor or nonexistent in the absence of bacteria, or when bacteria were replaced by soil extracts; in the 1970s, it was determined that some marine diatoms require vitamin B12 made by bacteria for growth in mixed laboratory cultures [39]. At the same time (1972), marine bacteria had been observed to exhibit chemotaxis towards algal exudates [3]. Oswald and Gotaas [23] brought in the engineering logic of using the wastewater-pond concept, with algae providing oxygen and bacteria providing oxidation. During the 1990s, the direct question of bacterial use of photosynthetic oxygen to explain the growth enhancement was asked and answered, and the conclusion was that oxygen relief is only part of the answer [46]. The 1990s witnessed the introduction of the vitamin B12 symbiosis [6], the 2000s the introduction of growth promoting bacteria as "helpers" for wastewater algae [8] and the 2010s saw the molecular level description of signaling and metabolite exchange [2], [26], [33]. Algal–bacterial interactions are hard to summarize due to three features. First, the phylogenetic range is broad and each of the green algae, diatoms, haptophytes, dinoflagellates and cyanobacteria have their own bacterial community, and bacterial partners are largely representatives of the *Alphaproteobacteria* (notably *Rhodobacteraceae*), *Gammaproteobacteria* and *Bacteroidetes* [33], [37]. Second, interactions can be species-specific or even strain-specific; the interaction between a diatom and its microbiota is demonstrated and is host specific [50]. Third, the outcome will also depend on the environment, and the same pair can exhibit mutualism in one environment and competition in another. The viewpoints on reviews are different from time to time and from place to place, some of them being from different angles like ecology [35], industrial production [45], aquaculture [47] and biotechnology [43].

2. INTERACTION MECHANISMS

2.1 Gas exchange

The O_2 / CO_2 loop is the most basic exchange. The photosynthetic production of O_2 by algae facilitates the oxidation of dissolved organic carbon and ammonium by aerobic heterotrophic bacteria. The resulting CO_2 is accessible to algae and partially relieves carbon limitation, especially in dense cultures at alkaline pH where free CO_2 is scarce [22]. The oxygenation benefit of algal-bacterial wastewater systems is based on this connection, which can also lower mechanical aeration, a significant energy expense in the treatment of activated sludge [30].

Another source of stress is gas exchange. Bacterial O_2 consumption can counteract the effects of supersaturating dissolved O_2 in closed photobioreactors, which can prevent algal development through photorespiration and the production of reactive oxygen species. Therefore, the heterotroph-to-alga ratio, mixing, and light regime all affect the overall benefit.

2.2 Nutrient and cofactor exchange

Vitamin B12. Because they lack the B12-independent methionine synthase isoform, around half of the algal species studied need exogenous cobalamin. According to Croft et al. [6], these algae obtain B12

through a symbiotic relationship with bacteria, who in turn receive fixed carbon. Later research showed that cyanobacteria and algae use chemically different B12 variations, and that this exchange is controlled and may be restored experimentally [12], [15].

Nitrogen fixation and nitrogen cycling. Under some circumstances, diazotrophic bacteria can provide algae with fixed nitrogen. *Chlorella vulgaris* and *Azospirillum brasilense* co-immobilization enhanced algal growth and changed cell shape; benefits were ascribed to several processes other than just nitrogen delivery [11]. The nitrogen forms accessible to algae in wastewater are also altered by bacterial nitrification and denitrification.

Phosphate solubilization. Algal absorption is improved by bacteria that solubilize inorganic phosphates or mineralize organic phosphorus, which increases P bioavailability. Compared to algae alone, co-cultures of *Chlorella* and *Azospirillum* demonstrated improved removal of phosphorus and ammonium from wastewater [8]. Carbon and sulfur. Bacterial development is fueled by dissolved organic matter (carbohydrates, amino acids, and organic acids) released by algae. In marine systems, bacteria and algae can reciprocally exchange sulfur metabolites such DMSP and its derivatives [9], [26].

2.3 Phytohormone signaling

Bacteria can modulate algal physiology via plant-hormone-like molecules. Indole-3-acetic acid (IAA) produced by *Azospirillum brasilense* promoted growth and altered cell size and pigment content in *Chlorella vulgaris*, with IAA-deficient mutants having a reduced effect [7]. In the marine roseobacter-diatom system, algae supply tryptophan that bacteria convert to IAA, which in turn promotes algal cell division, illustrating a closed signaling loop [2]. Cytokinin-like and gibberellin-like compounds have also been proposed, but evidence for their role in algae is thinner and warrants further work.

