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Potential of microalgae and cyanobacteria to improve soil health and agricultural productivity: a critical view

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Microalgae are a source of scientific curiosity and inspiration for their utilization as 'inoculants' in agriculture and the commercial production of high-value products. Their diversity and abundance in the soil environment highlight the fact that these integral members of the soil microbial community modify the physical and chemical conditions of soils and interact with other microorganisms and even with higher plants with varying degrees of association. However, to date, the agronomic benefits of the nitrogen fixation trait of cyanobacteria have not been fully realized. Thus, the ecological functions of these organisms in the biological soil crusts should be thoroughly evaluated and widely applied given that climate change events can increase desertification. Currently, the crop yield increments and pest control due to these biostimulants and the reclamation of saline and sodic soils by these bioameliorants are considered economically marginal. Similarly, the carbon capture and storage by eukaryotic microalgae and cyanobacteria in soils are poorly understood. Limitations in their commercial production for agricultural use include inadequate technological innovations and the enormous expectation for yield increments, together with the contemporary monetization of their environmental benefits. Thus, this critical review presents the desirable reappraisal of their agronomic benefits and the invigoration of research and culture collections to utilize these organisms or their metabolites, considering the evolutionary consequences and environmental advantages and finally their commercial production for widespread application in agriculture.

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Environmental significance

Microalgae, which include phylogenetically diverse microscopic organisms of eukaryotic algae (green algae and other microscopic algal forms), and prokaryotic cyanobacteria are abundant in agricultural soils. These organisms have beneficial traits such as N₂ and CO₂ fixation ability, cycling of nutrients, and plant growth promotion. However, their utilization as inoculants and metabolites requires new research and better understanding of environmental advantages, ranging from individual field plots to the planetary scale. Thus, the present review provides the recent developments in their agronomic and ecological assessments and the need for innovations in commercial production and cognizance of their evolutionary significance while promoting them for widespread applications in agriculture.

1. Introduction

Photosynthetic organisms are essential for life on Earth, the evolutionary developments ranging from anoxygenic to oxygenic photosynthesis determine the energetics of all carbon (C)-based life forms.¹ Almost all the atmospheric oxygen is derived from oxygenic photosynthetic organisms (autotrophic plants, algae, and cyanobacteria), which obtain electrons from light-driven reaction centres (RCs) to fix atmospheric carbon dioxide (CO₂). In addition, oxygenic photosynthetic organisms are responsible for fixing more than 99% of organic C annually.² The evolutionary consequences and environmental impact of microalgae, including cyanobacteria, are significant. Recently, molecular evidence has provided significant new evolutionarily

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insights into cyanobacteria, which are traditionally considered strictly oxygenic phototrophs. In the new cyanobacterial lineages (4C0d-2 and ML635J-21), *i.e.*, metagenome-assembled genome (MAG) representatives, the absence of genes for photosynthesis and CO₂ fixation was demonstrated.^{3–5} The primary endosymbiosis between a cyanobacterium and a heterotrophic eukaryotic host led to the formation of primary plastids (*e.g.*, chloroplast organelles) in the first photosynthetic eukaryotic lineages including green algae (and land plants as their descendants).⁶ Qiu *et al.*⁷ suggested that algae (endosymbionts) are the vectors of endosymbiotic and horizontal gene transfer in the evolutionary history of many photosynthetic lineages. The ‘red carpet hypothesis,’ proposed by Ponce-Toledo *et al.*⁸ suggests that the mixed heritage of green plastids in secondary algae is due to many previous red algal gene acquisitions. These evolutionary events and the diversity and abundance of eukaryotic microalgae and cyanobacteria in soils are significant in achieving success in the present in human agricultural endeavours. Although ‘blue-green algae’ are monerans (prokaryotes), they were included in one of the nine algal phyla, *i.e.*, ‘Cyanobacteria’, in 2008. Presently, this large and morphologically diverse group of photoautotrophic prokaryotes are classified as ‘Cyanobacteria’ in one of the three domains of life, *i.e.*, ‘Bacteria’, to clearly differentiate them from eukaryotic algae that belong to the other domain Eukaryota. Alternatively, microscopic forms of algae (microalgae), which play a major role in nutrient cycling and fixing atmospheric CO₂, are essentially eukaryotic forms. In the present review, the terms ‘microalgae’ and ‘cyanobacteria’ are used to separately represent two distinct microbial groups, *i.e.*, ‘eukaryotes’ and ‘prokaryotes’.

The systematic composition (diversity) and abundance of cyanobacteria in subaerial and freshwaters of the tropics, especially from the observations made in Ceylon (Sri Lanka now) and their presence and likely similarities in other parts of the world were reported by Fritsch⁹ in 1907. Harrison and Aiyer¹⁰ reported the beneficial effects of algal growth in aerating the upper layers of submerged rice soils. In contrast to the report by Bouilhac¹¹ on the absence of dinitrogen (N₂) fixation in *Nostoc* species, Molisch¹² showed the ability of two strains of *Nostoc* to grow well in nitrogen (N)-free solution. In 1939, De¹³ demonstrated N₂ fixation by cyanobacteria isolated from dried soil samples collected and brought from rice fields in India. Consequently, the contribution of cyanobacteria to cultivating rice in the same land for long periods was established.^{13,14} These beginnings have led to the widespread examination and utilization of the potential of cyanobacteria in improving soil fertility and plant growth promotion (see reviews by Renuka *et al.*,¹⁵ Abinandan *et al.*,¹⁶ Chittora *et al.*,¹⁷ and Santini *et al.*¹⁸). However, although the biochemical potential of microalgal resources has been previously considered by most researchers, the need for translational research into commercial production, cognizance of ecological consequences and environmental impact between farming communities and policy makers require reappraisal. In the present critical review, we present the potential contributions of eukaryotic microalgae and cyanobacteria to the soil structure and fertility improvements, plant

stimulatory effects related to nutrition and metabolisms, reclamation of saline and sodic soils, pest control, and soil C storage, and perspectives that should be considered for their commercial production and wide-spread applications in agriculture.

2. Microalgae and cyanobacteria in improving soil structure and fertility

Global food production depends on the soil, which acts as a home to several terrestrial species, thus significantly supporting biodiversity. The soil structure, influenced by the distribution of soil aggregates (*i.e.*, basic units of soil structure) and pore spaces, is an indicator of fertility and determines not only the ability of soil to retain water and nutrients for crop growth but also the drainage ability, water-holding capacity, and soil aeration. In this case, although compacted soil can retain moisture and nutrients better, it is poorly drained, and the emergence of seedlings and plants becomes difficult. On the contrary, ‘less compact’ soil cannot retain water and nutrients. Thus, depending on the soil type, the distribution of solids, air, and water determines whether it is an ‘ideal’ agricultural soil. Typically, the ‘ideal’ agricultural soil has about 50% solids (about 45% minerals and 5% organic matter), 25% air, and 25% water and has strong relationships with biodiversity and agricultural productivity. Hence, the soil structure determines and supports the biodiversity of terrestrial species, including plants and microorganisms, which consequently alter the soil structure. In agricultural soils, the inter-relationships between crop plants and microbial communities are complex, where certain species can improve the soil structure and increase crop yields. However, agricultural practices, such as use of heavy machinery and tillage, can damage the soil structure. Thus, management practices such as reducing or no-tillage become critical to improving the soil structure. Furthermore, management practices involving microbial entities can also have long-term benefits. Cyanobacteria are considered ecological engineers because of their ability to modulate the ecological processes in the soil and create habitats for other organisms.¹⁹ The experimental addition of cyanobacteria under laboratory and field conditions resulted in a significant improvement in soil structure and aggregate stability^{20–23} (see Fig. 1).

Chamizo *et al.*²⁵ inoculated two cyanobacterial species (non-N₂-fixing *Phormidium ambiguum* Gomont NIES-2121 of the order Oscillatoriales and the N₂-fixing *Scytonema javanicum* Bornet & Flahault NIES-1956 of the order Nostocales) in the microcosms of silt loam, sandy loam, loamy sand, and sandy soil types. After 90 days, the cyanobacterial inoculation led to the formation of biocrusts, and those by *P. ambiguum* were characterized by thin filaments enveloping soil particles, while that by *S. javanicum* exhibited thicker filaments as bunches between soil particles. Interestingly, the total exopolysaccharide content and soil penetration resistance improved with *P. ambiguum*, while the total organic C and N contents increased with *S. javanicum* with variable levels in different soil types. The cyanobacterial filaments and extracellular secretions (exopolysaccharides) act as





Fig. 1 Implications of cyanobacteria in (a) soil structure (based on data from Nichols²⁴). (b) Aggregate stability by *Phormidium ambiguum* and *Scytonema javanicum*. (c) Maximum penetration resistance of *P. ambiguum* and *S. javanicum* in different textured soils (based on data from Chamizo *et al.*²⁵). (d) Albedo properties (400–700 nm range of soil surface reflectance spectra) of three soils (A – Amoladeras, B – El Cautivo, and C – Gádorquarry) treated with different cyanobacterial inoculants (*Nostoc commune*, *Scytonema hyalinum* and *Tolypothrix distorta*) (based on data from Román *et al.*²⁶).

gluing agents for binding soil particles for the enhanced formation of soil aggregates.²⁷ ‘Cyanobacterization’ (soil inoculation with cyanobacteria) is effective for stabilizing burned soils and restoring post-fire ecosystems.^{28,29} Recently, Shantakumar *et al.*³⁰ demonstrated that the algalization of acid soils with acid-tolerant microalgae, *i.e.*, *Desmodesmus* sp. MAS1 and *Heterochlorella* sp. MAS3, resulted in the initial development of soil algal crust, followed by the release of exopolysaccharides, which facilitated the stability of the soil aggregates and increase in soil pH. Importantly, the most suitable species should be selected for the restoration of poorly structured soils, depending on the soil type, texture, and mineralogy composition, which influence the growth of cyanobacteria and exopolysaccharide production.²⁶ However, although the ecological and agronomic potential of micro algalization or cyanobacterization for restoring degraded lands has been reported, the technological advances for their widespread application are inadequate. Pelletized cyanobacteria facilitated the storage of inoculum for extended periods, which is a promising technological innovation for restoring arid lands.²⁶

Although Metting and Rayburn³¹ and Barclay and Lewin³² suggested the use of microalgal polysaccharides for the conditioning of agricultural soils, the necessity for frequent irrigation to maintain algal growth or high inoculant rates hinders the direct application of microalgae for soil conditioning. Eukaryotic green algae can enrich and enhance nutrient availability and improve the fertility and quality of soils by the production of polysaccharides, antimicrobial compounds, plant growth hormones such as abscisic acid, cytokinin, gibberellins, and ethylene, and other metabolites that can promote plant growth.^{33,34} The microalgal polysaccharides are generally heteropolymers with different proportions of galactose, xylose, and glucose linked by glycosidic bonds except for homopolymer polysaccharides of galactose and β -(-1,3)-glucan by *Gyrodinium impudicum* and *Chlorella vulgaris*. Together with sugars such as rhamnose, fucose, fructose, and methyl sugars, microalgal polysaccharides can serve as bio-stimulants for improving the nutrient uptake, growth performance and physiological status, and abiotic stress tolerance of crop plants *via* their mechanistic actions of enhanced root growth and metal chelation in soils



and enhanced scavenging of reactive oxygen species, Rubisco synthesis, photosynthesis and higher PSII activity in the above-ground parts of the crop plants.³⁵ In a recent study, Rachidi *et al.*³⁶ applied the crude polysaccharide extracts from three microalgal strains (*Arthrospira platensis* MS001, *Dunaliella salina* MS002 and *Porphyridium* sp. MS099) on tomato plants and observed an increase in the contents of carotenoid, chlorophyll, and proteins, enhancement in the activities of nitrate reductase (about 102%) and NAD-glutamate dehydrogenase (about 400%) and changes in metabolomics related to the synthesis of lipids, sterols, and alkanes in the leaves. In another study, Mutale-Joan *et al.*³⁷ found that the application of microalgal liquid extracts led to an increase in the accumulation of pyridine-3-carboxamide (active amide form of vitamin B3) and linolenic acid (C18:3), which are precursors involved in the jasmonate pathways in plants. However, it is necessary to standardize and optimize protocols for applying microalgal extracts for individual crop species at different growth and developmental stages.

