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Soil microalgae and cyanobacteria: the biotechnological potential in the maintenance of soil fertility and health

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ABSTRACT

The soil microbiota plays a major role in maintaining the nutrient balance, carbon sink, and soil health. Numerous studies reported on the function of microbiota such as plant growth-promoting bacteria and fungi in soil. Although microalgae and cyanobacteria are ubiquitous in soil, very less attention has been paid on the potential of these microorganisms. The indiscriminate use of various chemicals to enhance agricultural productivity led to serious consequences like structure instability, accumulation of toxic contaminants, etc., leading to an ecological imbalance between soil, plant, and microbiota. However, the significant role of microalgae and cyanobacteria in crop productivity and other potential options has been so far undermined. The intent of the present critical review is to highlight the significance of this unique group of microorganisms in terms of maintaining soil fertility and soil health. Beneficial soil ecological applications of these two groups in enhancing plant growth, establishing interrelationships among other microbes, and detoxifying chemical agents such as insecticides, herbicides, etc. through mutualistic cooperation by synthesizing enzymes and phytohormones are presented. Since recombinant technology involving genomic integration favors the development of useful traits in microalgae and cyanobacteria for their potential application in improvement of soil fertility and health, the merits and demerits of various such advanced methodologies associated in harnessing the biotechnological potential of these photosynthetic microorganisms for sustainable agriculture were also discussed.

Introduction

The human population is predicted to be over 9 billion by 2050 and this may result in a 70% increase in demand for food production [1]. Development and application of sustainable farming with the perspective of ecological and nutritional balance to feed human population have been the challenges to scientists in the 21st century [2]. The lack of interest to understand the natural phenomenon of sustainable farming paved the way for intensive agriculture for enhanced productivity [3]. Many agricultural soils lack major nutrients such as nitrogen, phosphorus, potassium, and iron, resulting in the consumption of ~200 million metric tons of chemical fertilizers [4,5]. Thus, there will be a huge investment in fossil fuels to produce the required amounts of fertilizers, which is economically tedious besides causing environmental pollution. The overwhelming response towards sustainable agriculture for the maintenance of soil fertility and a healthy ecosystem with low inputs gained much attention in recent years. The rationale of sustainable agriculture is critically dependent on soil, which is the major component of crop production and a complex life reservoir that needs nutrients for its prolonged stability and productivity [6]. Since soil serves as the largest sink for organic carbon and helps in regulation of fluxes of greenhouse gases, it is important to understand the soil ecology for ecosystem sustainability and restoration of habitats [7]. The role of soil microbiota is to increase organic compounds such as carbon, nitrogen, phosphates, and potassium, thereby improving soil health and quality [8].

Recently, Locey and Lennon [9] combined the scaling law with the lognormal model of biodiversity and predicted that the Earth is the home to more than 1.0 trillion microbial species. Of these, bacteria, fungi, actinomycetes, microalgae, and cyanobacteria are intimately associated and thrive in the uppermost part of the

soil, known as the biological soil crust (BSC), which plays a major role in improving soil fertility and agricultural productivity [10]. These crusts possess a diversity of microorganisms such as plant growth-promoting bacteria (PGPB), fungi, lichens, microalgae, and cyanobacteria. Among the diverse microbiota in the soil, microalgae and cyanobacteria are the primary producers in the food chain that can grow in intimidating environments such as arid, semi-arid and wetland ecosystems. Cyanobacteria have evolved over two billion years and are responsible for photogenic oxygenation. Certain cyanobacteria without the heterocyst can also perform nitrogen fixation, and some belong to chemoheterotrophs. The soil microalgae and cyanobacteria release nutritive products, organic products and active components that can serve as food for other organisms like bacteria, fungi, and invertebrates.

A perusal of the database from 1908 to 2018, retrieved from the Scopus, indicates that both microalgae and cyanobacteria received less attention when compared with fungi and rhizobia in soils (Figure 1). A total of only 2312 documents have been published on microalgae and cyanobacteria during 1919–2018, mostly originating from countries like USA, China, Germany, India, etc. Again, the quantum of research concerning microalgae as compared to cyanobacteria has been very limited, and never gained momentum! However, the significant contribution in this area of research was in agriculture and environment, which accounted for 43.2 and 45.3%, respectively. It is worthwhile noting that cyanobacteria, especially with their nitrogen-fixing ability, and species of microalgae such

as *Chlamydomonas, Scenedesmus* and *Chlorococcum* that produce polysaccharides, have a better ability compared to fungi and other microbes in soil [11]. Nevertheless, the diaspora of research on soil microalgae has decreased substantially when compared with other microbes. These "beneficial microorganisms" have great potential in nutrient recycling, organic waste decomposition, detoxification of harmful chemicals, control of plant pathogens, and the production of metabolites such as hormones, vitamins and enzymes [12–14]. Although the information on the population dynamics of microalgae and cyanobacteria helps to understand their role in soil ecology, the beneficial effects of these microorganisms are of utmost importance in soil ecosystems and have not been fully described so far. In this review, we critically discuss the potential of microalgal and cyanobacterial crusts in colonizing degraded soils, and their implication in the maintenance of soil fertility and health.

Biological soil crusts (BSCs) – role in the survival of microalgae and cyanobacteria

Earth has different habitats and drylands cover 45% of the terrestrial (semi-arid and sub-humid) ecosystem and is anticipated to expand in the near future [15]. Furthermore, elevated concentrations of CO_2 in the atmosphere, volcanic eruptions, UV radiation, and temperature could play a major role in the destruction of biota by nutrient limitation, and an unfavorable habitat for microbial activity thereby leading to soil infertility [16,17]. The primary organisms that colonized after
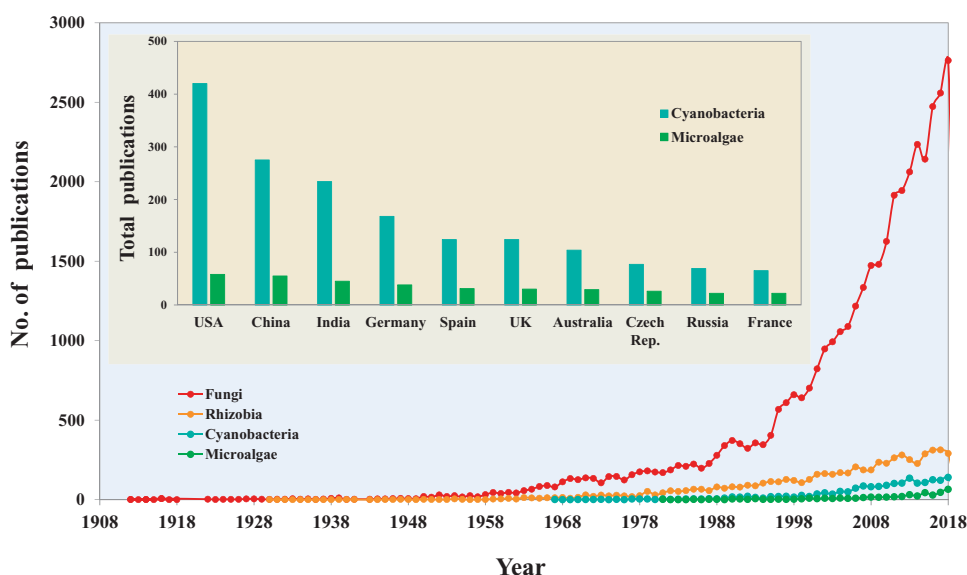