2.4 Quorum sensing and chemotaxis

Bacteria coordinate group behavior using diffusible autoinducers such as N-acyl homoserine lactones (AHLs) [20]. In algal-bacterial systems QS influences biofilm formation on algal surfaces, secondary metabolite production, and the transition between beneficial and harmful behaviors. Algae, in turn, can produce molecules that mimic or interfere with AHL signaling (quorum-sensing "mimics"), potentially steering bacterial behavior. Whether this is deliberate signaling or incidental chemistry is still debated. Chemotaxis positions bacteria within the phycosphere. Marine bacteria swim toward algal exudates [3], and the resulting spatial structure controls the efficiency of nutrient exchange; the physical scales involved are reviewed by Seymour et al. [28]. Designing reactors and mixing regimes with this microscale structure in mind remains largely unexplored.

2.5 Antagonistic and competitive interactions

Interactions are not uniformly cooperative. Algicidal bacteria lyse or inhibit algal cells via secreted enzymes, small molecules, or contact-dependent mechanisms, and play a role in terminating blooms [18]. The best-studied case is *Phaeobacter gallaeciensis*, which behaves as a mutualist, producing growth-promoting compounds and antibiotics that protect the host, until algal senescence products trigger production of algicidal roseobactin: the "Jekyll-and-Hyde" switch [27]. Competition for nutrients (especially N, P, and trace metals) can likewise suppress algae when heterotrophs dominate. For biotechnology, this means that the partner must be chosen and its dose controlled to avoid tipping the balance toward antagonism.

2.6 Physical association, EPS, and biofilms

Bacteria may live free in the medium, loosely associated with the algal surface, or attached within EPS matrices. Attachment shortens diffusion distances, so exchanged metabolites (vitamins, siderophores,

hormones) reach their targets at higher concentrations than they would in bulk liquid. It also protects cells from shear and from predation. Direct exchange of vitamin B12 between partners has been supported by dynamic growth modeling of co-cultures, which found that the data were best explained by cell-to-cell or near-cell transfer [38]. In benthic diatoms, the amount and composition of extracellular organic compounds released depended on the bacterial community present, showing that bacteria reshape the exudate that feeds them [34]. EPS also underlies floc formation (Section 4.3), so attachment is relevant both for mechanism and for harvesting.

2.7 Stress tolerance and host protection

Bacteria can improve algal resilience to abiotic stress. In *Chlamydomonas reinhardtii*, a B12-producing bacterium extended the thermal tolerance of the alga under heat stress, through a mutualistic interaction that did not simply reduce vitamin limitation [54]. Antibiotic production by bacteria such as roseobacters may protect hosts from other bacterial pathogens, and bacterial removal of excess O₂ can reduce oxidative stress. In genome analyses of the algal symbiont *Dinoroseobacter shibae*, genes for B12 and vitamin B1 synthesis, aerobic anoxygenic photosynthesis, and secretion systems were found, consistent with a lifestyle closely tied to a phytoplankton host [52]. Such genomic evidence helps in screening candidate partners before laboratory work.

2.8 The mutualism-parasitism continuum

Many pairs sit on a continuum rather than at a fixed point. The *Phaeobacter* example (Section 2.5) shows a switch triggered by host-derived signals that indicate senescence. In the *Sulfitobacter*-diatom case, the bacterium's IAA production depended on algal tryptophan, but reciprocal benefit depended on conditions in the culture [2]. A practical consequence is that consortium performance should be tested across the full growth cycle, including late stationary phase, and under stress, not only during exponential growth. A second consequence is that "growth-promoting" status should be treated as a property of a pair in a defined medium, not of a bacterium in general (Le Chevanton et al. [44] screened bacteria for *Dunaliella* and found that effects varied among strains and conditions).

3. CONSORTIUM DESIGN

3.1 Natural versus synthetic consortia

Natural or enriched consortia (for example, activated sludge combined with wastewater-borne algae) are cheap, adaptable, and often robust, but poorly defined and difficult to reproduce [30]. Defined co-cultures pair a characterized alga with one or a few bacteria, gaining reproducibility and mechanistic clarity at the cost of resilience. Synthetic consortia go further, engineering metabolic dependencies so that partners are obligately coupled. Examples from yeast and bacterial systems, such as cross-feeding auxotroph pairs [19], [29], and a synthetic community in which a heterotroph and a phototroph exchange carbon and nitrogen [32], provide design templates. Niche engineering has also shown that latent mutualism can be induced between organisms that did not co-evolve [14]. Critical reviews of algal co-cultures for biomanufacturing emphasize that the selection criteria should be tied to the target product [24].

3.2 Partner selection

Selection typically considers (i) growth promotion, demonstrated by controlled co-culture assays, (ii) absence of algicidal activity under process conditions, (iii) compatibility with temperature, pH, and salinity windows, (iv) genetic tractability if engineering is planned, and (v) biosafety classification.