Microalgal metabolites belonging to the chemical groups of phenols, fatty acids, indoles, terpenes, acetogenins, and volatile halogenated hydrocarbons possess antimicrobial, antiviral, and antiprotozoal activity. Alsenani *et al.*³⁸ reported that linoleic acid, oleic acid, docosahexaenoic acid (DHA), and eicosa-pentaenoic acid (EPA) in the extracts of three microalgae (*Isochrysis galbana*, *Scenedesmus* sp. NT8c, and *Chlorella* sp. FN1) are potential candidates for inhibiting the growth of Gram-positive bacteria. However, only a small percentage of microalgal species, about 50 species from the described species of 40 000 to 50 000, has been screened for antimicrobial compounds, while the global estimate of microalgal species is approximately 10 million.^{39,40} Furthermore, the culture collections of microalgae are limited, even at the global level, and their commercial cultivation is restricted to even less. Hence, the agronomic applications of microalgae-derived antimicrobial compounds for modulating the soil microbiomes and eukaryotes have not received sufficient attention to date.

Ancient microalgal species are considered the origin of modern higher plant phytohormone biosynthesis pathways.³³ Accordingly, a better understanding of the evolution, metabolism, and regulatory networks of microalgal phytohormone systems will provide new avenues for using phylogenetically divergent microalgal resources as feedstock for phytohormone production and their agricultural applications. The modulation of phytohormone systems in higher plants by the introduction, enhancement, or engineering of beneficial agronomic traits such as tolerance to high levels of salinity, drought, flooding, and temperature extremes in crop plants is considered significant to successfully realise the 'Green Revolution'. Interestingly, the application of phytohormones improves the growth and accumulation of lipids and metabolites in microalgae.⁴¹ Furthermore, the exogenous application of phytohormones can enhance the biomass of cultivated microalgae, where microalgal species can modulate plant growth and development. However, little has been done beyond the laboratory microcosm- and experiment plot studies to develop microalgal resources for agronomic applications.⁴² Because of the

limitations of the direct applications of microalgae, including cyanobacteria, for soil structure and fertility improvements, such as the need for frequent irrigation and high inoculant rates, only their practical applications as biofertilizers or biostimulants can become popular for the cultivation of crops.

3. Microalgae and cyanobacteria as biofertilizers: biological potential and technological constraints

The application of microorganisms for improved plant growth, especially nodulation in pulse crops, has been known for more than 125 years. The first US patented microbial inoculant was 'Nitragin' in 1896. Commercially, this bacterial fertilizer (a species of N₂-fixing *Rhizobium*) was sold as a soil inoculator for legume crops using the Nobbe-Hiltner process. However, the chemical process of ammonia synthesis, a German patent granted to Fritz Haber in 1908, led to the production of synthetic nitrogenous chemical fertilizers worldwide and eclipsed the utilization of bacterial fertilizers. Meanwhile in Russia, 'Phosphobacterin', a biofertilizer having the spores of *Bacillus megaterium* var. *Phosphaticum* with kaolin rocks for improving the availability of phosphorus (P) to crops, became popular in the 1950s. Cyanobacteria represent a dominant bacterial group, playing significant roles in providing photosynthetically fixed C, N, phosphorus, phytohormones and polysaccharides to promote rice growth and enhance the fertility of soils. Thus, cyanobacteria have been explored as biofertilizers in flooded rice paddies, especially in India, where they form mats on the surface of water and enable an increase in yield to the extent of 10–24%.^{13,43–46}

According to their types and guilds of microorganisms and benefits accrued due to their application, biofertilizers can be classified as N₂ fixers, phosphate- and potassium solubilizers, phosphate mobilizers, zinc- and iron-solubilizers and plant growth-promoting rhizobacteria or plant stimulants. In general, the selection of cyanobacteria as biofertilizers is based on their ability to fix atmospheric nitrogen and plant growth-promoting activity. Chemical fertilizers or bioinoculants are often applied to the soil, and their effect on the rhizosphere microbiome is beginning to be understood.^{47,48} Most soils are deficient in N for supporting higher crop growth and yields, and the application of nitrogenous fertilizers is a critical determinant of the condition of 'feast or famine' in many countries. Given that the N use efficiency associated with synthetic chemical fertilizers is often low at about 20–40%, the economic losses and environmental pollution necessitate intensive efforts in developing newer biological methods for nutrient management in agricultural soils. The global biofertilizer market size is estimated to increase from USD 2.6 billion in 2021 to USD 4.5 billion by 2026, with a CAGR of 11.9%⁴⁹ (see Fig. 2). In the following section, we present a critical analysis on the potential of eukaryotic microalgae and cyanobacteria as CO₂ fixers, N₂ fixers, phosphate solubilizers, and plant biostimulants. In fact, the potential of several species of microalgae, including cyanobacteria, as biofertilizers/biostimulants in enhancing the



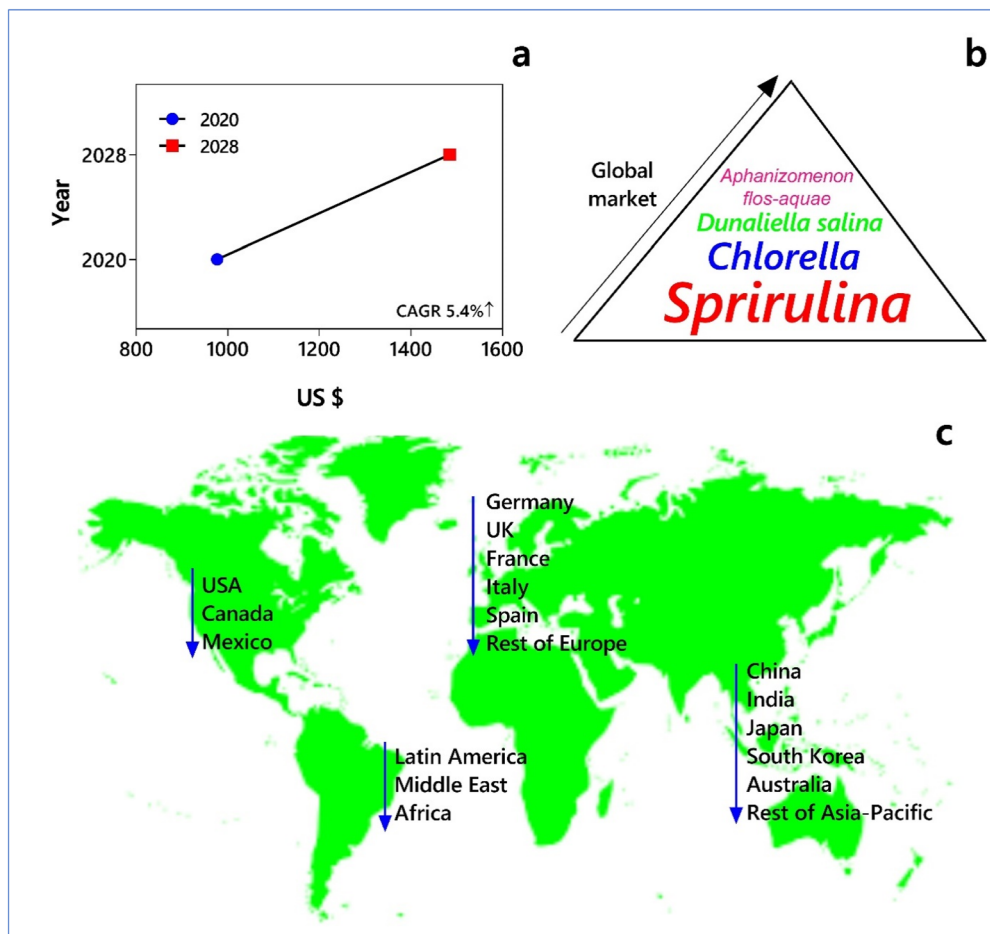


Fig. 2 Global biofertilizers market potential of microalgae and cyanobacteria. (a) Market size of microalgae for the years 2020 and 2028 (CAGR = compound annual growth rate). Key market consumption in terms of (b) microalgal/cyanobacterial type and (c) region globally (decrease in the order of arrow direction). (Source: <https://www.alliedmarketresearch.com/microalgae-market-A13419>).

yield components and/or yield of certain crop plants has been well realized (Table 1 and Fig. 3).

3.1. Role as CO₂ fixers

Terrestrial C cycling processes are critical for plant growth and development and higher agricultural productivity. 'Green carbon' refers to the C stored in plants and soils of the natural ecosystems. In this case, forests can accumulate and have large stocks of C, whereas agricultural croplands have relatively lower stocks due to their release with the short cycles of plant production and harvest. About 75% of soils have already been degraded, resulting in a negative impact on food security and family farming. Thus, the measures of reforestation and afforestation have become necessary to enhance the stocks of 'green carbon'. The primary producers, such as plants, algae, and autotrophic prokaryotes, including cyanobacteria (aerobic) and anaerobic photosynthetic organisms, assimilate by transforming CO₂. In contrast, animals (consumers), microbial decomposers, and primary producers release CO₂ through dissimilatory (chiefly respiratory) processes. The biotic interactions among the primary producers, microbial decomposers,

and consumers determine the rates of the assimilatory and dissimilatory processes. Higher plants modulate the activity of microbial decomposition by influencing the microbial availability of oxygen, nutrients, and labile substrates. Given that most of humanity depends on terrestrial soils for food, feed, and fiber, soils without sufficient C will make agricultural cultivation less profitable and environmentally catastrophic. Accordingly, nature-based solutions for conserving and restoring the C content of soils necessitate a shift from chemical fertilizer-based, modern agriculture to sustainable farming that can regenerate C-rich soils and reduce the emissions of greenhouse gas emissions and minimize the use of energy and inputs (www.4p1000.org).

