Cyanobacterial Contributions on Agriculture– A Review

Abstract :

Purpose: This paper reviews the diverse agricultural applications of cyanobacteria for improving soil health, plant growth, and agricultural sustainability.

Research Method: The paper provides a literature review summarizing recent research on cyanobacteria's roles in soil aggregation, biofertilization, abiotic/biotic stress tolerance, yield improvements, carbon sequestration, and bioremediation. Both laboratory studies and field trials evaluating cyanobacteria's effects on soil properties and plant growth are discussed.

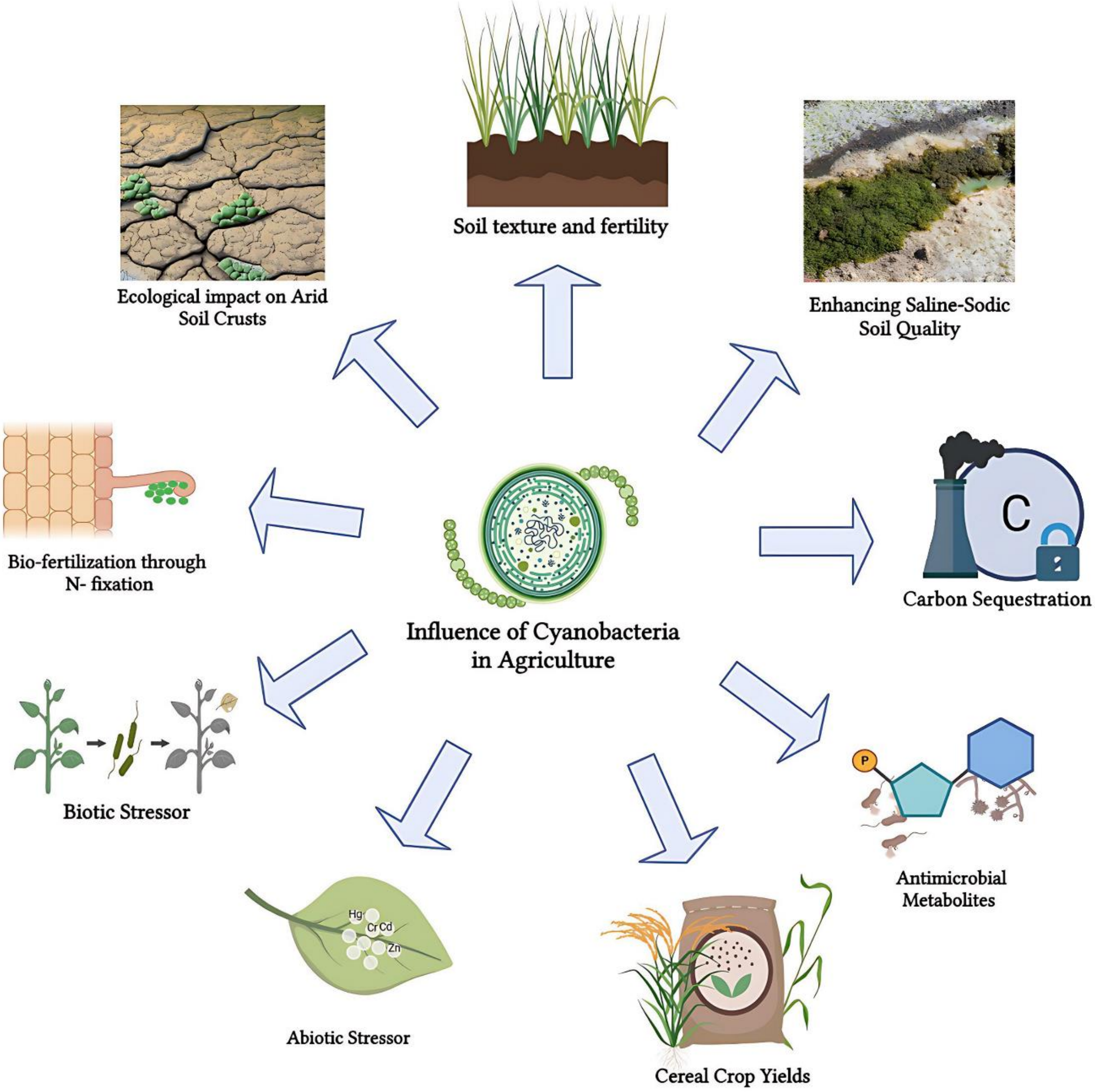
Findings: Cyanobacteria can enhance soil structure, provide fixed nitrogen, mitigate salinity stress, increase crop yields, and sequester carbon. Their stress adaptations, antimicrobial metabolites, and synergies with plants and microbes underpin many benefits. However, translating laboratory research into effective field inoculants remains challenging.