Growth-promoting genera frequently reported include *Azospirillum*, *Bacillus*, *Rhizobium*, and members of the *Rhodobacteraceae* [8], [13], [16].

3.3 Inoculation ratios

The initial alga-to-bacteria ratio strongly affects outcome, because it sets the early balance between co-operation and competition. In wastewater systems, algae-to-sludge ratios shift the balance between pollutant removal, biomass settling, and algal growth, with intermediate ratios often performing best [30]. Optima are strain and medium specific, so ratio screening in factorial designs is advisable, with ratios reported on a cell-count or dry-weight basis explicitly stated to permit comparison across studies.

3.4 Co-culture conditions

Key operating variables play a critical role in maintaining a stable and productive algal–bacterial co-culture system. Light intensity and photoperiod regulate oxygen supply through algal photosynthesis, while excessive light may increase oxidative stress in both partners. Organic carbon supplementation in small amounts can support bacterial growth, but excessive carbon may shift the system toward heterotrophic bacterial dominance. pH and temperature must also be carefully controlled, as algal photosynthesis can increase the pH, potentially inhibiting bacterial partners and promoting ammonia stripping. Mixing conditions and cell immobilization influence mass transfer and partner stability; previous studies have shown that co-immobilization in alginate beads can enhance early-stage growth [11], while combining immobilized algae with suspended sludge can improve the treatment of real wastewater [21]. In addition, nutrient stoichiometry, particularly the N ratio, determines the relative growth and activity of the algal and bacterial partners and can strongly influence the dominant interactions within the co-culture system.

3.5 Model-assisted design

Mathematical models help to narrow the experimental space before laboratory work. Genome-scale metabolic models of two-species communities were used to explain a mutualism based on cross-feeding [51], and computational searches can identify environments that induce obligate cooperation among partners [42]. Reviews of synthetic ecology describe how kinetic, flux-based, and agent-based models can be matched to different design questions [55]. For algal systems specifically, Kazamia et al. [41] argued that synthetic ecology could help create stable consortia for biofuel production, and ecological analyses highlight trade-offs that apply to algal production systems [49]. In a synthetic photosynthetic consortium, sucrose-secreting cyanobacteria supported heterotrophic partners, and the study defined the interactions that led to robustness and production [40]. Together these studies suggest a workflow: build a draft model from genomes, predict exchanged metabolites and their sensitivity to medium composition, test predictions in microplate co-cultures, and then refine the model with the measured data.

3.6 Reactor formats and immobilization

Four formats are commonly used. Suspended co-cultures in photobioreactors are simplest and allow direct monitoring but suffer from washout of the slower-growing partner. Open raceway ponds use natural or wastewater-derived consortia and have the lowest cost but the least control. Biofilm and immobilized systems retain both partners, as shown with alginate-bead co-immobilization [11] and immobilized *Chlorella* combined with suspended sludge [21]. Granular or flocculated systems use self-aggregating biomass, which simplifies solid-liquid separation. Immobilization improves retention and protects against grazers, but mass-transfer limits (light, O₂, nutrients) inside beads or granules cap productivity, and cells may be damaged during encapsulation.

3.7 Online monitoring and control

Real-time parameters such as dissolved oxygen, pH, and redox have been used to follow the evolution of real municipal wastewater treatment in photobioreactors and algae-bacteria consortia, and to infer which process (photosynthesis, nitrification, or organic oxidation) dominates at a given time [36]. Because algal and bacterial processes shift dissolved O₂ and pH in opposite directions during light and dark phases, such signals contain information about community balance that can be used for control, for example by adjusting light, aeration, or hydraulic retention time.

4. APPLICATIONS

4.1 Wastewater treatment

Algal-bacterial systems remove organic carbon, nitrogen, and phosphorus, and can degrade or sequester hazardous contaminants, including some xenobiotics and heavy metals, while cutting aeration energy [22], [31]. Co-immobilized or suspended configurations have achieved high nutrient removal on municipal and industrial effluents [8], [21]. Open raceway ponds, photobioreactors, and algal-bacterial granular sludge are the principal configurations. Open questions include seasonal variability, light limitation in turbid effluents, and fate of pathogens and micropollutants.

4.2 Biofuel and lipid production

Bacterial partners can enhance biomass and lipid productivity, as in the *Rhizobium*-enhanced biomass of *Chlorella* [16], and consortia grown on wastewater couple fuel feedstock production with remediation, improving process economics relative to freshwater monocultures [4], [10]. Lipid content may trade off against growth rate, and the effect of bacteria on lipid profile is inconsistent across studies, so product-specific optimization is needed.