Figure 1. Analysis of research-based documents powered by SCOPUS accessed on 15 March 2019. Scattered plot shows the overall documents published on fungi, rhizobia, cyanobacteria and microalgae in soil. The bar diagram (inset) indicates the number of articles published on cyanobacteria and microalgae by top 10 countries.

volcanic eruptions were microalgae that formed a gelatinous sheath [18]. Over the soil's surface, microalgae together with cyanobacteria initiate the formation of BSCs. Cyanobacteria also synthesize phytochelatin molecules for their defense against UV-B radiations that are more prevalent in desert regions [19,20]. Treves et al. [21] observed desert soil microalgae modifying photosynthetic functions such as PSII activities that will withstand elevated radiations. Heterocystous cyanobacteria possess thick extracellular sheaths that prevent the damage of nucleic acids from radiation and help to survive in extreme environments [22]. Lynch and Bragg [23] hypothesized that survival of microalgae in dryland silt soils would be delicate as the moisture plays an important role. Besides, the algae cyanobacterial crusts require only small amounts of moisture to initiate their living compared to other microbes [24]. Subsequently, by being confined to the top layer of soil, these crusts form into mounds thereby prevent moisture evaporation and shelter other crusts dominated by lichens and mosses [25]. The major factors that influence algal crust formation in the desert are the wind, water, and dust. Due to the wind factor, microalgae tend to adapt by distributing themselves in deeper layers of the sand and move to the surface when it is wet [26]. Under these conditions, they also tend to secrete copious amounts of hydrophobic amino acids in order to prevent the soil from erosion by wind and water and they will be utilized by other organisms as an organic source [27]. Bhatnagar et al. [28] observed considerable diversity of algal crusts in a desert due to its infrequent distribution. Similarly, Zhang et al. [29] suggested that mineral contents along with soil texture were responsible for the growth at extreme habitats and the heterogeneity of algal crust distribution in the desert. Similarly, Hu and Liu [30] explored the relationship between the five algae from a desert habitat, which consists of high molecular weight proteoglycans, different monosaccharides and methylated monomers in secreted extracellular polysaccharide (EPS). However, the amount of the initial inoculum and soil properties must ensure the trend-setting ability of microalgae. Trivedi et al. [31] reported that cyanobacterial abundance was significant in natural as well as agroecosystems. Based on analysis of the scientific database of NCBI on soil algae, predominant groups present in different zones such as arid, semi-arid, wetland were: *Oscillatoriales*, *Nostocales*, *Chroococcales*, *Synechococcales*, *Chroococcidiopsidales*, *Pleurocapsales*, *Microcoleaceae, Chlorellales*, etc.

In eroded and degraded lands, microalgae help to bind soil particles by forming sheaths and filaments [32]. Due to the oxygenic photosynthesis mediated by algae, the soil becomes aerobic by absorbing O_2

through diffusion that is required for initial setting. For instance, the relatively slow formation of the crust by cyanobacterial inoculation in burned soils compared to unburned soils due to the surface disturbance caused by heating [33]. In contrast, Acea et al. [34] observed that inoculation of heated soil samples with cyanobacteria resulted in proliferation and crust formation. Most of the algae are isothermal in nature, and the survival is dependent on protoplasm but not insulation layers [35]. Due to modified light intensity, temperature and moisture levels in arid environments, the diaphanous strata are the favorable habitats for algae [36]. In addition, algae form an association with minerals to produce water-stable organomineral aggregates [37].

Kheirfam et al. [38] demonstrated that the application of native soil cyanobacteria in erosion-prone zone increased the chemical properties such as carbon, nitrogen and organic matter. Furthermore, the synthesis of intracellular metabolites such as superoxide dismutase, proline, and carotenoids tend to help microalgae in drought-mediated stress conditions [39]. The secretion of these metabolites increases the soil compressive strength to remain stable even after cell lysis [40]. Under desiccation stress, the algal filaments are subjected to an increase in surface volume ratio in order to uptake nutrients and prevent loss of water from the cell [41]. Cellular structures such as zygotes, heterocysts, resting spores, and akinetes enable them to survive, but not necessarily withstand high temperatures [42]. Spores and cysts are morphologically distinct that help microalgae in actively dispersing over long distances [43]. By developing cysts, a microalga, *Protosiphon botryoides*, survived 50 years in soil without moisture and was active again [44].

Since topsoil dries out rapidly at high temperatures, suppressed growth of microalgae is resumed after adaptation by changing the physiological conditions [45]. Holzinger and Lütz [20] observed that under desiccation stress, a green alga, *Klebsormidium crenulatum*, was able to tolerate as a result of subsequent changes in the cell wall, cytoplasm, and mitochondria. Furthermore, algae survive photosensitivity during desiccation by enduring inside the microsites within crust formation [46]. Microalgae and cyanobacteria can resurrect once there are no supporting factors for the growth despite the presence of CO_2 and nitrogen. Thus, it is clear that microalgae and cyanobacteria are inclined to adapt to extreme conditions with various physical, metabolic and other forms of alterations mediated by immunity and change the surface quality of soils and provide organic and inorganic bioavailable nutrients to other organisms.