In agricultural lands, microbial inoculants can improve C sequestration by capturing CO₂, forming carbonates by sedimentation, producing recalcitrant compounds, and enhancing the soil C stability.⁸⁴ In algae, the CO₂-concentrating mechanism (CCM) involves carbonic anhydrase, which provides CO₂ for C fixation by Rubisco. The natural ability and efficiency of CO₂ sequestration of several microalgal species are poor. However, In-na *et al.*⁸⁵ recently used loofah-based microalgal



Table 1 Impact of eukaryotic microalgae and cyanobacteria as biofertilizers or biostimulators on selected crop plants

Crop plant	Microalgal/cyanobacterial species	Effect (increase)	References		
Rice	<i>Calothrix</i> sp.	Plant growth	48, 50 and 51		
	<i>Oscillatoria</i> sp.				
	<i>Anabaena</i> sp.				
	<i>Phormidium</i> sp.				
	<i>Aulosira</i> sp.				
	<i>Plectonema</i> sp.				
	<i>Nostoc spongiaeforme</i>			Yield components such as tillers per hill, panicles per hill, length of panicle, straw, and grain yield	52
	<i>Nostoc commune</i>				
	<i>Calothrix marchica</i>				
	Wheat			<i>Stigonema</i> sp.	Plant growth
<i>Scytonema hofmannii</i>					
<i>Chlorella vulgaris</i>		Salt stress tolerance	53		
<i>C. pyrenoidosa</i>				Seed germination and growth	
<i>Nostoc</i> sp.		Plant growth (length and dry biomass)	59 and 60		
<i>Calothrix</i> sp.					
<i>Anabaena</i> sp.					
<i>Chlorella sorokiniana</i>					
Maize	<i>C. sorokiniana</i>	Plant growth (root development)	61		
	<i>Chlamydomonas reinhardtii</i>				
	<i>Pseudanabaena</i> sp.			Nutrient content	62
	<i>Phormidium</i> sp.				
	<i>Geitlerinema</i> sp.			Seed germination	62
	<i>Arthrospira</i> sp.				
	<i>Oscillatoria</i> sp.				
Lettuce; capsicum; tomato	<i>Calothrix anomala</i>	Plant growth, and nutrient content	36, 63 and 64		
	<i>Arthrospira platensis</i>				
	<i>Aphanothece</i> sp.				
	<i>Dunaliella salina</i>			Salt tolerance	36 and 65
	<i>Chlorella</i> sp. (in consortium)				
		Metabolomics profile			
		Plant growth	66		

and cyanobacterial biocomposites for enhancing CO₂ capture. Also, some attempts have been reported on genetically engineering cyanobacteria for enhanced carbon capture and storage (CCS) in photobioreactor systems.⁸⁶ Presently, agricultural practices do not include the utilization of eukaryotic microalgae and cyanobacteria as microbial inoculants for biological C sequestration. However, the 'soil carbon debt' due to human land use suggests that 1200 years of human agriculture has led to the loss of 133 billion tonnes of C, *i.e.*, about 8% of total global soil C stocks (estimated at 2400 petagrams of C, PgC) or equivalent to 65 ppm of atmospheric CO₂, from the top two meters of the soil worldwide.⁸⁷ The global 'hotspots' of C losses include agricultural lands, which are not equally distributed. In addition, the annual loss of topsoil is about 75 billion tons, with an economic loss of approximately US\$ 400 billion.⁸⁸ Moreover, the functions of plant roots include the absorption of CO₂ and carbonate with the β-carboxylation of keto acids and movement of dicarboxylic acid to leaves.⁸⁹ Thus, the continuing soil C loss and soil erosion through the loss of top soil due to agriculture, increasing concentrations of atmospheric CO₂ as a greenhouse gas, and the ability of plants to utilize CO₂ provide incentives to screen, select and use eukaryotic microalgae and cyanobacterial species and other autotrophic microorganisms for improved CO₂ fixation in soils or rhizospheres. Nevertheless, tracking the

below-ground processes and differentiating the CO₂ fixers from soil-derived and plant-derived C-utilizing microorganisms, and their efficiencies are essential to develop methods for rationally manipulating plant–soil microorganism systems for promoting soil C storage. In a recent report, Chen *et al.*⁹⁰ showed that the CO₂ fertilization effects due to increased land-use management through croplands were greater in India (82%) than in China (32%), while it was the opposite for greening through forests with 42% and 4.40% in China and India, respectively. Interestingly, the net primary productivity of soil algae in croplands is estimated to be the highest (157 g C m⁻² years⁻¹) among the biomes, equalling about 6% of the net primary production of terrestrial vegetation⁹¹ (see Table 2). The CO₂ fertilization efforts through soil algae can benefit croplands, not only through plant growth stimulation but also through improved terrestrial carbon uptake.

3.2. Dinitrogen fixers

Biological N₂ fixation by prokaryotic microorganisms is an ancient process that probably originated in anaerobic methanogens about 1.5 to 2.2 Ga (Giga annum or billions of years). The distribution of nitrogenase enzyme among biological organisms is limited to bacteria and archaea. The presence of





Fig. 3 Metabolic potential of microalgae and cyanobacteria. (a) CO₂ bio-fixation rate (mg L⁻¹ day⁻¹) under different cultivation systems (based on data from Basu *et al.*,⁶⁷ Duarte *et al.*,⁶⁸ Kumar and Das,⁶⁹ Nayak *et al.*,⁷⁰ Swarnalatha *et al.*,⁷¹ Yeh and Chang,⁷² and Yun *et al.*⁷³). (b) Carbon fixation efficiency (%) of absorption-microalgae hybrid (based on data from Cardias *et al.*,⁷⁴ da Rosa *et al.*,⁷⁵ Kim *et al.*,⁷⁶ and Kim *et al.*⁷⁷) (DEA – diethanolamine; MEA – monoethanolamine; AMP – 2-amino-2-methyl-1-propanol; TEA – triethanolamine). (c) Nitrogen (% w/w) in *Chlorella vulgaris* biomass harvested after 10 days (in the presence of different initial nitrate concentrations) and 7 days (in nitrogen-free medium) from algal batch culture system (based on data from Farooq *et al.*⁷⁸). (d) Efficiency of nitrogen savings by a microbial consortium containing cyanobacteria during crop cultivation (based on data from Prasanna *et al.*^{79–83}). (A, B and C = *Anabaena* spp. + *Nostoc* spp.; D = *Anabaena torulosa* + *Trichoderma viride*/A. *torulosa* + *Azotobacter* sp.; E = A. *torulosa* + T. *viride*/A. *torulosa* + *Pseudomonas* sp.; F = A. *torulosa* + T. *viride*).

nif gene clusters is limited to a few terrestrial (*i.e.*, *Cyanothece* and *Synechococcus*) and marine (*Crocospaera*) cyanobacterial strains. Besides, the genomes of *Firmicutes*, *Chloroflexi*, *Chlorobi*, and *Bacteroidetes* and the lineages of *Actinobacteria* and

Proteobacteria have *nif* gene clusters. Cyanobacteria are the only diazotrophic lineage capable of fixing N₂, while producing molecular oxygen as their metabolic product. They employ different mechanisms to protect the oxygen-sensitive

Table 2 Abundance and net primary productivity of soil microalgae and cyanobacteria across different biomes^a

Ecosystem	Abundance (median value × 10 ³ cells g ⁻¹ dry soil)	Net primary productivity (NPP) (g C m ⁻² years ⁻¹)	Contribution to total terrestrial NPP (%)
Croplands	161	157	>30
Drylands	85	<15	<10
Wetlands	1036	<15	<10
Alpine and polar lands	20	<15	<10
Grasslands	410	22.6	<15
Broadleaf and mixed forests	59	28.2	<10
Broadleaf evergreen forests	202	18	>15
Average	550 ± 340	30	

^a Data from Jassey *et al.*⁹¹



nitrogenase, as follows: (i) up-regulation of N_2 fixation at night on a diurnal cycle with reduced oxygen tensions due to decreased photosynthetic oxygen production, especially in non-filamentous cyanobacteria and (ii) spatial segregation of nitrogenase in heterocysts with the involvement of the Mehler reaction.⁹² Cyanobacteria, with their 'introvert' lifestyle of maintaining C/N homeostasis, tightly interconnect the fixation of CO_2 with N-assimilation. The complex network of signal transduction pathways involves 2-oxoglutarate to sense the cellular C/N status. The accumulation of carbon or nitrogen storage polymers in the cells cope with the imbalance in the homeostatic control.⁹³ Recently, Hirose *et al.*⁹⁴ sequenced the genomes of 28 cyanobacterial strains that can form heterocysts, which are morphologically distinct cells for fixing N_2 from a collection of 827 strains in the National Institute for Environmental Studies (NIES), Japan.

Cyanobacteria can establish symbiotic relationships with bryophytes (hornworts and liverworts), algae, *Azolla*, *cycads*, fungi (*Geosiphon* together with yeasts forming lichens), and *Gunnera* because of their ability to differentiate heterocysts (specialized N_2 -fixing cells) and hormogonia.^{95,96} Thus, the only angiosperm species that can form symbiotic relationships with cyanobacteria is *Gunnera*. Besides, in higher plants, the symbiotic relationships with mycorrhizal fungi and N_2 -fixing bacteria (symbiotic nitrogen fixation, SNF) began about 540–420 million years ago (Ma), with the occurrence of the first peak in CO_2 , and the second peak occurred about 150–100 Ma.⁹⁷ Hence the selection of N_2 -fixing cyanobacteria as bacterial inoculants for higher plants is primarily limited to free-living members. Nevertheless, both the free-living N_2 -fixing cyanobacterial strains are utilized as biofertilizers, and the symbiotic *Azolla*-*Anabaena* system is used as 'green manure' in many rice-cultivating countries such as India, Nepal, Vietnam, China, Thailand, and the Philippines. Although the application of free-living cyanobacteria can fix about 25–30 kg N ha⁻¹ season⁻¹, the *Azolla*-*Anabaena* system can contribute about 20–40 kg N ha⁻¹ to the rice crop in about 25 days.^{98–100} Chittora *et al.*¹⁷ detailed the steps required to mass-produce cyanobacterial biofertilizers. They introduced affordable (rural) technology to economically poorer farmers, with the soil-based inoculum consisting of *Aulosira*, *Nostoc*, *Anabaena*, and *Tolypothrix*, is now a commercial enterprise of cyanobacterial biofertilizer technology in India.¹⁰¹ The symbiotic relationships between eukaryotic microalgae and cyanobacteria, such as that between various genera of diatoms with the diazotrophic cyanobacterium *Richelia intracellularis* still have not been investigated for their potential for N_2 fixation and their utilization as inoculants to date. Interestingly, diazotrophic cyanobacteria with an alternative nitrogenase (V-nitrogenase, encoded by *vnfH*, *vnfD*, *vnfG*), in addition to molybdenum nitrogenase have been reported.¹⁰² Thus, it is necessary to prepare comprehensive genomic data of cyanobacteria to benefit from their nitrogenases with different metal co-factors.

3.3. Phosphorus cycling by microalgae and cyanobacteria

The P content of most soils is about 0.5% (w/w), while the plant available form is only 0.10% of the total P content. The P use

efficiency of phosphatic fertilizers is about 46%, leading to the environmental problems of groundwater contamination and eutrophication.¹⁰³ The P availability in soil is an essential determinant of global food security. The current global reserves of phosphate rocks, a non-renewable source for chemical P fertilizers, may be depleted in the next 50 to 100 years.¹⁰⁴ In this case, soil microorganisms, including eukaryotic microalgae and cyanobacteria, are capable of phosphate solubilization. The solubilization of rock phosphate (*i.e.*, Mussoorie rock phosphate, MRP) by cyanobacteria was demonstrated by Roychoudhury and Kaushik,¹⁰⁵ and organic sources by Whitton *et al.*¹⁰⁶ Yandigeri *et al.*¹⁰⁷ showed the differential response of two diazotrophic cyanobacteria, *Westiellopsis prolifica* and *Anabaena variabilis*, to solubilize extracellular insoluble tricalcium phosphate (TCP) and MRP. Nevertheless, the mineral phosphate solubilizing (mps) phenotype is not common among cyanobacteria. Microalgae (*e.g.*, *Chlorella* sp. and *Scenedesmus* sp.) and cyanobacteria (*e.g.*, *Aphanothece* sp., *Spirulina* sp., *Arthrospira* sp., and *Phormidium* sp.) are capable of assimilating P as polyphosphates as linear polymers of orthophosphate residues linked by phosphoanhydride bonds to mitigate stress conditions.¹⁰⁸ These microalgal and cyanobacterial strains can be used as biofertilizers for the slow and moderate release of P, supplying it within the 'critical value' for the crop rhizosphere, thus reducing the probability of excess supply.