4.3 Bioflocculation and harvesting

Harvesting can account for a large fraction of biomass production cost. Algae-associated bacteria can induce flocculation by secreting extracellular polymeric substances (EPS) or by altering surface charge, enabling gravity settling with reduced chemical input [17]. Bioflocculation is attractive because it avoids metal salts that contaminate biomass, though flocculation efficiency depends on species pairing and conditions.

4.4 High-value compounds

Bacterial partners can raise yields or modify composition of pigments (carotenoids, phycobiliproteins), polyunsaturated fatty acids, polysaccharides, and vitamins; the evidence is summarized by Fuentes et al. [10]. Bacterial signals such as IAA can shift algal pigment content [7]. A particular opportunity is production of B12-containing or B12-enriched biomass, exploiting the natural B12 exchange [6].

4.5 CO₂ capture

Algal photosynthesis is a route to biological CO₂ fixation, and bacterial respiration recycles carbon within the system while improving inorganic carbon availability. Consortia may increase net fixation per unit area by sustaining higher biomass density [25]. Credible claims, though, require full carbon balances, including the carbon supplied as organic substrates and the fate of the biomass.

4.6 Aquaculture and feed

Microalgae are the base of many aquaculture food chains, and their bacterial microbiota affects larval health. Reviews have outlined how algal-bacterial interactions influence the success of hatchery cultures, including through probiotic effects and pathogen suppression, and how bacterial communities in live-feed cultures can be managed [47]. Biomass grown on wastewater is attractive as feed, but contaminant and pathogen limits must be met (see Section 5).

4.7 Bioremediation of hazardous contaminants

Beyond nutrients, algal-bacterial systems have been applied to phenols, hydrocarbons, pesticides, and metals. The usual logic is that bacteria perform the initial catabolic steps, while algal O₂ supports aerobic degradation and algae take up or detoxify metabolites and metals [22]. The advantage is the lower aeration demand and, in some cases, the removal of toxic intermediates that would inhibit the bacteria alone. The limitation is that contaminant toxicity to the alga can set an upper bound on loading, so acclimation and staged dosing are often needed.

4.8 Dual-role systems: remediation and biomass

Reviews of phycoremediation of domestic wastewater describe the "dual role" of microalgae, treating the effluent while generating biomass for fuels, which improves the economics of both [48]. Consortia strengthen this logic, since bacteria raise treatment rates and can aid harvesting. A realistic assessment, however, requires data on year-round productivity, the energy needed for mixing and harvesting, and the value of the end product, which remain thin for consortia.

5. CHALLENGES

Stability. Cooperation can be exploited by non-contributing "cheaters", and shifts in environmental conditions can turn a mutualist into a pathogen [27]. Long-term continuous cultures commonly show composition drift. Metabolic coupling (obligate dependency) is a leading strategy to lock composition [29], [32].

Contamination. Open systems are invaded by grazers, algicidal bacteria, fungi, and competitor algae. A resident consortium can offer colonization resistance, but this is not guaranteed, and unintended partners can destabilize the system.

Scale-up. Laboratory observations in small flasks with defined media often fail to translate to large reactors with gradients in light, oxygen, and nutrients, and with real, variable wastewater. Few pilot studies report multi-month performance, and techno-economic and life-cycle analyses of consortium processes are scarce.

Regulation and biosafety. Using genetically engineered strains in open systems raises containment questions, and biomass from wastewater consortia faces restrictions for feed, food, and fertilizer uses owing to pathogen and contaminant concerns. Regulatory frameworks differ among jurisdictions and are not yet tailored to engineered microbial communities.

Reproducibility and reporting. Heterogeneous reporting of ratios, media, and strain identity hampers meta-analysis. Standardized reporting would greatly help the field.

6. FUTURE PERSPECTIVES

Omics-guided design. Metagenomics, transcriptomics, metabolomics, and exometabolomics are revealing which compounds are exchanged and which genes are induced during interaction [5], [26]. Integrating these layers with spatial methods should clarify phycosphere structure and identify biomarkers of community health that can be monitored in reactors.

Synthetic biology. Engineered auxotrophies, orthogonal signaling, kill switches, and tunable cross-feeding could create stable, containable consortia [19], [32]. Genetic tools for non-model algae remain a bottleneck.

AI and modeling. Genome-scale metabolic models, flux balance analysis of community interactions, and dynamic models can predict compatible pairs and optimal ratios; machine learning trained on high-

throughput co-culture data and sensor streams may support real-time control and optimization of reactors. Such models require high-quality, standardized datasets and experimental validation to avoid overfitting to a few model systems.

Systems integration. Linking consortium performance to techno-economic and life-cycle assessments, and demonstrating multi-product biorefineries that combine remediation, fuels, and co-products, will be essential for commercial adoption.

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