Soil microalgae/cyanobacteria – a very helpful factor for soil fertility

Agricultural lands are susceptible to the loss of soil fertility due to the practice of intensive farming practices, which may lead to 30% of the cultivable land being subject to soil degradation. Among other soil microbiota, microalgae alone account for 27% of the total biomass in agricultural land [47]. As evidenced by their response in different agro-ecosystems, cyanobacteria are the most suitable group of microorganisms to consider as a soil bioindicator of land use [48]. The information available in the literature signifies the potential of microalgae and cyanobacteria to improve various parameters related to soil health and fertility (Table 1). Cyanobacteria and green algae tend to enrich organic plant production particularly during climate change [54]. In addition, an increase in oxidizable C by way of releasing exopolysaccharides during algal cell lysis increases soil organic matter [55]. The soil organic matter is the readily available form of C for the growth of soil microbiota [56]. The cyanobacterial inoculation can increase soil organic carbon (SOC), total availability of nutrients in the topsoil. It is observed that cyanobacteria inoculated in a pot without seeding showed a higher content of carbon, nitrogen, and minerals than seeded pots [57]. However, the plant can also induce priming of soil organic matter (SOM) mineralization, which is due to factors that influence plant growth [58]. Yet, the bioavailability of a complex SOM fraction to support the growth of microbiota is scarce as its solubility and reactivity vary greatly depending upon the environment.

It is also postulated that algae compete with higher plants and prevent leaching of minerals and maintain the reserves for bioavailability [59]. Cyanobacteria such as *Nostoc* sp. are able to colonize plant root systems, and by a tight association facilitate the transfer of nutrients as well as metabolites with the help of hormogonia [60]. The use of native cyanobacterial strains as an alternative supplementation for nitrogen improved paddy yield [61]. Similarly, the use of cyanobacterial biofilms under non-flooded conditions improved N_2 fixation and phosphate solubilization thereby increasing the growth of crop plants [62]. Cyanobacteria not only improved the paddy yield but also showed the highest increase in oxidizable C and soluble C in postharvest soil compared to preharvest soil [63]. In extreme habitats, genera of Cyanophyceae cause retention of silt and clay with an increase in organic C (300%) and N (400%) [64]. Cyanobacterial inoculation contributes to the yield of grains besides leaving C residues that can enhance plant growth without the help of manure [65]. Interestingly, the predominantly growing native algae can reduce the diversity of other diazotrophic organisms and enhance nitrogen fixation [66]. However, the algal inoculation followed by population build-up in the soil will vary depending on the habitats under field conditions. For instance, the density of algae in arable soils ($<1 \times 10^2$ g^{-1}) was less than water-logged soils ($>1 \times 10^7$ g^{-1}) [67,68]. Mayland et al. [69] observed a two-fold nitrogen content increase in nutrient-limiting semi-arid soil indicating the role of cyanobacteria with active heterocyst.

Table 1. The potential of microalgae and cyanobacteria to improve various properties related to soil fertility.

Soil type	Major soil characteristics	Cyanobacterial/ microalgal inoculants	Soil fertility improvement	Reference
Sandstone, granite, schist and lime	Poor micronutrients	*Oscillatoria* sp., *Nostoc* sp. and *Scytonema* sp.	Formation of microbial crusts with high carbon and nitrogen content.	[34]
Silt loam soil	Poor micronutrient availability	*Anabaena* sp. and *Providencia* sp.	Iron concentration in soil was >2–3 folds.	[10]
Desert soil	Low organic carbon and total nitrogen	*Microcoleus vaginatus* Gom. and *Scytonema javanicum* Born et Flah	>5-Fold increments of soil organic carbon and nitrogen.	[49]
Sterile soil	Low nutrients	*Chlorella* sp., *Scenedesmus* sp., *Chlorococcum* sp., and *Chroococcus* sp.	Microbial biomass carbon.	[50]
Clay loam	Low nitrogen	*Chlorella vulgaris*	Improved nitrogen and soil enzyme activities.	[51]
Semi-arid soil	Organically poor	*Anabaena doliolum* HH-209, *Cylindrospermum sphaerica* HH-202, and *Nostoc calcicola* HH-201	Improved carbon and nitrogen mineralization by promoting soil microbial activities.	[52]
Ferruginous tropical soil	Poorly aggregated soils	*Nostoc* sp.	Improvement of aggregate stability.	[53]
Glade soil	Poor nutrients and hydro-physical parameters	*Tribonema minus*, *Choricystis minor*, and *Klebsormidium subtile*	Increase in organic carbon content, water drop penetration and decreasing evaporation during dry periods.	[25]

Table 2. Potential traits of soil microorganisms and their merits and demerits to improve soil fertility.

Microorganisms	Potential soil traits	Advantages	Limitations	References
Microalgae	Carbon fixation, extracellular polysaccharides, and initiation of BSCs.	Carbon supplementation to promote soil health. Extra cellular polysaccharides for soil aggregation. Enhancing hydraulic conductivity.	Soil moisture. Carbon limitation. Requirement of pH, mostly slight acidic to basic.	[45] [78] [79]
Cyanobacteria	Nitrogen fixation through heterocyst and non-heterocyst, CO_2 fixation, and extracellular polysaccharides.	Carbon and nitrogen supply for soil fertility. Extra cellular polysaccharides for soil aggregation. IAA production.	Phosphorus limitation. Decreased N_2-fixing ability. Oxygen affects N_2 fixation.	[80] [81] [82] [83]
PGPR	Development of resistance to pathogens, plant growth promotion, phosphate solubilization, and osmotic stress mitigation.	Fix N_2 into plants through complex enzymes system. Phosphate mineralization. Organic acid for solubilization of potassium.	Requires phosphates and carbon for efficient activity.	[84] [85–88]
Fungi	Decomposing old recalcitrant soil organic matter, and increased nutrient availability to plants.	Accommodating bacterial enzymes to fix N_2 without oxygen influence. Entrapment of soil particles. Mucilage, polysaccharides, and soil protein production.	Requires organic carbon for survival. Prefer acid pH.	[5,89]

The essential nutrients next to nitrogen to enrich crops are Phosphorus and potassium. In general, the upper layer in soil consists of organic Phosphorus that ranges from 20–80% of the total phosphorus [70]. In addition, Phosphorus availability to plants decreases in the highly weathered soil and is heavily dependent on microbial activity in such soils [71]. Many studies reported that phosphate-solubilizing bacteria play a major role in converting insoluble phosphate to soluble Phosphorus [72]. Nevertheless, soil microalgae accumulate inorganic phosphate and produce polyphosphates, the easily available form of phosphate to plants [73]. In addition, cyanobacteria can also release enzymes that degrade inorganic phosphate in the soil to increase its bioavailability to plants [74]. During phosphate-starved conditions, cyanobacteria are capable of solubilizing mineral rock containing phosphate by phthalic acid production [75]. However, nitrogen fixation in cyanobacteria ceased in the presence of soluble phosphate whereas the insoluble phosphate helped to maintain the rate of nitrogen fixation [76]. Other possible mechanisms include chelation and phosphate solubilization through the release of organic acids by cyanobacteria [77]. Table 2 presents the merits and demerits of potential traits in microalgae, cyanobacteria, plant growth-promoting rhizobacteria (PGPR) and fungi to improve soil fertility.