Research Limitation: Variability in effectiveness across cyanobacterial strains, plant species, and environments limits current understanding. More field testing is needed along with assessment of potentially negative impacts.

Originality/Value: This review highlights promising areas for cyanobacteria to promote agricultural sustainability while identifying knowledge gaps in genetics, plant-microbe interactions, and soil ecology that require further study. It emphasizes the need for locally-adapted, integrated solutions leveraging cyanobacteria's multifunctional traits.

Keywords: Cyanobacteria, Agriculture, Soil health, Biofertilizer, Bioremediation

GRAPHICAL ABSTRACT:



1. INTRODUCTION

Agriculture plays a pivotal role in sustaining human life and ensuring food security for the growing global population. It is a scientific practice that involves cultivating plants and rearing animals for various purposes, such as producing food, fibre, and raw materials for industries. The importance of agriculture lies in its ability to provide nourishment, support economic development, and contribute to the overall well-being of societies. Through the application of scientific methods and advancements, agriculture has the potential to optimize crop yields, enhance livestock productivity, and mitigate environmental impacts, making it an indispensable field of study and practice.

Cyanobacteria, historically characterized as proficient oxygenic phototrophs, adeptly employ photosynthesis to convert atmospheric CO_2 and water into organic compounds (Ward *et al.,* 2011). Recent revelations have unveiled novel cyanobacterial lineages marked by the absence of genes linked to photosynthesis and CO_2 fixation mechanisms (Di Rienzi *et al.,* 2013; Soo *et al.,* 2014). Prominent among these non-photosynthetic cyanobacterial groups are 4C0d-2 and ML635J-21, delineated through the assembly of metagenomic genomes (Soo *et al.,* 2014; Soo *et al.,* 2019).

Cyanobacteria wield ecological significance across diverse ecosystems, spanning aquatic and terrestrial realms. Their propensity for symbiotic associations with various organisms including bryophytes, fungi, and Azolla underscores their ecological importance (Rai *et al.,* 2000). Within terrestrial landscapes, particularly in biological soil crusts, cyanobacteria occupy a pivotal role in shaping soil structure and influencing nutrient dynamics. Certain filamentous cyanobacteria produce extracellular polymeric substances that foster soil particle aggregation and enhance stability (Chamizo *et al.,* 2018). Notably, specific cyanobacterial strains, such as Nostoc and Anabaena, have been harnessed as biofertilizers, particularly in rice cultivation, leveraging their nitrogen-fixing abilities to mitigate reliance on conventional nitrogen fertilizers (De, 1939; Zhang *et al.,* 2021).

Cyanobacteria have also demonstrated adaptive mechanisms for salinity stress, exemplified by their active expulsion of sodium ions and efficient transport of potassium ions (Singh *et al.,* 2022). This adaptability has incited explorations into their potential applicability for remediating saline-affected soils. Additionally, the nexus between cyanobacterial filaments and oxygenic photosynthesis has been associated with prospective soil organic carbon sequestration, bearing implications for ecosystem carbon dynamics (Crouzet *et al.,* 2019).