Microalgae are acclimated to low-P conditions because of their capabilities related to the 'luxury uptake' of P and storage as polyphosphate whenever P is available. The expression patterns of Pi (inorganic orthophosphate) transporters are a function of the P availability of microalgae.¹⁰⁹ Mukherjee *et al.*¹¹⁰ proposed the development of technology to recover P from waste and effluent (*e.g.*, parboiled rice mill effluent) using microalgal and cyanobacterial strains capable of sequestering P as polyphosphate inclusions and recycling these strains as biofertilizers for the slow and moderate release of P. Golzary *et al.*¹¹¹ reported the potential of *Azolla filiculoides* (*Azolla*-*Anabaena* system) to remove about 40–44% of P from secondary effluents.

3.4. Plant biostimulants

Because of phototrophic and aerobic growth requirements, cyanobacteria are conventionally considered plant biostimulants, although some strains were isolated from rhizospheres. The N_2 -fixing trait of cyanobacteria is the primary choice for their screening, selection, and utilization. However, recent reports suggest that diverse bioactive molecules such as osmolytes, phenolics, vitamins, phytohormones, and others act synergistically for plant growth promotion and tolerance to abiotic stresses¹⁸ (see Table 1). Singh *et al.*¹¹² suggested that two biological processes, *i.e.*, biological fixation of CO_2 and atmospheric dinitrogen, make them biostimulants, especially in paddy fields. Ördög *et al.*¹¹³ applied freeze-dried biomass of *Nostoc piscinale* after resuspending it in tap water (1.0 g L⁻¹ DW) as a single foliar treatment (400 L ha⁻¹) to maize (*Zea mays* SY Zephir hybrid) and found that the number of leaves, the contents of chlorophyll (SPAD value) and grain protein, and



grain yield (6.50–11.50%) were significantly higher. Seed priming and soil application of cyanobacterial strains, with or without other bacterial biofertilizers have shown variable plant growth-promoting effects in different crops.^{79,114} Since the 1940s, extracts of seaweed (macroalgae) have been applied to improve the stress tolerance and crop yields due to their elicitors and phytohormones.¹¹⁵ Similarly, microalgal extracts have diverse biological activities and are potential agents for mitigating stresses and plant growth promotion.^{116,117} In fact, Colla and Rouphael¹¹⁷ identified the bottlenecks such as high cost of microalgal production and application, poorly characterized products with varying performance, lack of knowledge about the mechanisms, and lack of awareness among farmers in deriving the benefits from microalgal and cyanobacterial biostimulants.

4. Microalgae and cyanobacteria in biological soil crusts: significance in drylands

Arid and semiarid environments occupy 41% of the global land area and support more than 38% of the total human population. Desertification affects about 25% of the global land area due to climatic change, human activities, and other factors, and more than 40% of the Earth's terrestrial area is in danger of desertification.¹¹⁸ The desertification risks are about 13%, 7% and 9% of the global land area at moderate, high, and very high levels, respectively.¹¹⁹ The significant features of these dry lands include the presence of biological soil crusts, which are of two types, as follows: (i) hypoliths, also referred to as biocrusts, consisting of microscopic cyanobacteria, algae, fungi, and bacteria, and (ii) poikilohydric organisms consisting of macroscopic lichens, mosses, and microarthropods.¹²⁰ Fossil records suggest that biocrusts, one of the earliest and dominant types of community terrestrial life forms, appeared about 2.6 Ga. The biocrusts determine the structure, surface morphology, capture and retention, organic matter and other resources, and fertility of soil by influencing the atmospheric fixation of C and N. In drylands, the critical zone (described as the 'heterogeneous, near-surface environment in which complex interactions involving rock, soil, water, air, and living organisms regulate the natural habitat and determine the availability of life-sustaining resources') (US National Research Council, 2001) is chiefly characterized by biocrusts, endoliths, and hypoliths, whereas sporadically by vascular plant roots at, on or in the top few cm of the soil surface or rock. This critical zone mediates: (i) the exchange of all gaseous, nutrients, and water inputs and outputs; (ii) the deposition, transformation, and availability of nutrients; (iii) the structuring of the vascular plant community at the temporal, spatial, and compositional levels; (iv) the direct delivery of C, nutrients, and water by biocrusts to plants; (v) the creation of biodiversity hotspots by biocrusts and (vi) the cover and composition of biocrusts, which can modify the soil stability, fertility, and hydrology and be used as an index of soil health.¹²⁰

In 1729, Micheli¹²¹ described the thallus of *Nostoc*, which occurs in most biocrust communities worldwide. The oldest fossil record of biological soil crusts of 2.6 Ga presumably had cyanobacteria. The cyanobacteria associated with biocrusts can be grouped as follows: (i) filamentous cyanobacteria (e.g., *Microcoleus*) stabilizing soils by gluing and forming soil aggregates with extracellular matrix; (ii) either unicellular or filamentous cyanobacteria (e.g., *Chroococciopsis*, *Scytonema*, and *Stigonema*) contributing to C and N cycling, and (iii) stochastically occurring cyanobacteria (e.g., *Chroococcus*, *Gleocapsa*, *Gleocapsopsis*, *Cylindrospermum*, *Phormidium* and *Tolypothrix*). The molecular clock estimates suggest that the formation of biocrusts by eukaryotic algae occurred about 600 million years ago (Ma). The eukaryotic algae are not exclusively found in biocrusts, with the major functional groups as follows: (i) crust-forming algae due to filamentous nature and/or mucilage secretion (e.g., *Klebsormidium* and *Zygonium*), (ii) algae attached to soil particles and crust-forming algae (e.g., *Spongiochloris*, *Neochlorosarcina*, and diatoms); (iii) algae that occur within lichens as symbionts, free-living within the biocrusts and those living epiphytically (e.g., *Myrmecia* and *Stichococcus*), and (iv) freshwater algae originating from aquatic habitats (e.g., *Chlorococcum*, *Chlamydomonas*, *Scenedesmus* and *Mychonastes*). Besides cyanobacteria, the members of Proteobacteria (e.g., β -Proteobacteria – *Massilia* and *Comamonas*), Actinobacteria (e.g., *Streptomyces*, *Sphaerobacter*, *Actinomadura*, *Rubrobacter*, *Nonomuraea* and mycelia genera), Bacteroidetes (*Flexibacter*, *Spirosoma*, *Flavobacterium*, and *Sphingobacterium*), and those of Armatimonadetes, Gemmatimonadetes, Planctomycetes, and Verrucomicrobia are present in the biological soil crusts. The fungal diversity, which varies with the age and type of biocrusts, includes the lineages of the class Dothideomycetes with the representatives of *Pleosporales* and the genus *Alternaria* but with no arbuscular mycorrhizal fungi.¹²² Applying molecular, culture-independent approaches coupled with physiological and biochemical assessments and their cultured isolates can improve our understanding of the functioning of individual constituents of biological soil crusts.

Human activities, even compressed stress due to footsteps or the use of machinery, and air pollutants from industrial activities have adverse environmental impacts on biological soil crusts. The agronomic importance of biological soil crusts in improving the soil structure and stability, minimizing soil erosion, and plant growth-promoting effect as biofertilizers and biostimulants has received significant attention.¹²³ Kheirfam and Roohi¹²⁴ examined an inoculation-based technique for forming biocrusts using the soil profile collected from the dried region of Lake Urmia. After 120 days, the microbial inoculation significantly improved the biocrusts indicators such as the contents of total C (225%) and N (3200%), available P (70%) and potassium (19%), pH (–1.20%), soil moisture (15.70%), bulk density (–2.50%), aggregate stability (133%), and surface roughness (34.80%). Thus, inoculation-based techniques can be considered for restoring dried-up and degraded lands. Earlier, Zhou and Zhang¹²⁵ reported the feasibility of artificially cultivated biological soil crusts for increasing the runoff efficiency with less runoff sediment and recommended them as green



materials for harvesting rainwater. In arid or semiarid environments, algae employ diverse survival strategies including the synthesis of intracellular antioxidants (e.g., carotenoids lutein in microalgae) and anti-oxidative enzymes, the strengthening of the cell wall by the secretion of extracellular polymeric substances (EPSs) and cellular membranes (water stress protein and trehalose), and the formation of microbial consortia with fungi and bacteria. These survival strategies have a significant contribution to the ecological functions of biocrusts.

Together with these strategies, the soil fertility improvements by biocrusts make them excellent agents for practical applications to control desertification.¹²⁶ Recently, De Oliveira and Maciel-Silva¹²⁷ compared the Brazilian biocrust communities with that from different ecosystems and proposed the utilization of biocrusts as 'ecosystem engineers' for colonizing other ecosystems. The meta-analysis of the biocrusts suggested that the soil organic carbon (SOC) concentration increased by 70.9% compared to the uncrusted soil, and the random forest analysis showed that the total N was an essential determinant of the concentration of SOC, followed by climate ($p < 0.01$).¹²⁸ Because of their ecological advantages, improvements in soil physical structure and stability, and enhanced concentrations of soil labile C and microbial C and N, biological soil crusts were applied (as broken-skin inoculation, moss) as a nature-based strategy (Nbs) in the fields of semiarid rainfed alfalfa (*Medicago sativa* L.).¹²⁹ The restoration efforts of degraded lands can significantly benefit from the soil microbiota,¹³⁰ where biocrusts can be more effective than individual microbial inoculants.

5. Amelioration of saline and sodic soils by microalgae and cyanobacteria

Soil salinization has failed many human civilizations, including the early Mesopotamia from 1200 and 900 BC and now the river basins of the Indo-Ganges in India, the Murray-Darling in Australia, the Yellow River in China, and the San Joaquin Valley in the United States of America. About 23% (0.34×10^9 ha) and 37% (0.56×10^9 ha) of the cultivated lands are saline and sodic soils, respectively, predominantly located in arid and semi-arid regions distributed worldwide. These soil environmental services and agricultural productivities are adversely affected due to natural causes and human activities such as irrigated agriculture, when poorly managed with over-irrigation, seepage, and silting.¹¹⁹ The annual cost of land degradation in irrigated areas due to salinity and sodicity can lead to the lost crop production of about US\$ 27.3 billion worldwide. Cyanobacteria colonize the habitats of saline soils because of their salinity sensing-signaling (e.g., activation of K^+ transport system, glycosyl glycerol (GG) synthesizing enzyme, histidine protein kinase (HIK), response-regulator protein (RRE) two-component signaling system, and salt overly sensitive (SOS) pathway) and tolerance mechanisms such as active Na^+ efflux, K^+ transport system, phospholipid modifications, osmotically active molecules and activation and deactivation of enzymes although growth, photosynthesis, plasma membrane composition, cellular homeostasis, reactive oxygen species (ROS) generation,

other biochemical pathways, and gene expression and protein synthesis are adversely affected under high salinity stress.¹³¹ Thus, the microbial remediation of saline soils has been attempted by employing halophilic and halotolerant strains, consortia, and bacterial enzymes. These approaches are successful to some extent, but many complex factors such as their poor adaptability and application methods limit their widespread acceptance.¹³²