New advancements are very helpful to understand the mechanism and response of algae to soil function, and are more attractive for scaling heights and achieve more promising results. The use of cyanobacterial biofilm fertilizer gauge increased attraction due to a reduction in the quantity of chemical fertilizer, cost savings, etc. Cyanobacterial biofilm formulation of

Anabaena–Trichoderma viride resulted in the production of maize hybrids with an associated saving of 60 kg ha^{-1} nitrogen and an increase of 20–60 kg ha^{-1} available nitrogen in the soil [90]. The biofilm of Phormidium sp. showed higher phosphatase activity under different phosphate regimes [91]. Similarly, the biofilms of Anabaena–Serratia, Anabaena–Pseudomonas exhibited high acetylene reduction and phosphate activities during wheat cultivation [92]. Prasanna et al. [93] reported a 12–25% increase in yield of soybeans with the use of Anabaena–T. viride biofilm formulation along with the compost (paddy straw and vermiculate) as a carrier. Under the SRI system, biofilm formulation of cyanobacteria increased the bioavailability of nitrogen and phosphates to rice plants that resulted in savings of 60 kg N ha^{-1} season^{-1} [66,94]. Biofilm formulation increased the levels of soil micronutrients such as zinc (15–41%) and iron (13–46%) over controls in Oryza sativa [95]. The biofilms consisting of Anabaena laxa and Rhizobium sp. showed the higher activity of nitrogenase which resulted in 1724 kg ha^{-1} yield in chickpea [96]. Microalgae/cyanobacteria as biofilm vectors show a higher degree for nutrient enrichment compared to other suppliers.

Soil health maintenance by microalgae/ cyanobacteria – an underexplored option

According to Nkonya et al. [97], an increase in land degradation stretched to 30% compared to the total land area in the world, costing about US$300 billion to improvise the degraded cover. Other subjugated degraded soils include acid sulfate soils, salinity soils, arid cover, etc. that are prevalent in certain countries
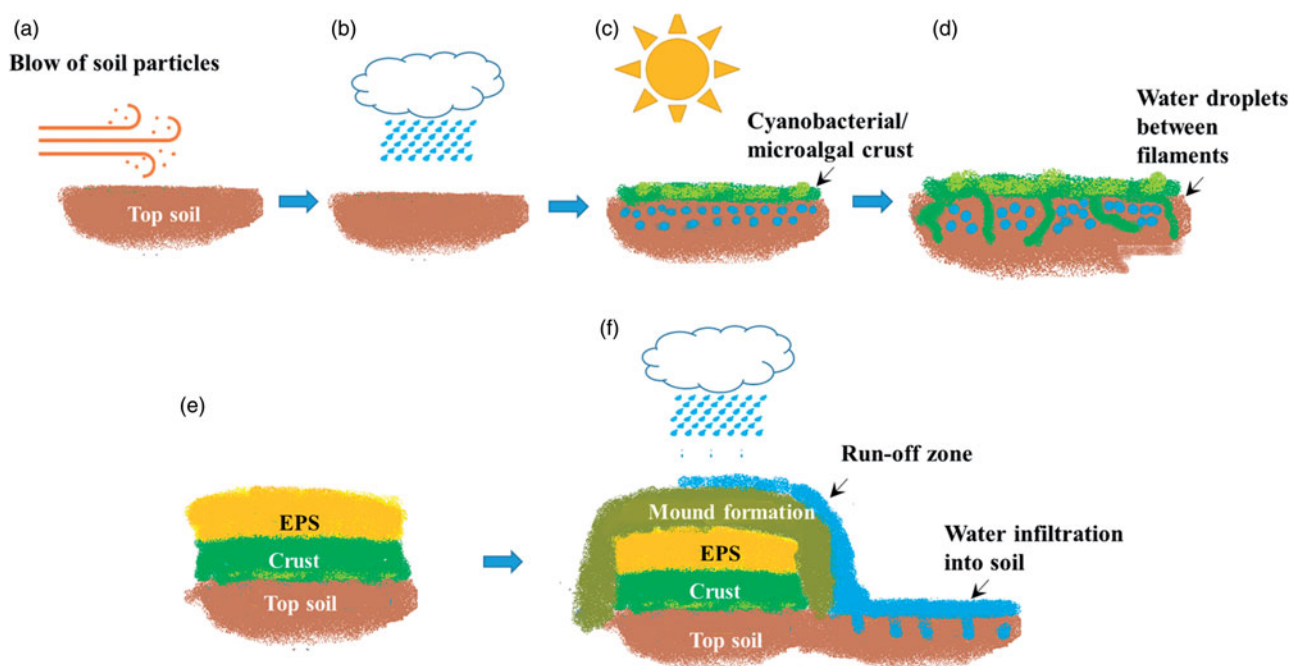
Figure 2. Formation of microalgal/cyanobacterial-based biological soil crusts. (a) Wind drives soil particles from top soil; (b) Infiltartion of rain droplets into the soil layer; (c) Colonization of cyanobacteria and microalgae to form a sheath; (d) Soil and water entrapment in sheath to form a cyanobacterial/microalgal crust; (e) Extracellular polysaccharides (EPS) are produced from the crust; and (f) The mound formed acts as a run-off zone to divert rainwater into soil and enhances water infiltration.

such as India and Australia. The use of improved practices along with the application of fertilizers can improve the decreasing rate of land degradation [98]. However, it is evident that the routine application of synthetic fertilizers adversely affects the arable soil characteristics. Organic fertilizer amendment reduced the relative abundance of algal communities even after a year of application [99]. Long-term (82 years) applications of chemical and organic fertilizers in a rice field affected the diversity of eukaryotic microorganisms [100]. This situation, therefore, necessitates the use of alternative approaches like the application of promising microorganisms to restore soil characteristics. Induction of BSCs helps to initiate the restoration of microbial diversity in soil and vegetation cover. Hence, overwhelming interest in developing BSCs to improve the soil quality and its characteristics is vital for restoring regions with soil degradation over the world [101,102]. For instance, the combined application of cyanobacterial formulations with natural chemical additives will help to form BSCs at a faster rate than with the natural processes and enhance soil stability and water-holding capacity (WHC) in degraded soils [102].