The exploration of non-photosynthetic cyanobacterial lineages presents an evolving domain necessitating comprehensive investigation concerning their roles in carbon and nitrogen cycling processes (Soo *et al.,* 2017). nevertheless, knowledge gaps persist, spanning cyanobacterial diversity, taxonomy, ecological functions, and mechanistic insights (Hirose *et al.,* 2021). Addressing these gaps entails expanding culture collections and conducting comprehensive genomic analyses encompassing both cultivated and uncultured cyanobacterial cohorts (Fawley & Fawley, 2020).

2. SOIL TEXTURE AND FERTILITY

Cyanobacteria play a major role in improving soil structure and fertility. They act as ecological engineers that can modulate ecological processes in the soil and create habitats for other organisms (Jones *et al.,* 1994). The type of crust that forms on the soil surface depends on the amount of moisture present. Cyanobacteria are the first organisms to establish biological soil crusts in arid environments. As the crusts develop, other organisms may also thrive in them.

The addition of cyanobacteria under laboratory and field conditions has resulted in significant improvements in soil structure and aggregate stability (Wang *et al.,* 2009; Park *et al.,* 2017; Mugnai *et al.,* 2018). Cyanobacteria improve soil aggregate stability by producing filaments and extracellular secretions that act as binding agents (Mazor *et al.,* 1996). Chamizo et al. (2018) inoculated two cyanobacterial species, the non-N2-fixing *Phormidium ambiguum* and the N2-fixing *Scytonema javanicum*, into different textured soils. After 90 days, cyanobacterial inoculation led to increased total exopolysaccharide content and soil penetration resistance with *P. ambiguum*, while total organic carbon and nitrogen contents increased with *S. javanicum*. The filaments and extracellular polysaccharides of cyanobacteria act as gluing agents to bind soil particles for enhanced aggregate formation (Chamizo *et al.,* 2018).

Cyanobacterization, or soil inoculation with cyanobacteria, is effective for stabilizing burned soils and restoring post-fire ecosystems (Chamizo *et al.,* 2019; Muñoz-Rojas *et al.,* 2021). Recently, Shantakumar et al. (2021) showed inoculation of acid soils with acid-tolerant cyanobacteria species led to improved soil aggregate stability. The cyanobacteria tested were able to decrease soil pH through organic acid production, as well as increase exopolysaccharide content which aids in soil aggregation (Shantakumar *et al.,* 2021). Cyanobacteria can establish symbiotic relationships with bryophytes, fungi, Azolla, and Gunnera due to their ability to form heterocysts and hormogonia (Rai *et al.,* 2000). Heterocysts are specialized N2-fixing cells that provide microoxic conditions for the oxygen-sensitive nitrogenase enzyme. Hormogonia are short mobile filaments that allow dispersal and colonization of new environments. The only angiosperm that can form symbiotic relationships with cyanobacteria is Gunnera (Rai *et al.,* 2000). This is likely because Gunnera stem glands provide an anaerobic environment suited for the oxygen-sensitive nitrogenase enzyme of cyanobacteria.

Cyanobacteria are a dominant group in biological soil crusts, where they contribute to soil fertility and structure (Büdel *et al.,* 2016). Cyanobacterial diversity varies in crusts depending on factors like crust age, soil texture, climate, and geography. Common cyanobacteria in biocrusts include Microcoleus, Chroococcidiopsis, Nostoc, Scytonema, Phormidium, Oscillatoria, and Nostoc (Büdel *et al.,* 2016). The filamentous forms aid in soil binding and aggregation. Other physiological adaptions also allow crust cyanobacteria to survive in dry, high light conditions. The filaments and extracellular matrices of edaphic cyanobacteria improve soil aggregate stability by binding soil microbiota and particles over aggregates (Crouzet *et al.,* 2019). The exopolysaccharide sheath surrounding cyanobacterial filaments helps maintain soil moisture as well as protects cells from desiccation. Cyanobacteria synthesize specialized UV-absorbing pigments like scytonemin and mycosporine-like amino acids to shield from high irradiation in biological crusts (Lu *et al.,* 2022).