Thomas¹³³ found that the repeated cultivation of *Anabaena torulosa* in the saline Kharland soils led to a reduction in salinity by 12–35%, which was attributed to an active photosynthesis-linked mechanism for the extrusion of sodium according to the studies using ^{24}Na and ^{22}Na . Kaushik and Subhasini¹³⁴ reported that algalization decreased the electrical conductivity, soil pH, and exchangeable sodium content in saline soils. On the contrary, Rao and Burns¹³⁵ found that cyanobacteria were ineffective in alleviating highly degraded alkali soil, with an insignificant increase in the contents of C and N from the soil column studies, even after 17 weeks. Due to their inability to mobilize calcium from native soil calcite for exchanging with sodium in the exchange complex, these organisms were considered ineffective. Pandey *et al.*¹³⁶ reported that the sequence of appearance of cyanobacteria, the dominant species in usar soil (alfisol, solonetz, alkaline and widespread in India) was *Nostoc calcicola*. Its bicarbonate-resistant mutant (HCO_3^-R) was better in modifying soil pH compared to the wildtype in the laboratory incubation study for two years. Similarly, in another laboratory simulation experiment, Jaiswal *et al.*¹³⁷ showed that *N. calcicola* lowered the pH of usar soil in a 20% soil extract compared to the basal medium. However, the bicarbonate mutant (HCO_3^-R) could grow at a higher percentage of soil extract (60%). The bicarbonate mutant strain was suggested to be a potential bio-ameliorant after further evaluation at the field level. Srivastava *et al.*¹³⁸ found that *Aulosira* was more prevalent than *Nostoc* in soil samples collected in Eastern Uttar Pradesh after the denaturing gradient gel electrophoresis profiling of cyanobacterial communities. In this case, the selection of salinity-adapted cyanobacterial species specific to the location to be facilitated is vital for the success of its utilization. Li *et al.*¹³⁹ suggested the potential of co-culture of cyanobacteria and bacteria as bio-remediating agents for salt-affected soils. Likewise, Naorem and Udayana¹⁴⁰ considered cyanobacteria as add-ons of the beneficial soil microbiota to remediate salt-affected soils under organic farming. In a recent report, Brito *et al.*¹⁴¹ showed that the soil application of a new terrestrial cyanobacterial species (*Oculatella lusitanica* LEGE 161147) on lettuce (*Lactuca sativa* L. cv Marvel of Four Seasons) had a limited priming effect. However, there were beneficial effects by mitigating the deleterious salinity stress by eliciting non-enzymatic antioxidant (i.e., proline, H_2O_2 , and reduced glutathione) responses. However, the cyanobacterial priming effect, including the enhanced activity of N metabolism-related enzymes such as glutamate dehydrogenase, glutamine synthetase, and nitrate reductase, was observed in lettuce plants under non-stress conditions.

The eukaryotic microalgal forms and cyanobacteria are beneficial, renewable resources for agriculture, even in saline



and sodic soils.⁴² Mutale-joan *et al.*¹⁴² examined the potential of microalgae–cyanobacterial extracts as stimulators of salt stress tolerance responses in tomato (*Solanum lycopersicum* L. JANA F₁). The extract formulations (MEF) of microalgae (*Dunaliella salina* MSD 002 and *Chlorella ellipsoidea* BEA 0337) and cyanobacterial species (*Aphanothece* sp. BEA O₉₃₅B and *Arthrospira maxima* MSS₀₀₁) at different levels (MEF1%, MEF5%, and MEF10%) were applied to tomato plants grown under four NaCl concentrations (0, 80, 120, and 150 mM) by soil drenching. The application of MEF5% was found to enhance the vegetative growth, photosynthetic pigments due to improved osmotic adjustment and ion homeostasis, proline accumulation, the activities of CAT and SOD, and absorption of N, P, and K in the plants grown at 80 and 120 mM NaCl. In contrast, leaf lipid peroxidation through ROS oxidative stress was significantly decreased together with a decrease in fatty acid content. The application of MEF led to the enhanced uptake of K⁺ and reduced Na⁺/K⁺ ratio in leaves, suggesting its role in re-establishing ion homeostasis. Thus, the combined microalgal–cyanobacterial formulations can better stimulate the salt tolerance responses, nutrient uptake, and growth of plants. In an earlier study, Grzesik *et al.*¹⁴³ observed that the foliar application (*i.e.*, sprayed three times on leaves at three-week intervals during vegetation season) with intact cells of *Microcystis aeruginosa* MKR 0105, *Anabaena* sp. PCC 7120 and *Chlorella* sp. influenced the growth and physiological performance, such as the stability of cytomembranes, chlorophyll content, intensity of net photosynthesis, transpiration, and stomatal conductance of willow plants (*Salix viminalis* L.), a horticultural plant whose flexible branchlets are used in basketry. Similar investigations on the potential of intact or cellular extracts of microalgae–cyanobacteria in crop plants for improving salinity tolerance are necessary. Up to 2010, the utilization of microalgal and cyanobacterial resources was about 10 000 tons per year, while their commercial production will increase to 27 500 tons per year with a market value of US\$ 1.10 billion, especially as food, feed, dietary supplements, cosmetic care products, and biofuels.^{144,145} Because of their potential to stimulate plant growth and improve stress tolerance, the biomolecules from these organisms can increase their commercial production and agronomic applications.

6. Microalgae and cyanobacteria as biocontrol agents of pathogens and pests

Pathogens and pests are integral to agricultural ecosystems, where pathogens including members of fungi, bacteria, viruses, oomycetes, and Chromista and ‘animal pests’ such as insects, mites, and weeds cause economic losses of crops at the local, regional, national, and global levels. The major food crops such as wheat, rice, maize, potato, and soybean have about 137 pathogens and pests. Their global burden in terms of yield losses ranges from 17% (potato) to 30% (rice), with more losses associated with food-deficit regions and frequently with the emergence or re-emergence of pests and diseases.¹⁴⁶ The annual

cost of plant diseases is more than US\$ 220 billion, which may increase due to global climate change events, a major threat to food security and the environment.¹⁴⁷ Evolutionarily, plant-pathogen or pest interactions help develop defense mechanisms to protect plants, pest host breadths and impacts, and maintain the ecological balance in the wild and human-managed systems.¹⁴⁸ However, intensive agriculture with pesticides to control pathogens and pests has caused environmental disturbance and non-targeted effects, with long-lasting and far-reaching consequences.¹⁴⁹ The theory of ‘trophobiosis’, which was proposed by Chaboussou,¹⁵⁰ suggests that the increased availability of soluble nutrients in plant tissues and modification of morphological and chemical defensive traits due to intensive use of chemical fertilizers and pesticides can promote the damage by pathogens and pests in crops. Thus, the vicious cycle of chemical input applications, either repeated or with new compounds, becomes undesirable in agricultural ecologies.

Presently, almost 50% of all crop production compounds available are based on natural products (NP), their semi-synthetic derivatives (NPDs), compounds inspired by NPs (NP mimics, NPMs), and especially NP synthetic equivalents, which constitute about 30%.¹⁵¹ Pratt¹⁵² described the use of the anti-bacterial substance, chlorellin, against human pathogenic Gram-positive (*Staphylococcus aureus*, *Streptococcus pyogenes*, and *Bacillus subtilis*) and Gram-negative bacteria (*Bacterium coli* and *Pseudomonas pyocyanea*) extracted from *Chlorella* sp. (*C. vulgaris* and *C. pyrenoidosa*), which also could inhibit the further multiplication of their cells. Shaima *et al.*¹⁵³ reported the anti-bacterial activity of microalgae such as *C. sorokiniana* (UKM2), *Chlorella* sp. (UKM8), and *Scenedesmus* sp. (UKM9), which is attributed to the presence of phenol, hexadecenoic acid, phytol, 9,12-octadecadienoic acid, and bicyclo[3.1.1]heptane. Kulik¹⁵⁴ reviewed the potential of cyanobacteria and algae to produce antibacterial and antifungal compounds against plant pathogens for biological control. Fungal pathogens (soil-borne, foliar, or fruit pathogens) can cause the most plant diseases with severe economic losses and produce mycotoxins, which are harmful to humans and livestock (see Dean *et al.*¹⁵⁵ for top 10 fungal pathogens). The data presented in Fig. 4 clearly highlights the important role of microalgae and cyanobacteria as potential biocontrol agents against fungal and bacterial pathogens.

The extracts prepared with methanol, acetone, diethyl ether, ethanol, methyl chloride, and other solvents, using *Microcystis*, *Anabaena*, *Nostoc*, *Scytonema*, *Lynghya*, *Oscillatoria*, *Trichodesmium*, and *Synechococcus* were inhibitory to *Aspergillus* spp. *Fusarium* spp. and other pathogens under many *in vitro* and some *in vivo* studies (reviewed by Righini *et al.*¹⁵⁷). Roberti *et al.*¹⁵⁸ reported that when a water extract of *Anabaena* sp. BEA0300B was applied to cotyledonary leaves (two leaves, with other cotyledonary and true leaves untreated) of zucchini (*Cucurbita pepo* cv. Consul Semencoop, s. r. l, Italy) and challenged with a conidial suspension of *Podosphaera xanthii*, it resulted in the induction of systemic defense responses (systemic acquired resistance (SAR) and induced systemic resistance (ISR)). On 1, 2, and 3 days of treatment, the total





Fig. 4 Biocontrol properties of microalgae and cyanobacteria. (a) Inhibition (%) of *Fusarium oxysporum* by *Synechocystis sp.*, *Tetradesmus obliquus*, *Chlorella protothecoides*, and *Chlorella vulgaris* at different levels of biomass (g L^{-1}) (based on data from Ferreira *et al.*¹⁵⁶). (b) Anti-bacterial activity of *Isochrysis galbana*, *Scenedesmus sp.* NT8c and *Chlorella sp.* FN1 against bacterial pathogens, *Listeria monocytogenes*, *Staphylococcus aureus*, *Bacillus subtilis*, *Clavibacter michiganensis*, *Staphylococcus epidermidis* and *Enterococcus faecalis*. (c) Fatty acids methyl esters (FAME) in *I. galbana*, *Scenedesmus sp.* NT8c and *Chlorella sp.* FN1 implicated in antimicrobial activity (based on data from Alsenani *et al.*³⁸) EPA – Eicosapentaenoic acid and DHA – Docosahexaenoic acid.

chitinase activity increased (15–38%) and the transient increases of β -1-3-glucanase and peroxidases further increased. The powdery mildew symptoms were reduced by 25%, while the water extract had direct antifungal activity by reducing the pathogen sporulation. Based on the results from this greenhouse experiment, Roberti *et al.*¹⁵⁸ suggested the use of microalgal extracts, after further evaluation, in environmentally friendly disease management.

Zhou *et al.*¹⁵⁹ reported the biocontrol effect of *Nostoc piscinale* SCAU04 and *Anabaena variabilis* SCAU26 against the sheath blight pathogen (*Rhizoctonia solani* Kühn) in rice (cv. Huanghuazhan) under microchamber and micro-area experiments. Diisooctyl adipate, among other cyanobacterial metabolites, had the highest inhibitory effect, and the phytohormone production of salicylic acid, *trans*-zeatin-riboside, and isopentenyl adenine increased several folds. Thus, the biocontrol mechanisms of the selected cyanobacteria against the sheath blight pathogen include the direct inhibitory effect of

biologically active compounds against the fungus, improved production of phytohormones for plant growth and induction of disease resistance, and soil nutrients through N_2 -fixing ability. In another study, Bao *et al.*¹⁶⁰ demonstrated the inhibitory effect of *Anabaena variabilis* SCAU30 against not only the rice sheath blight fungal pathogen (*R. solani* AG-1 IA strain GD-118 by 62–70%) but also bacterial blight pathogen (*Xanthomonas oryzae* pv. *oryzae* CCTCC AB 91122 by 45–50%) in microchamber experiments. In the field experiments (12 m \times 8 m plots with rice variety Yuexiangzhan and 20 m \times 5 m plots with rice variety Gengxiangyou-8), the rice yield increments were 13.90% to 22% due to the combined treatment of *A. variabilis* SCAU30 and 50% topdressing fertilizer, respectively. *A. variabilis* SCAU30 is considered a biofertilizer-biopesticide agent for 'Green Super Rice variety-Huanghuazhan' production under green agriculture and advocated as 'a resource-saving and environmentally friendly agriculture system'.¹⁶¹ More importantly, the field-level evaluation of microalgae or their cellular



extracts is critical for the widespread acceptance of their application as an agronomic practice in green agriculture.