Soil quality primarily deals with soil aggregate properties such as gradient, texture, water repellence, WHC and hydraulic conductivity [23]. On the other hand, soil health provides the balance amongst organisms within the soil, and between soil organisms and their environment [103]. Thus, soil health is of utmost importance for the survival of crop plants. It has been established that algae are responsible for this in the crust formation and for inducing water repellence upon drying. The role of microalgae and cyanobacteria in the formation of BSCs and their implication in soil health is depicted in Figure 2. These crusts also tend to cause retention of clay, which helps in rearranging soil particles for improving soil structure [64]. Furthermore, the hydrophobic compounds synthesized by soil algae play a primary role in establishing water repellence [104]. The hydrophobic derivatives of algal metabolites tend to stabilize water aggregation, bind mineral particles and reduce break down of soil [105]. It should also be noted that filamentous algal crusts can also lead to the clogging of pores, thereby reducing the water infiltration rate [106]. Inevitably, a change in structure and function in soil due to the release of metabolites and hydrophobic derivatives allows preferential flow paths that result in developing wetting instability and improving evaporation loss [107]. These preferential flow paths possess higher substrate and nutrients bioavailability compared to other regions in soil indicating hot spots for elevated microbial activity [108,109]. However, hydrophobic surface chemistry can lead to super hydrophobicity with the help of water droplets that subsequently promotes water repellence [110]. Nevertheless, cyanobacteria and microalgae increase water repellency

during initial crust development and result in slower infiltration due to the crust succession [111].

Microalgae synergistically can also activate quorum sensing among cyanobacteria and other prokaryotes that render them to move or grow towards the substrate and thereby increasing the soil stability [107]. The EPS from cyanobacteria holds water movement in soil by absorption, and thus creates a microenvironment in the soil for water regulation [112]. Similarly, EPS serves as a reservoir of water storage in order to manage the abnormal conditions and can be metabolically active during rewetting [113]. In addition, wetting also increases the size of cyanobacterial colonies by swelling the polysaccharides present in the mucilage and thereby decreasing water runoff in the soil [105]. This makes EPS to increase soil WHC and reduce the trans-evaporation loss to the atmosphere [114]. It was also reported that cyanobacterial inoculation increased WHC, nutrient availability and aggregation of soil particles [115]. Cyanobacterial crusts increase water retention time by decreasing the bulk density and soil porosity along with organic matter and cation-exchange capacity (CEC) [116]. Roger and Reynaud [117] observed that the algal crusts helped prevent erosion from rain and did not slow the water infiltration rate. However, in the presence of cyanobacteria, the soil porosity prevented the damage of water addition due to the breakup effects of periodic wetting [118]. There will be immediate availability of organic matter from cyanobacteria to the food chain, and this contribution is significant [42].

It has also been reported that intensive agricultural practices lead to loss of soil stability, reduction in water infiltration and formation of bio pores, all of which are important for water movement and root development. These associated problems can be abridged by using organic amendments that would help to increase soil quality and properties [119,120]. When applied to the soil, gypsum binds to the polysaccharide sheath of cyanobacteria and protects them from physical breakage [81]. The use of microalgae will also increase the hydraulic conductivity of minimizing other soil amendments in order to improve soil fertility [121]. Filamentous algae have the potential in proliferating in soil within 10–50 mm from the surface thereby enhancing the hydrologic condition of the soil [122]. The sheaths from cyanobacterial crusts that are undisturbed for long periods can penetrate up to 10 cm below the soil surface and thus possess ameliorating influences on WHC, CEC and soil stability [81]. Chamizo et al. [123] observed that cyanobacteria in BSCs with higher

electrical conductivity have aggregate water stability and water content at -33 kPa and -1500 kPa, respectively.

Soil enzymes and phytohormones from microalgae/cyanobacteria – role in soil fertility and plant growth

It has been well established that microalgae and cyanobacteria can produce several important components of varying applications. Enzymes from microalgae and cyanobacteria are exploited to increase soil fertility. The phosphatases are the enzymes that catalyze the hydrolysis of organophosphates in soil and make Phosphorus bioavailable to plants. The presence of microalgae and cyanobacteria increases the metabolic activity of willow plants by inducing the activity of phosphatases (acid and alkaline). For instance, synthesis of alkaline phosphatase, that cleaves the phosphate residues of polyphosphate, in cyanobacteria was high under phosphate-deficient conditions [54], and consequently helps in increasing the activity of nitrogenase enzyme [124,125]. Even in extreme habitats, there was no reduction in the activity of phosphatase in cyanobacterial mats whereas other enzymes such as lipase; and glucosidase were significantly affected under these conditions [126,127]. Cyanobacteria also synthesize hydrolytic enzymes that exhibit fungicidal activity such as protease, carboxymethyl cellulase (CMCase), cellobiase and filter paperase (Fpase), all of which are responsible for hastening nutrient recycling of carbon, nitrogen, and phosphate which are necessary for plant growth [84]. Rao and Burns [67] reported a significant increase in the activities of dehydrogenase, urease, and phosphatase with cyanobacterial inoculants that resulted in increased organic matter mineralization.

De Caire et al. [128] reported that *T. tenuis* and *Microchaete tenera* inoculants in soil increased the activities of extracellular enzymes such as glucosidase, phosphomonoesterase, arylsulfatase, protease, and urease besides the accumulation of intracellular dehydrogenase. The role of enzymes associated with the antioxidant defense mechanisms towards pesticides has been known in microalgae and cyanobacteria as it is important to identify the activities of these resistant enzymes [129]. It is noteworthy that certain enzymes in microalgae are responsible for the degradation of pesticides [12]. For instance, an esterase in the marine cyanobacterium, *Phormidium valderianum* BDU 20041, transformed chlorpyrifos [130]. Phosphatase enzyme in soil microalgae was not affected by the insecticide, fenamiphos [131]. Such enzymes in microalgae or cyanobacteria, which

Table 3. Enzymatic resistance in cyanobacteria/microalgae towards pesticides as soil contaminants.