3. BIO-FERTLIZATION THROUGH NITROGEN FIXATION.

Cyanobacteria are able to fix atmospheric nitrogen (N_2) through spatial segregation of nitrogenase in heterocysts and temporal separation of N_2 fixation at night (Boyd & Peters, 2013). This ability has led to their use as biofertilizers, especially in flooded rice paddies (De, 1939). The enzyme nitrogenase is highly sensitive to oxygen, so cyanobacteria have evolved mechanisms to protect it and separate oxygenic photosynthesis from N_2 fixation (Boyd & Peters, 2013). These include upregulating N_2 fixation at night when oxygen levels are lower, and differentiation of heterocysts that have thicker cell walls and lack photosystem II to maintain an anaerobic cellular environment.

In rice fields, cyanobacterial biofertilizers can fix 25-30 kg of N ha/season/(Prasanna *et al.,* 2015). The symbiotic Azolla-Anabaena system can contribute 20-40 kg N ha-1 to rice crops in about 25 days (Roger & Ladha, 1992). *Anabaena azollae* is the N_2-fixing cyanobacterium that lives in leaf cavities of the aquatic fern Azolla. The cyanobacteria receive carbon from the Azolla host while providing fixed nitrogen. This symbiotic association allows *Azolla* to grow rapidly and accumulate high levels of nitrogen (Kellar & Goldman 1979). The steps for mass producing cyanobacterial biofertilizers for applications in rice cultivation in India have been established, with inoculum containing Aulosira, Nostoc, Anabaena, and Tolypothrix (Chittora *et al.,* 2020). Aulosira, Nostoc and Anabaena are common filamentous, heterocystous cyanobacteria used in rice agriculture.

The cyanobacterium *Anabaena azotica* can partially substitute nitrogen fertilizers in rice fields by 30-50% while sustaining yields (Zhang *et al.,* 2021). *Anabaena azotica* is a heterocystous, filamentous cyanobacterium capable of providing significant amounts of biologically fixed nitrogen. Replacing a portion of chemical nitrogen fertilizers with this organism can reduce costs and environmental impacts while maintaining crop productivity. Cyanobacteria solubilize phosphates to a limited extent. They can sequester phosphorus as polyphosphates to mitigate stress (Mukherjee *et al.,* 2015). Polyphosphate metabolism allows cyanobacteria to accumulate and store phosphorus when it is available in excess, and then utilize it for growth during phosphorus starvation conditions. This adaptation helps cyanobacteria thrive in soils and waters where phosphorus levels fluctuate.

Cyanobacteria are mostly used as phototrophic plant biostimulants that provide fixed carbon, nitrogen, and phytohormones to promote plant growth (Santini *et al.,* 2021). However, high inoculum rates and need for frequent irrigation hinder direct applications of cyanobacteria for soil conditioning (Metting & Rayburn, 1983). Their agronomic applications as biofertilizers or bio-stimulants depend largely on successful commercial production. Mass culturing cyanobacteria can be challenging due to their relatively slow growth compared to other microbes. Contamination issues also commonly impact large-scale cyanobacterial cultivation intended for agricultural uses (Borowitzka, 1999).

4. ECOLOGICAL IMPACT ON ARID SOIL CRUSTS

Biological soil crusts containing cyanobacteria are abundant in arid and semi-arid environments, where they play a major role in improving soil structure, fertility, hydrology, and C and N fixation (Belnap *et al.,* 2016). Crusts dominate ground cover in drylands across about 35% of the Earth’s land surface (Smith *et al.,* 2019).Filamentous cyanobacteria like Microcoleus contribute to soil stabilization in crusts by producing extracellular matrices that bind and glue together soil particles (Büdel *et al.,* 2016). Microcoleus produces copious amounts of exopolysaccharides that aid in soil aggregation and moisture retention. The filamentous morphology also facilitates binding of soil particles (Rossi *et al.,* 2017).