The insecticidal properties of several macro- and microalgae as well as cyanobacteria have been reported and recently reviewed by Asimakis *et al.*¹⁶² The crude ethanolic extracts of a cyanobacterium (*Nostoc carneum*), green algae (*Parachlorella kessleri*, *Ulva intestinalis*, and *Cladophora glomerata*), and stonewort (*Chara vulgaris*) showed insecticidal activity against cotton leafworm (*Spodoptera littoralis*) when treated against the 2nd and 4th instars in the *in vitro* assay.¹⁶³ The ethanolic crude extracts contained an array of saturated and unsaturated fatty acids (particularly polyunsaturated ω -6 linoleic, palmitic, oleic, myristic, α -linolenic, and 7,10-hexadecadienoic acids), essential oils, and phytol and other terpene compounds, and their effects were inhibitory to larval duration, percent pupal formation, pupal duration and weight, moth emergence (%), fecundity and longevity of adults, hatching of eggs, sex ratios, and even larval-pupal-moth malformations. The water- and ethanol-extracts (diluted with distilled water to prepare concentrations of 3%, 5% and 7%) of *Spirulina platensis*, which contained phenolic compounds such as quercetin, kaempferol, resorcinol, and naphthaline, were found to be toxic to the larvae (newly hatched 2nd and 4th instars) of *Spodoptera littoralis*.¹⁶⁴ Earlier studies indicated that microalgal and cyanobacterial extracts may contain toxic metabolites to higher plants.^{165,166} Hence, utilizing microalgal and cyanobacterial resources needs scrutiny against individual crop species and at the field levels. However, these organisms can be a source and inspiration for developing synthetic pesticides, especially their applications in organic or green agriculture.

7. Microalgal forms and cyanobacteria in improving grain yield and yield components

The trait of N₂ fixation has attracted attention from researchers and agronomic utilization of cyanobacterial strains, especially in rice cultivation. The first report was by Fritsch,⁹ who examined the abundance and contributions of cyanobacteria to soil fertility through biological N₂ fixation in paddy fields. The cyanobacterial symbiosis with *Azolla*, a heterosporous pteridophyte, was traditionally used in rice cultivation in China as early as 540 AD.¹⁶⁷ Shukla and Gupta¹⁶⁸ reported that the extract of *Phormidium foveolarum* (Mont.) Gomont when treated with rice seeds (type 21) by pre-soaking for 24 h in 0.5%, 1% and 5% water led to an increase in the total weight of all ears per plant, the weight of a single ear and weight of 1000 grains. Generally, cyanobacterial strains and microalgae are utilized as biostimulants, which are defined as 'certain substances, mixtures, and microorganisms, not as inputs of nutrients, that can stimulate the natural nutrition processes in plants. The use of these products is aimed solely at improving the nutrient use efficiency, tolerance to abiotic stress, and quality traits of plants or increasing the availability of confined nutrients in the soil or rhizosphere, which can act in addition to fertilizers to optimize the efficiency of fertilizers and reduce the nutrient application rates.¹⁶⁹

During the developmental stages of crop growth, the potential of a yield component is determined by environmental and management conditions and the yield components interact to achieve a given yield. For example, yield components such as the number of plant parts (*i.e.*, tillers per unit area or the number of kernels per head) limit yield more than the size of parts such as kernels. In rice, the grain-yield contributing traits include tillering ability, panicle length, and spikelet fertility, when cultivated under dry-direct seeded conditions and those such as plant height, number of primary branches, secondary branches and filled grains per panicle, dominant effects for yield per hill, yield per tiller and 1000 grain weight are associated with rice under submerged conditions, respectively.^{170,171} Generally, higher grain yields of rice can be achieved with increasing numbers of tillers and/or panicles per plant and grain setting rates. In intensive agriculture, applying chemical N fertilizer is the most common practice to increase the yields. Generally, biofertilizers and biostimulants are considered as substitutes for chemical fertilizers. Zhang *et al.*¹⁷² reported that the partial substitution of nitrogenous chemical fertilizers with the N₂-fixing cyanobacterium, *Anabaena azotica* FACHB-119, at 30% and 50% significantly increased the number of tillers and panicles per plant compared to higher substitution rates, where the substitution by 30% sustained the rice yields.

Organic agriculture offers a multitude of environmental and soil health benefits. In Brazil, the use of microalgae is allowed for organic vegetable production. Mógor *et al.*¹⁷³ examined the potential of lyophilized biomass of *Arthrospira platensis* (also known as *Spirulina platensis*) at 1 and 3 g L⁻¹ on the yield gains of organic red beet (*Beta vulgaris*) and found significant increases in hypocotyl diameters and consequent yield gains. In another study, Geries and Elsadany¹⁷⁴ found that the foliar spraying of *Spirulina platensis* 100 and 120 days after transplanting (DAT) and seedling inoculation with endophytic, N₂-fixing *Pseudomonas stutzeri* (10⁸ CFU mL⁻¹) in onion (*Allium cepa* L., var. Giza red), even in the presence of different N doses (100% and 75% of the recommended dose), improved the marketable yield, total bulb yield, bulb weight and diameter, lowest cumulative weight loss percentages of bulbs during storage and reduced the cull weight. On the contrary, Soppelsa *et al.*¹⁷⁵ found that the microalgal extract prepared using *Spirulina* spp. (4.0 g L⁻¹) when applied to strawberry (*Fragaria ananassa* cv. *Elsanta*) as foliar spray from the pre-flowering stage led to lower fruit firmness (-18%).

Faheed *et al.*¹⁷⁶ reported that seeds of lettuce (*Lactuca sativa*) after germination in culture medium containing *Chlorella vulgaris* and the addition of 2 and 3 g dry microalga kg⁻¹ soil significantly increased both the fresh and dry weight of the seedlings. The yield potential in maize (*Zea mays* L.) under the influence of *Spirulina platensis* and *Chlorella vulgaris* was shown to be significant by Dineshkumar *et al.*¹⁷⁷ (Fig. 5). Garcia-Gonzalez and Sommerfeld¹⁷⁸ applied the green algal cellular extracts and dry biomass of *Acutodesmus dimorphus* as a seed primer, foliar spray, and biofertilizer to tomato and evaluated the seed germination, plant growth, and fruit production. Although the experiment was terminated early, the higher fruit



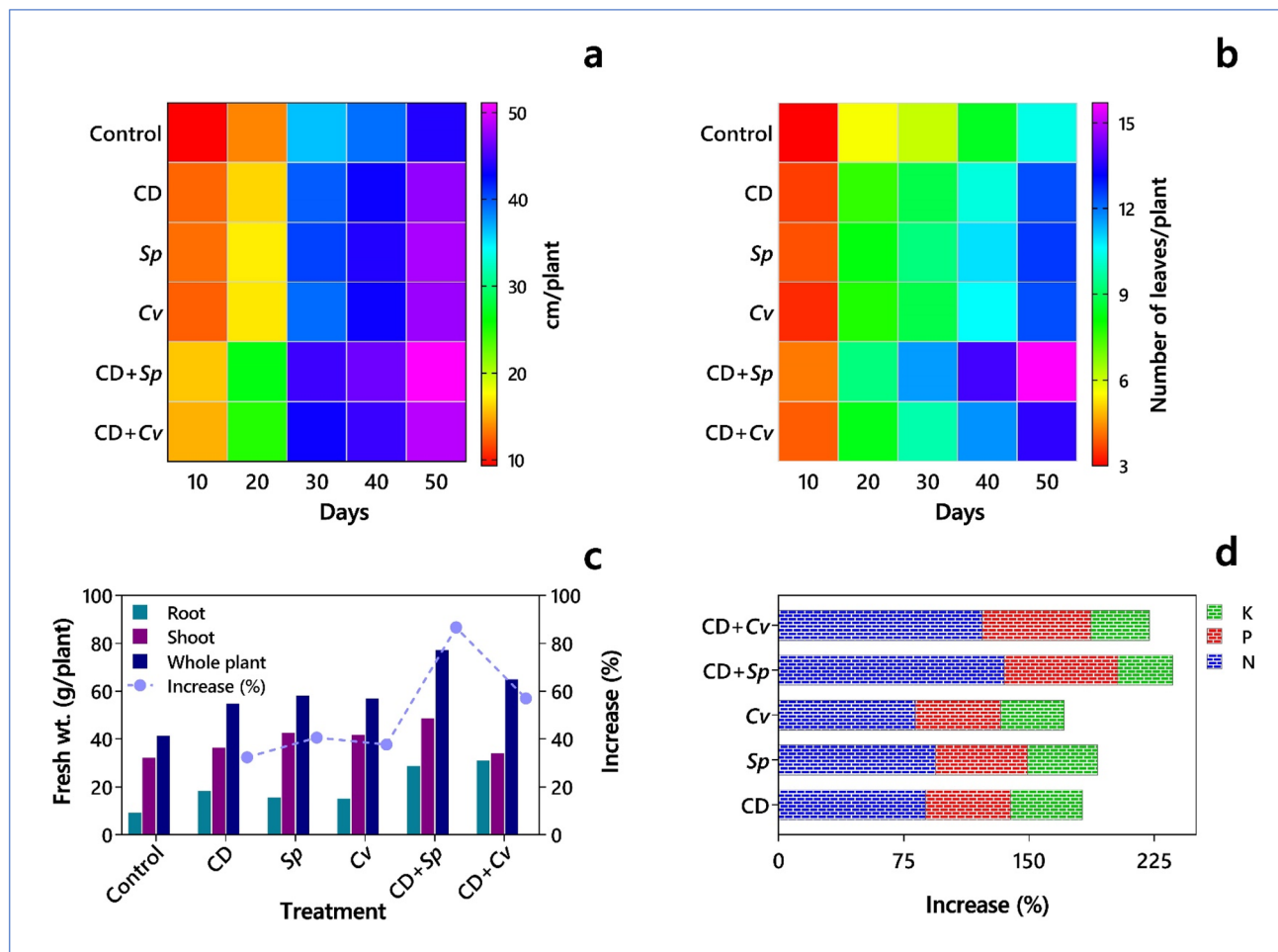


Fig. 5 Impact of microalgae and cyanobacteria on the yield potential of maize (*Zea mays* L.) yield potential (based on data from Dineshkumar *et al.*¹⁷⁷). Impact of *Spirulina platensis* and *Chlorella vulgaris* on (a) shoot length, (b) number of leaves, (c) fresh weight, and (d) nutrient composition in maize plant. CD – Cow dung, Sp – *S. platensis*, and Cv – *C. vulgaris*.

numbers suggested the likely effectiveness of 100 g biofertilizer 22 days before transplant. Presently, there is renewed interest in microalgae for improving global food security. Vigani *et al.*¹⁷⁹ proposed that the strategies adopted by the European Union entitled 'Innovating for Sustainable Growth: A Bioeconomy for Europe'¹⁸⁰ and 'Microalgae-based Products for the Food and Feed Sector: An Outlook for Europe',¹⁸¹ and their scientific and technological capacity can be employed to prepare novel microalgae-based products for foreign markets, leading to the strategic acquisitions of foreign companies. Biotechnological innovations can improve microalgal productivity and utilize waste and cheaper substrates to reduce production costs.