Pesticide/group	Cyanobacterium/microalga	Responsible enzyme	Reference
Glyphosate (H)	*Anabaena* sp.	Enol-pyruvyl-shikimate-3-phosphate (EPSP) synthase	[133]
	Nostoc sp.		
Chlorpyrifos (I)	*Spirulina platensis*	Alkaline phosphatase	[134]
Organophosphates	*Synechococcus* sp. PCC7942	Organophosphorus hydrolase	[135]
Fluroxypyr (H)	*Chlamydomonas reinhardtii*	Glutathione S-transferase	[136]
Chlorpyrifos (I)	*Phormidium valderianum* BDU 20041	Polyphenol oxidase	[115]
Carbofuran (I)	*Nostoc hatei*	Glutamine synthetase	[137]
Norflurazon (H)	*Synechocystis* sp.	Phytoene desaturase	[138]
Metflurazone (H)	*Chlorella fusca*	Cytochrome P450	[139]
Bentazon(H)	*Anabaena cylindrica*	Glutathione S-transferase	[140]
Methyl parathion (I)	*Anabaena* sp. PCC7120	NADP + reductase	[141]
Mancozeb (F)	*Nostoc ellipsosporum*		
	Tolypothrix tenuis		
Bagalol (F), Thiodan (I)	*Scytonema simplex*		
Phorate (I)	*Tolypothrix tenuis*	Isocitrate lyase	[142]

I: Insecticide; F: Fungicide; H: Herbicide.

confer resistance towards pesticides, have a greater role in their biodegradation by fortuitous evolution [132]. Several enzymes of microalgae and cyanobacteria are involved either in biodegradation of environmental pollutants or confer resistance towards such chemicals (Table 3). The presence of these enzymes could help to screen algae-based upon *in vivo* tolerance [133].

Phytohormones are important molecules commonly found in plants and microbes (microalgae, fungi, bacteria, etc.), and are involved in regulating their cellular processes. These phytohormones help to alleviate the abiotic stress in plants and maintain growth [143]. Both cyanobacteria and microalgae, which establish a symbiotic association with plants, synthesize hormones such as auxins (indole acetic acid, IAA), cytokinin, abscisic acid, gibberellins and ethylene [83,144,145]. Moreover, certain phytohormones, produced by cyanobacteria and microalgae, are implicated in improving plant growth (Table 4). It has been established that the synthesis of phytohormones in microalgae is dependent on the bioavailability of precursors, amino acids, from plants [149]. For example, synthesis of auxins in cyanobacteria was only observed with the accumulation of tryptophan, an amino acid, excreted by plants [83]. On the contrary, certain cyanobacteria cannot synthesize IAA even in the presence of tryptophan [150]. However, it has been observed that unicellular cyanobacteria release auxins and filamentous cyanobacteria accumulate them within the cells [151]. In general, phytohormones produced by cyanobacteria during cocultivation, are transferred to the plants through their roots along with other nutrients [152].

It was also postulated that phytohormones from cyanobacteria or microalgae could influence the endogenous phytohormones of the plant cell [153]. Likewise, cytokinin-binding protein from cyanobacteria was transported into the plant for the synthesis of endogenous phytohormones [83,154]. Although the transportation of phytohormones into the plant is clearly understood, the molecular mechanism of transportation has yet to be established. The symbiotic association of cyanobacteria and other bacteria is quite common, and the mutualism is for exchanging organic substrates, such as vitamins [62,155–158]. Among other microorganisms, *Nostoc* sp. was high in abundance associating it with the root system of rice plants by developing hormogonia [159]. This association was particularly due to the presence of a gene *ipdc* in the cyanobacterium which is responsible for the IAA synthesis needed for plant growth [151]. A schematic diagram provided in Figure 3 represents the association between a cyanobacterium, microalga, and PGPR in the plant rhizosphere. Meza et al. [160] reported that IAA supplied by a growth-promoting bacterium, *Azospirillum brasilense*, was used by *Chlorella vulgaris* for utilizing inorganic phosphate intracellularly. The intracellular accumulation of ammonium was enhanced by the release of IAA by PGPR [160]. Metabolites such as tryptophan from microalgae will exchange with IAA that is produced from PGPR, indicating an alternative way of obtaining phytohormones by algae [161,162].

Co-cultivation of *A. brasilense* with *Chlorella sorokiniana* resulted in an increase of tryptophan in the microalga and the exudation of IAA from the bacterium during their interaction [163]. A similar observation under stress conditions was where microalgae and bacteria released thiamin during co-cultivation [164]. Thus, the release of phytohormones may be a plausible solution to stress tolerance in microalgae. Similarly, the exogenous role of abscisic acid supported stress tolerance mechanism in *Chalmydomonas reinhardtii* [165]. A green alga, *K. crenulatum*, could significantly withstand desiccation stress by producing phytohormones such as ethylene, cytokinin and abscisic acid [166]. It is also reported that the utilization of phytohormones

Table 4. Phytohormones produced by cyanobacteria/microalgae that enhance plant growth.

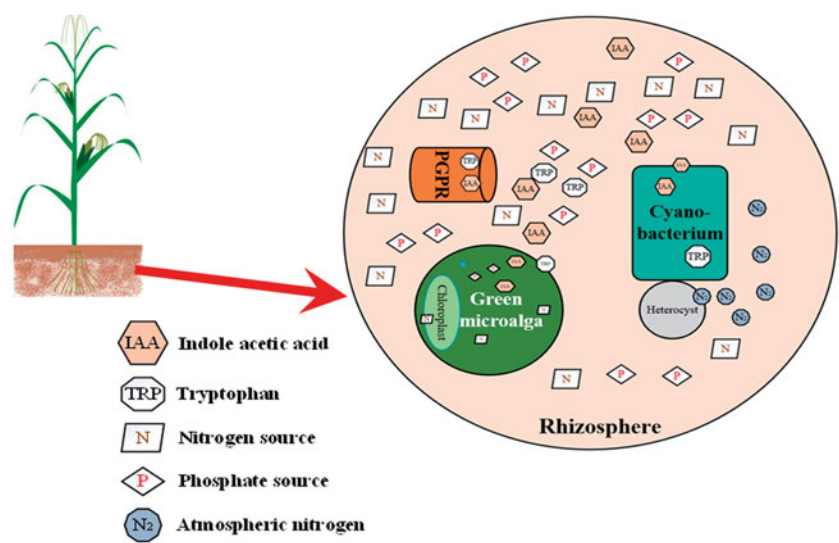| Cyanobacterium/microalga	Phytohormone	Plant	Reference
Anabaena vaginicola Cylindrospermum michailovskoense, Nostoc calcicole	Auxins (IAA, indole 3-acetic acid; IBA, indole 3-butyric acid)	Triticum aestivum L.	[146]
Calothrix sp. (403)	Auxin (IBA)	Cucumis sativus	[147]
Calothrix sp. (405)	Cytokinins (Kinetin)	Glycine max	
Chlorella sp. (519)			
Coenochloris sp. (534)			
Tetracystis sp. (479)			
Chlamydomonas sp. (460) Chlamydomonas sp. (693)			
Anabaena oryzae	Auxins (IAA, IBA)	Oryza sativa	[13]
Anabaena doliolum			
Phormidium fragile			
Calothrix geitonos			
Hapalosiphon intricatus			
Aulosira fertilissima			
Tolypothrix tenuis			
Oscillatoria acuta			
Plectonema boryanum			
Aphanothece sp. MBDU 515	Auxin (IAA)	Arachis hypogaea L. Moringa oleifera Lam.	[148]

Figure 3. Symbiotic relationship between a microalga, cyanobacterium, and PGPR in plant rhizosphere.

improves growth as well as lipids (fatty acids) in microalgae [167–169]. The phytohormones can also detoxify or modify the toxic compounds that inhibit plant and algal growth. For example, phytohormones help to modify the phytotoxicity of heavy metal and prevent algal inhibition [170]. Thus, the coexistence of microalgae and PGPR in plant roots will be not only mutually beneficial but also help to release plant growth-promoting substances.

Genetic engineering potential of microalgae and cyanobacteria for improving soil fertility and health

The use of advanced techniques in algal engineering helps to induce traits for enhancing their role in soil functioning. Figure 4 provides a general schematic representation of approaches for developing potential traits in microalgae and cyanobacteria to improve soil fertility and health that is essential for sustainable agriculture. Gene transfer is a signature for the manipulation of the rubisco gene from cyanobacterium to plants through endosymbiosis [171]. Even genetic rearrangements have been observed in cyanobacteria from ancient viruses [172]. Nevertheless, a significant paradigm shift is enhanced hydrogenase production by cyanobacteria through genetic manipulation [173]. Such a paradoxical swing can be one of the reasons why the potential of exploring microalgae is still in its infancy. Moreover, earlier research on mutagenic cyanobacteria has suggested that N_2 fixation was higher compared to wild strains especially when ferredoxin hydrogenase was expressed in the mutants [174]. However, iron concentrations, at $1\,\mu M$, promoted
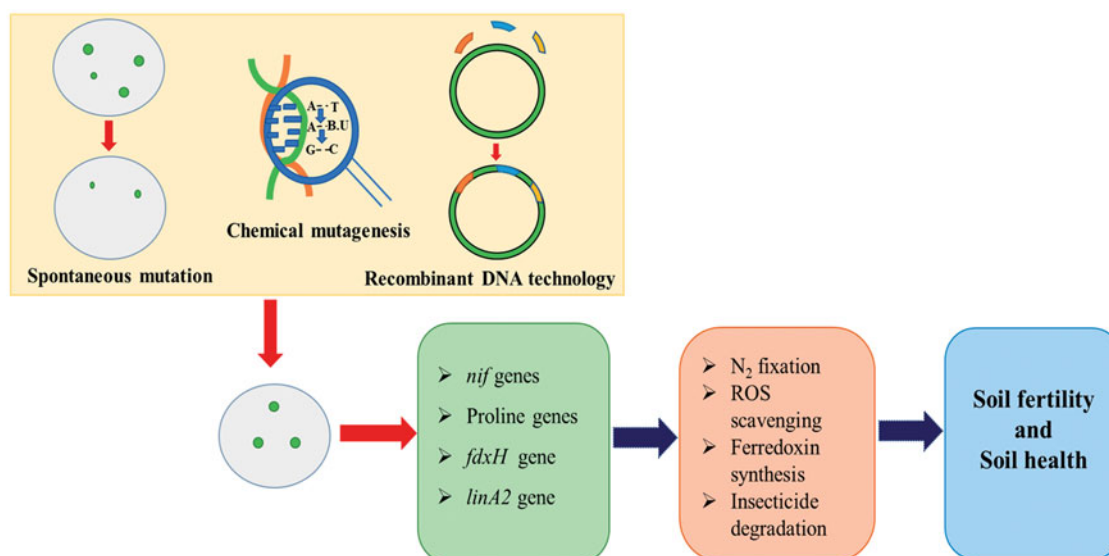
Figure 4. Approaches to develop potential traits in microalgae/cyanobacteria for their application to improve soil fertility and health.

ferredoxin biosynthesis but not the growth of mutant strains, suggesting that the FdxH was not replaced by NifJ-flavodoxin. In fact, the hetR protein is mainly responsible for regulating N_2 fixation in heterocysts especially in N_2-fixing dominant strains of *Anabaena* and *Nostoc* [175]. It was also observed that chemical mutagenesis resulted in defects with no heterocyst formation under any conditions. However, Zhou et al. [176] observed that the nitrogen-depleted environment provided higher production of hetR protein predominantly located in heterocysts only for a limited time. Furthermore, it was postulated that hetR could play other roles in non-heterocystous cyanobacterial species. Nevertheless, additional copies of *hetR* the gene, placed under the promoter, has alleviated the stress and exhibited overexpression of hetR protein in *Anabaena* strains [177]. Spiller et al. [178] developed a mutant strain, which can produce the nitrogenase enzyme and excrete ammonium in the environment thus exhibiting excellent fertilizer traits.

The application of recombinant DNA technology involving genomic integration in all the above studies, overproduced heterocysts and reduced further risks of lateral transfer of transgenes. It is also imperative to identify external stress (such as herbicides) and the response of cyanobacteria and microalgae in order to produce resistant biofertilizers. Singh et al. [179] identified hetero-specific DNA-mediated genetic transformation responsible for herbicide resistance in *Gloeocapsa* sp. which could be later expressed in a *Nostoc* species for their application in the field as a biofertilizer. They also suggested that the absence of a hetero-specific barrier in crosses of DNA-mediated genetic