8. Microalgae and cyanobacteria in biosequestration of soil organic carbon (SOC)

C-containing compounds, also present in the complex organic material of soil, are a critical component of soil organic matter (SOM). The SOC is primarily from the fixation of atmospheric

CO₂ by photosynthetic higher plants and microorganisms. Globally, the stock of SOC in the top 1 m and 3 m soil profiles is about 1500–2400 Pg C (1 Pg = 1 Gt) and 2300 Pg C, respectively.¹⁸² Because of land cultivation (*i.e.*, about 45% of global soils), arable soils contribute more to agricultural greenhouse gas emissions than that under permanent crops and pastures. Given that all living forms are C-based, soil biodiversity is critical to many ecosystem functions, including C cycling, which occurs over long- and short-term time scales, ranging from a few minutes to a few billion years. The SOC, which is captured, sequestered, and mineralized by microorganisms and an indicator of soil health, significantly contributes to food production, mitigation, and adaptation to climate change. Intensive land management and the vast degraded land areas warrant efforts to improve future C storage, the capacity of soil to buffer against climate change events, and the resilience of agricultural food production systems. The most crucial constraint with aggressive targets for soil C sequestration is the requirement of N to maintain the C : N stoichiometry in soils. In general, agricultural soils have about C : N at the ratio of 10–12. Then, about 100



million tons of N is required to increase 4 billion tons of CO₂ annually.¹⁸³ Any synthetic chemical N fertilizer application will increase nitrous oxide emissions, another highly potent greenhouse gas from soils. Hence, many 'best management practices' and 'frontier technologies' for which many technological and economic barriers need to be overcome are being evaluated worldwide to enhance the soil C sequestration potential in the long-term. The biological negative emission (BNE) strategies involving management practices that can regulate the biotic processes for improved soil C balance in the long-term have gained significance. In the present context, reducing atmospheric CO₂ with almost no enhanced emission of nitrous oxide due to the fertilizer application is desirable.¹⁸¹

Among the 'best management practices', reduced tillage or 'no-till' can improve the soil C capture, sequestration, and storage, depending on the soil texture, type and the prevailing climate. Navarro-Noya *et al.*¹⁸⁴ reported that tillage practice affected the relative abundance of Actinobacteria, β -Proteobacteria, and α -Proteobacteria more, while that of Bacteroidetes, β -Proteobacteria, Cyanobacteria, and Gemmatimonadetes was

affected by residue management. Both edaphic cyanobacteria and microalgae can improve the soil aggregate stability by producing exopolymeric matrices and enmeshing filamentous microbiota over aggregates, improving the soil C sequestration.¹⁸⁵ Haiming *et al.*¹⁸⁶ showed that even short-term tillage managements influenced the soil autotrophic bacterial community in the double-cropping rice fields. There have been several surprises regarding cyanobacterial clades from phylogenetic studies although they are the most studied aerobic and phototrophic microorganisms. Recently, two new clades (*i.e.*, 4C0d-2 (Melainabacteria) and ML635J-21 (Sericytochromatia)) with chemoheterotrophic and fermentative metabolisms were proposed.^{5,187} Cano-Diaz *et al.*¹⁸⁸ showed the environmental preferences of different cyanobacterial clades from a field survey and co-occurrence network analysis. The members of the photosynthetic Oxyphotobacteria-dominated cluster were abundant in arid and semi-arid areas, while that of non-photosynthetic Sericytochromatia- and Melainabacteria-dominated clusters are in hyper-arid oligotrophic and acidic/humid environments, respectively. Recently, Larsson *et al.*¹⁸⁹

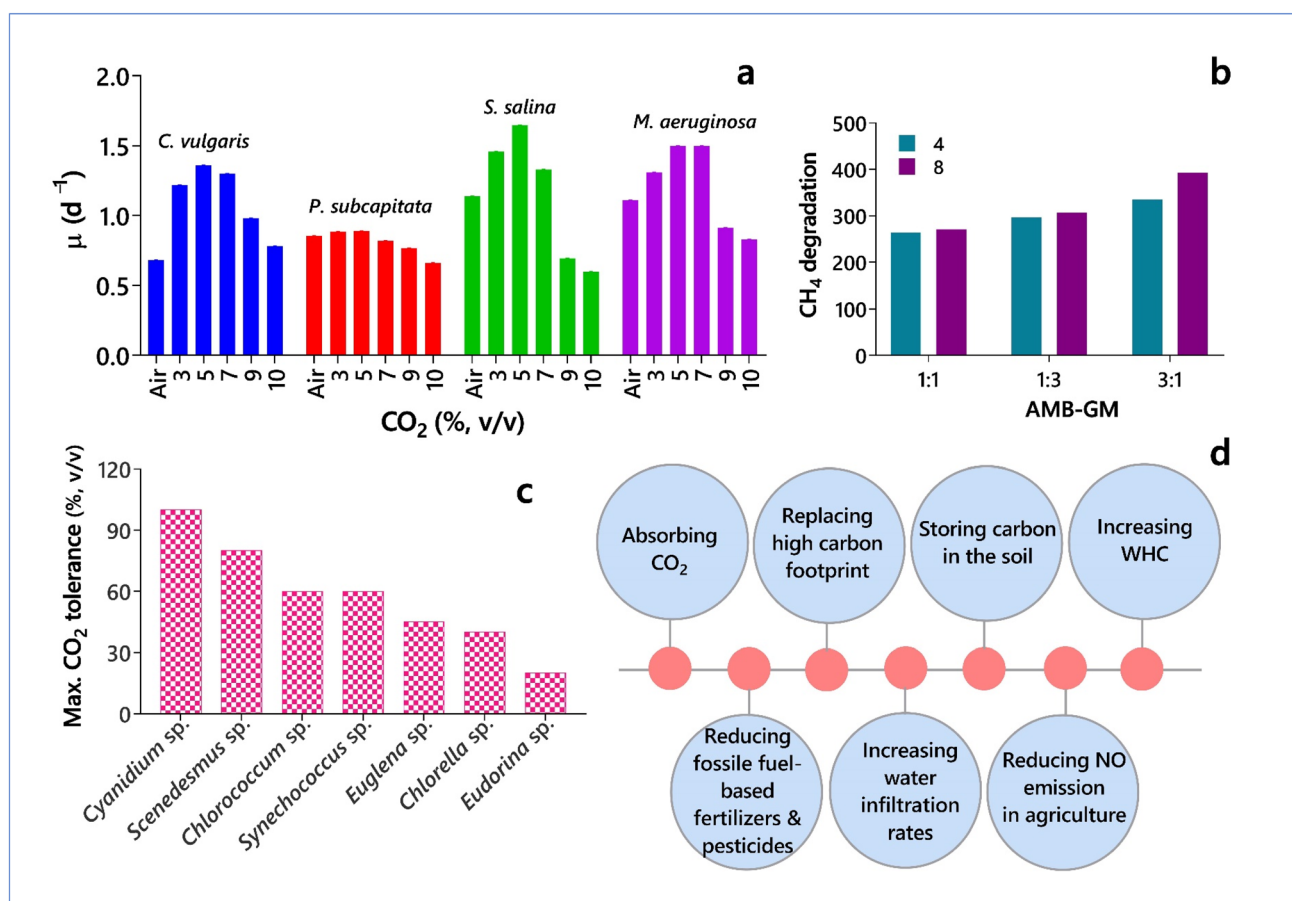


Fig. 6 (a) Specific growth rates of microalgae (*Chlorella vulgaris* and *Pseudokirchneriella subcapitata*) and cyanobacteria (*Synechocystis salina* and *Microcystis aeruginosa*) at different levels of CO₂ (based on data from Gonçalves *et al.*¹⁹³). (b) Methane degradation rate (mg CH₄ g_{biomass}⁻¹ day⁻¹) by the coculture of an alkaliphilic methanotrophic bacteria consortium (AMB) and green microalga (GM) *Scenedesmus obtusiusculus* at different methane concentrations (4% and 8%) (based on data from Ruiz-Ruiz *et al.*¹⁹⁴). (c) Maximum CO₂ tolerance by different microalgal species (based on data from Onyeaka *et al.*¹⁹¹). (d) Climate resilience and mitigation by microalgae and cyanobacteria (based on data from Nichols²⁴).



demonstrated the involvement of mixotrophic protists capable of both phototrophy and phago-heterotrophy in the production of C-rich ‘mucospheres’ in disproportionately contributing to the vertical flux in the ocean C cycling. In soils, the mixotrophic and fermentative metabolisms of cyanobacteria associated with C cycling have been overlooked to date. Besides the agronomic application of N₂-fixing and plant bio-stimulatory cyanobacteria, the utilization of CO₂-fixing (photosynthetic) cyanobacteria warrants attention and future research to improve the soil C sequestration.

In arid and semi-arid environments, bacteria, cyanobacteria, or their combination collected from the biological soil crusts and inoculated into the soils were found to have higher potential for C sequestration.¹²⁴ The sequestered C increased from 0.232 to 0.294 g m⁻² days⁻¹, and when scaled up, it could increase from 0.84 to 1.07 ton ha⁻¹ year⁻¹, equivalent to the atmospheric CO₂ removal of 3.11 to 3.93 ton ha⁻¹ year⁻¹. The addition of biochar is one of the options among the ‘frontier technologies for soil C sequestration.’¹⁸³ The C capture by photosynthesis in microalgae is more efficient than by higher plants due to the presence of active bicarbonate pumps, which can elevate the internal concentrations of CO₂ and inhibit photorespiration. Earlier, Sayre¹⁹⁰ suggested three strategies for algal C capture and sequestration, as follows: (i) permanent burial of total fresh biomass, (ii) permanent burial of algal lipids, and (iii) soil amendment with algal biochar, each having some advantages and liabilities as well. Algal biochar can sequester about 50% of C present in biomass. Many microalgal species, including *Endornia* sp., *Chlorella* sp., *Euglena gracilis*, *Chlorococcum littorale*, *Scenedesmus* sp., and *Cyanidium caldarium* can tolerate CO₂ up to the level of 20% to 100% (v/v).¹⁹¹ The successful implementation of microalgae-based C capture and sequestration requires many improvements and innovations and the application of biorefinery principles. Earlier, Beal *et al.*¹⁹² evaluated the techno-economic and life-cycle assessment of an integrated 2800 ha production facility of algae with bioenergy carbon capture and storage (ABECCS). They reported the financial break-even achieved for algal biomass, sold as fishmeal replacement for US\$ 1400 per ton with a \$ 68 per ton carbon credit and as soybean replacement for \$ 600 per ton with a \$ 278 per ton C credit. Thus, ABECCS can sustainably reduce atmospheric CO₂ with economic, energetic, and environmental benefits.¹⁹² In a recent report, Jassey *et al.*⁹¹ showed that soil algal capture about 3.60 Pg C annually, corresponding to about 6% of the net primary production of terrestrial vegetation (Table 2). Although certain species of eukaryotic microalgae and cyanobacteria have been identified as potential agents in soil C capture, sequestration, and storage (Fig. 6), the biodiversity and global implications of these organisms demand more research efforts and the development of technological opportunities.