transformation maintains stable expression. Similarly, herbicide-resistant markers could be used in microalgae to resist toxic potential [180]. Chaurasia et al. [181] used the *linA2* gene from *Sphinogomonas* and inserted it into an *Anabaena* strain to confer resistance towards the toxicity of lindane through the light-inducible promoter. Both an integrative approach and a light-inducible promoter minimized the chances of lateral gene transfer to non-target organisms and were found suitable for their application in agriculture fields. The induction of gene encoding modified norflurazon-resistant phytoene desaturase (PDS) also enhanced the herbicide resistance efficiently in *Chlorella zofingiensis* by 91%, suggesting that the use of a dominant selectable marker is a pre-requisite for efficient transformation of microorganisms [182]. Similarly, expression of the *hsp* gene to produce a heat shock protein, that serves as the backbone for stress tolerance in certain cyanobacteria with respect to desiccation and temperature, has been well used to improve the strains in biofertilizer application. Nevertheless, expressing the *groESL* operon encoding the heat-shock protein genes enhanced nitrogen fixation levels and photosynthetic activity even in stress-mediating environments [177]. Use of recombinant technology to enhance nitrogenase activity led to catering the demand of nitrogen in rice seedlings. A mutated cyanobacterial strain, resistant to azetidine carboxylate, was used to over-accumulate proline, which helps to withstand salinity stress [183]. The practice of developing spontaneous mutants did not favor the overaccumulation of proline either from stress or resistance. However, toxicity was exerted if the mutant cells are defective also in other assimilatory

Table 5. Potential of genetically modified traits and their merits and demerits in maintaining soil fertility and health.

Microorganism	Genetic modification	Potential trait	Methodology used	Limitations	Reference
Anabaena sp. PCC 7120	*fdxH* gene	*FdxH* is necessary for maximum nitrogenase activity and optimal growth under N_2-fixing conditions.	Plasmid DNA isolation, restriction enzyme analysis, agarose gel electrophoresis, and cloning.	Iron limitation causes a decrease in growth.	[174]
Synechocystis sp. PCC 6803	*nif* genes	First example of nitrogenase activity detected in photosynthetic non-diazotroph.	Five-step homologous recombination together with the *cnfR* gene encoding the transcriptional activator of the *nif* genes	Low but significant nitrogenase activity was detected in all transformants.	[188]
Azotobacter sp.	FeSII protein	Forms a protective complex with nitrogenase during periods when nitrogenase is exposed to oxygen.	Subcloning gene and site-directed mutagenesis.	The nitrogenase component bearing the double lysine mutation is degraded much more rapidly under carbon substrate-limited conditions.	[189]
Synechocystis sp. PCC 6803	Hydrogenase genes	Functional way to improve nitrogenase enzyme activity under micro-oxic conditions.	Recombinant plasmids, DNA assembler and Gibson assembly.	Further removal of genes from both directions resulted in a decrease of N_2 fixing activity.	[190]
Chlamydomonas reinhardtii	*chlL* gene	Introduces N_2-fixing genes directly into a chloroplast genome.	Plasmid construction and construction of chloroplast transformation vectors.	NifH product can at least partially substitute for the function of the putative "chlorophyll iron protein".	[191]
Azotobacter vinelandii	Fe–Fe nitrogenase system	Metallocluster biosynthesis under molybdenum limiting conditions.	Construction of recombinant plasmids and construction of multiple gene deletion mutants.	Limitation in ratio of ethane/ethylene produced by Fe–Fe nitrogenase is dependent upon electron flux.	[192]

pathways involved in nitrogen [184]. Interestingly, it was also demonstrated that a mutant lacking nitrate accumulation could grow without any damage in an herbicide-treated paddy field [185]. Some mutant strains withstand methylamine (an inhibitor of metabolic activity) that is induced by the action of herbicidal activity [186]. In fact, the spontaneous occurrence of mutants switched off the pathway and conferred resistance against the herbicide. Apart from other activities, the role of EPS in microalgae and cyanobacteria has an extensive function in soil activities. Recently, Liu et al. [187] mutated a microalga, *Crypthecodinium cohnii,* that resulted in higher secretion of EPS compared to the wild type strain indicating that mutagenesis plays a significant role. However, the use of optimal conditions for mutation is required for effective transformation in microbes.

For exploiting the potential traits in maintaining soil fertility and health, several microalgae and cyanobacteria have been genetically modified (Table 5). Although promising results are associated with the use of such advanced techniques, it is essential to overcome certain disadvantages while developing better strains of microalgae and cyanobacteria for their application as potential soil inoculants in a win-win situation.

For instance, soil health improvement through spontaneous gene mutation requires optimization with the reaffirmation of the expressed genes as it results in the shutting of other pathways [183,186,187]. Furthermore, the use of chemicals to mediate mutagenesis is also known to affect the organisms upon genetic modification [175]. However, the approach of recombinant technology for genetic modification has been quite promising, especially in the area of nitrogen fixation by soil microorganisms [177]. Engineering microbes are vulnerable in complex environments due to the presence of other microbes and substrates necessitating proper attention. An integrated approach for genetic modification reduces the risk of gene transfer to other microbes [178,181]. Genetic markers, excess plasmids, stable transformation, and expression are some of the key factors to be addressed in any genetic modification technique. This situation is warranted because the use of microalgal − cyanobacterial consortia in field studies results in more agricultural productivity even in abiotic stress environments and degraded lands. In fact, there is a huge gap since the late 2000s in this area of research because of a shift in interest toward the generation of value-added products such as biofuels. Furthermore, an understanding based on the OMICS

technology to explore the mechanistic and other arenas of mutation is also limited. However, the use of genetically modified organisms remains controversial due to the associated undesirable effects on ecological balance and living beings [193].

Conclusions

Microalgae and cyanobacteria are the primary colonizers that pave the way for other organisms to survive and establish under different climatic and edaphic conditions ranging from desert to wetland. As detailed in the present review, it is very factual that microalgae and cyanobacteria play a major role in maintaining the soil health and fertility necessary for sustained agriculture. The most significant advantage of exploiting microalgae and cyanobacteria is the balance in the dynamics of nutrients such as carbon, nitrogen and phosphate for the productivity of agricultural crops. Metabolic activities, such as the release of phytohormones, enzymes and allelochemicals from microalgae, play a pivotal role in enhancing plant growth, establishing interrelationships among other microbes, and detoxifying chemical agents such as pesticides, herbicides, etc. Moreover, biofertilizer applications using microalgae or cyanobacteria is a promising and beneficial approach for a better nitrogen economy in modern agriculture, reduction in greenhouse gas emissions, and maintenance of soil fertility. Hence, better insights into molecular aspects of microalgae and cyanobacteria are essential in order to realize their full potential in biotechnological applications. The present review underlines the further need to harness soil microalgae and cyanobacteria in the area of environmental biotechnology.

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