9. Algalization of soils: successes and limitations

‘Algalization’ which was referred earlier to the process of cyanobacterial application as biofertilizer in rice fields can include

microalgal species or their products as plant biostimulants.¹⁹⁵ The potential of the microalgae- and cyanobacteria-based products has been evaluated at various levels, more often by researchers. Recently, Abinandan *et al.*¹⁹⁶ demonstrated that algalization of two acid soils with *Desmodesmus* sp. MAS1 and *Heterochlorella* sp. MAS3 significantly enriched bacteria belonging to rhizobacteria and diazotrophs such as *Acetobacter*, *Azospirillum*, *Bradyrhizobium*, *Gluconacetobacter*, *Nitrobacter*, *Burkholderia*, *Comamonas*, *Herbaspirillum*, *Enterobacter*, *Nitrosococcus*, *Brevibacillus*, *Enterococcus*, *Frankia*, and *Anabaena*, which are largely implicated in promoting soil health and plant growth. Successful field-scale algalization has been reported in a few states in India and in other countries such as China, Egypt, Vietnam, and the Philippines.^{13,101,197} Although the agronomic importance of algae has been known since the 1900s, the commercial production of algal biofertilizers or biostimulants is in its infancy. Interestingly, several microalgal species are cultured and produced as human health food and nutraceuticals, animal/aquaculture feed, and feed additives in the industries. As human food and animal feed, *Spirulina* (*Arthrospira platensis*) has been collected as the blue-colored ‘techuitlats’ and as ‘dihe’ and eaten by the Aztecs living in the valley of Mexico and the Kanembu people along the shore of Lake Chad, respectively, for centuries.^{198,199} The industrial production of this well-known microalgal product only commenced in man-made ponds in 1978.²⁰⁰ Similarly, the first commercial production of *Chlorella*, marketed as a health food product for immune stimulation, reducing blood lipids, and treating gastric ulcers, wounds, and constipation, was by the Nihon *Chlorella* in Taiwan during the 1960s.²⁰¹ In a recent report, Beal *et al.*¹⁹² suggested that the sustainability of global fisheries and aquaculture can be improved by the commercial production of microalgal products as a replacement for fishmeal and fish oil. Their proposed model of establishing and deploying about 100 facilities (based on microalgal production in Hawaii, each of 111 ha with a hybrid system of photobioreactors and raceway ponds for the cultivation of *Desmodesmus* sp.) can replace all the domestic production of fishmeal in Thailand.

Many algal products are produced from low-tech farming (harvesting from the wild or simple man-made structures of ponds and tanks, *i.e.*, ‘open’ systems) and high-tech bioprocess engineering industries (using fermenters and photobioreactors, *i.e.*, ‘closed’ systems).^{202,203} The need for light, relatively slow growth rate, the requirements for temperature, C, oxygen, source and supply of nutrients, selection of strains suitable either for out-door cultivation or in bioreactors, the capital-intensive bioreactors, and the contaminants and diseases of both the ‘open’ and ‘closed’ systems continue to be significant challenges in scaling up and realizing the potential of microalgae, especially from laboratory to land applications. Besides understanding the foundations of good science, skilled and experienced personnel are required to produce high value bio-products or biomass of microalgal species. Most commercially successful companies have chosen high-priced products, either metabolites or whole cells of microalgae.

The agronomic applications of cyanobacteria as bio-fertilizers for improved N₂ fixation and/or microalgae as biostimulants depend largely on their commercial production. In



the global market, the popular biofertilizers with N₂-fixing ability are Cell-Tech, Nitragin Gold, TagTeam, Mamezo, R-Processing seeds and Hyper Coating seeds from Novozymes and Tokachi Federation of Agricultural Cooperatives, respectively, and the popular genera used for production are *Bradyrhizobium*, *Sinorhizobium*, *Azorhizobium*, *Mesorhizobium*, and *Allorhizobium* (www.mordorintelligence.com). The global biofertilizers market is predicted to have a CAGR of 12.10% during the period 2022–2028. In fact, the market projection exclusively for microalgae during 2020–2028 is expected to have a CAGR of 5.40%. In addition, the global area under organic farming will increase to more than 75 million ha during this period. In this case, increased awareness, environmental benefits, and government policies can make the commercial production of biofertilizers and biostimulants including microalgae more relevant. To date, the regional and national markets, especially in India, have more rhizobacteria-based products than phototrophs-based products. The increases in crop yields due to biofertilization compared to uninoculated crops remain insufficient to motivate farmers and industrialists to utilize microalgal resources. According to the global meta-analysis, Schütz *et al.*²⁰⁴ showed that the yield responses due to biofertilization by microbial inoculants ranged from 6.10% to 21.70%, with better responses in the areas under dry climate, followed by that under tropical climate. The soil P concentration, organic matter content, and pH are also important determinants of the yield responses due to microbial inoculation. These limiting factors and inconsistencies due to climate variabilities thwart the efforts of governments, industries, and farming communities to rely on biofertilizers and biostimulants for yield increments. However, the environmental benefits of CO₂ sequestration by microalgae can now provide the necessary impetus for their commercial production. More importantly, the collective benefits from the metabolism of C, N, and oxygen of phototrophic inoculants, in addition to their bio-stimulatory effects on crop yields, need better agronomic- and environmental auditing. Furthermore, the benefit-to-harm ratio of microalgal applications needs to be considered, especially during their long-term usage. Compared to microalgae, certain species of cyanobacteria can produce toxic metabolites known as cyanotoxins. These cyanotoxins are hepatotoxins (*i.e.*, microcystins, nodularins and cylindrospermopsins) and neurotoxins such as anatoxin-a, saxitoxins, and beta-N-methylamino-L-alanine. These toxins, of which microcystins have been examined the most, can inhibit germination and plant growth, and accumulate in plants, adversely affecting other micro- and macroorganisms, and eventually entering the food web of soils.²⁰⁵ Future studies should examine the genomic potential for all the traits of microalgae, including those related to the production of toxins and antimicrobial compounds.

10. Future perspectives

There are many challenges related to the technological advances for agricultural applications and environmental benefits from microalgae and cyanobacteria, beginning with

taxonomic identification, evaluation of genomic potential and functional capabilities, and availability of authentic cultures. The conventional phenotype-based classification of algae has several limitations, in addition to modern taxonomy, guided by the rRNA relationships inferred from the DNA sequences associated with different subunits. Both Park *et al.*²² and Parks *et al.*²⁰⁶ proposed the Genome Taxonomy Database (GTDB; <http://gtdb.ecogenomic.org>, a normalized genome-based phylogenetic framework) based on the phylogenetic inferences from the concatenation of ubiquitous, single-copy proteins (covering about 254 090 bacterial and 4316 archaeal genomes and metagenome-assembled or single-cell genomes of uncultured members). In addition, there is a proposal of the suffix -ota to denote phyla.²⁰⁷ These considerations have led to a new proposal on cyanobacteria. Presently, the phylum Cyanobacteriota encompasses three classes: (i) *Cyanobacteria* (previously called *Oxyphotobacteria* – all oxygenic phototrophs), (ii) *Vampirovibrionia* (replacing the Candidatus name *Melainabacteria*) and Candidatus *Sericytochromatia*.²⁰⁸ Interestingly, *Vampirovibrio chlorellavorus*, the first cultured representative of Candidatus *Melainabacteria* is an obligate predator of *Chlorella vulgaris*.²⁰⁹ Similar to the difficulties associated with the identification of cyanobacteria, the systematic process for identifying eukaryotic microalgal strains requires curated databases on the DNA barcodes and repositories.²¹⁰ These advances in microalgal taxonomy present a major disadvantage, where all the described cultures need renaming and revision of their classification. However, the chief opportunity of polyphasic, molecular taxonomic methods is the inclusion of uncultured microalgae (such as the representatives of Metagenome-Assembled Genomes, MAGs) in our understanding. The genomic and metagenomic elucidation of culturable and uncultured cyanobacterial and microalgal lineages will help to re-evaluate their diversity, distribution, and ecological functions.

The primary and high-order endosymbiosis and the diversification of many eukaryotic photosynthetic lineages strongly suggest the global ecological importance of microalgae and demand greater appreciation for their conservation and avoiding the disruption of the evolution of eukaryotes. Nevertheless, the benefits of microalgal evolutionary developments are difficult to account for in monetary terms. Recently, Altman and Mesoudi²¹¹ showed how plant genes (*e.g.*, domestication) coevolve with human agricultural activities by applying frameworks and concepts such as Gene-Culture Coevolution (GCC), Niche Construction (NC), and Cumulative Cultural Evolution (CCE). Similar investigations are necessary for the soil microbiomes of agro ecosystems to gain insights into the potential and limitations of soil C sequestration, atmospheric N₂ fixation, and oxygen cycling in the rhizospheres. Earlier, Thrall *et al.*²¹² also proposed the need for applying the evolutionary approaches to the management of pests and pathogens (biotic interactions) in agroecosystems.

Microbial culture collections are critical in understanding the metabolic lifestyles and genome characteristics of individual organisms. Globally, the microbial culture collections of 146 centers situated in 51 countries have about 67 812 and 61



421 plant-associated strains and those of soil origin, respectively (<https://gcm.wdcm.org>). Hirose *et al.*⁹⁴ noted that there are only about major 15 culture collections that maintain about 7000 cyanobacterial strains. The British Phycological Society reported that algal culture collections are necessary to 'generate solutions to societal challenges by stimulating interaction between academia and bioindustry' (<https://brphycesoc.org/algal-culture-collections-in-the-omics-age/>).

The transformation of 'energy to matter' is important in living soils, which are central to most agricultural activities.²¹³ Recently, Gunina and Kuzyakov²¹⁴ provided an experiment-based review on the soil microbial communities using organics as the source of energy, not as a source of C. Hence, the plant litter and rhizodeposition are sources of energy, rather than sources of C, in most soil microbial communities. This hypothesis strengthens the importance of phototrophic microorganisms in the C cycling processes of soils. There is also a strong need to understand the ecological roles of nitrogenases present in N₂-fixing prokaryotes. Oehlmann and Rebelein²¹⁵ reviewed the 'side reactivities' of three isozymes of nitrogenases (Mo-, V- and Fe-only) for the reduction of carbon monoxide (highest activity by V nitrogenase) and CO₂ (highest activity by Fe-only nitrogenase). The cyanobacterial members also possess genes coding for the structural components of V-nitrogenase.¹⁰¹ Hence, the nitrogenases and alternative nitrogenases (V- and Fe-only) of the N₂-fixing cyanobacteria warrant future research on their ecological significance in the soil N and C cycling processes.

Heterotrophic bacteria can promote the growth of cyanobacteria, for example, *Pannonibacter* sp. and *Chryseobacterium* sp. had a positive effect on the growth of *Microcystis aeruginosa* FACHB-905.³⁴ Earlier, Borowitzka and Vonshak²⁰³ suggested that the microbiome (bacterial flora associated with microalga) could be the causal agent for the collapse of large-scale heterotrophic algal cultures under stressed and poorly mixed systems. Presently, we know that *Vampirovibrio chlorellavorus* is a cyanobacterial obligate predator of *Chlorella vulgaris*.²⁰⁹ Thus, the inadequacies in culture collections, inconsistencies and changing taxonomic assignments, and limited innovations in commercial production pose serious challenges to their utilization in agriculture. More importantly, the commercial production of microalgae for agricultural applications will remain difficult to achieve if profitability is limited to yield increments and contemporary monetary gains.

11. Conclusions

Microalgae and cyanobacteria are effective in improving the nutrient contents, structure, and fertility of soils. Several microalgal species are selected based on traits, such as the fixation of carbon dioxide and dinitrogen and phosphorus cycling, which are beneficial to plants. However, their potential to ameliorate drylands and saline and sodic soils is yet to gain widespread acceptance. Similarly, their biocontrol properties and potential to improve the yield and yield components and the biosequestration of soil organic carbon demand more research efforts and technological innovations. The benefit-to-

harm ratio of microalgal applications needs to be considered based on their genomic potential, especially during their long-term application. Nevertheless, the new hope for utilizing these microalgal resources in agriculture is their abundance, which is underestimated by the present-day culture-based methods and improved understanding of their evolutionary benefits and their ecological services. Future work should improve their pure-culture collections, understand their metabolic lifestyles, examine their ecological roles, know their evolutionary significance, advance new knowledge and create awareness among the farming communities and policymakers.

Author contributions

B. R.: writing-original draft, investigation, and data curation. N. R. M.: visualization and writing-original draft. K. V.: conceptualization, writing-review & editing, and supervision. M. M.: conceptualization, data curation, resources, validation, writing review & editing, and supervision.

Conflicts of interest

There are no conflicts to declare.

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