Other common crust cyanobacteria are *Chroococcidiopsis, Nostoc, Scytonema, Phormidium, Oscillatoria*, and *Nostoc* (Büdel *et al.,* 2016). Chroococcidiopsis, in particular, has remarkable adaptions to survive extreme aridity. It has a multilayered, highly melanized cell wall and the ability to enter long-term dormancy (Caiola & Billi, 2007). Nostoc and Scytonema can fix N_2 in crusts, while *Oscillatoria* contributes to C cycling. Inoculation of cyanobacteria from biological crusts into soils can increase carbon and nitrogen fixation, thereby improving fertility in arid lands (Kheirfam & Roohi, 2020). For example, inoculation of *Nostoc commune* into degrade soils significantly increased total nitrogen and organic carbon content compared to uninoculated soils (Roncero-Ramos *et al.,* 2019). The added C and N from cyanobacteria improve conditions for plant establishment.

Cyanobacteria-based biocrusts have potential for restoring degraded drylands and mitigating desertification (Gholamhosseinian *et al.,* 2021; Wang *et al.,* 2022). Biocrusts can be cultivated on-site then inoculated into degraded soils to kickstart ecological succession (Ayuso *et al.,* 2016). They improve fertility and provide microbial community structure lacking in eroded desert soils.Zhou and Zhang (2012) showed artificially cultivated biocrusts increased water runoff efficiency and reduced runoff sediment. Biocrusts can be used as green materials for rainwater harvesting in dry environments (Zhou & Zhang, 2012). The complex matrices formed by cyanobacterial exopolysaccharides absorb water like a sponge, capturing rainfall and reducing erosion (Rossi *et al.,* 2017).

Cyanobacteria in crusts possess various survival strategies to thrive in arid conditions, including synthesis of protective pigments and compounds, secretion of extracellular polysaccharides, and formation of microbial consortia (Lu *et al.,* 2022). To survive prolonged desiccation, crust cyanobacteria produce trehalose, a disaccharide sugar that helps preserve membranes and proteins (Harel *et al.,* 2015). Specialized UV-absorbing pigments like scytonemin and mycosporine-like amino acids shield cells from high irradiation (Xu *et al.,* 2022). Exopolysaccharides also aid in moisture retention (Bhunia *et al.,* 2018).

5. ENHANCING SALINE-SODIC SOIL QUALITY

Cyanobacteria can tolerate and even thrive in saline and sodic soils due to various physiological adaptions. They possess salinity sensing and signaling mechanisms as well as tolerance mechanisms to cope with the adverse effects of high salinity (Singh *et al.,* 2022). Some key adaptions include active sodium efflux to prevent toxic accumulation, potassium transport systems to maintain homeostasis, production of organic osmolytes for osmotic balance, and modulation of enzymes to maintain metabolism under salt stress (Singh *et al.,* 2022).

Certain cyanobacteria strains can decrease the electrical conductivity, pH, and exchangeable sodium content in saline-sodic soils. Kaushik and Subhasini (1985) showed algalization with Anabaena spp. lowered these parameters. The ameliorative effect is attributed to active photosynthesis-driven sodium extrusion, based on radiotracer studies using 22Na and 24Na (Thomas, 1977). However, the ability to mobilize calcium for exchanging with sodium is likely needed for effective remediation of degraded alkali soils (Rao & Burns, 1991).

Pandey et al. (2005) found the alkali-tolerant cyanobacterium *Nostoc calcicola* was prevalent in the sodic soils of India. Further, its bicarbonate-resistant mutant strain was more effective than the wild type in decreasing soil pH in laboratory incubations (Pandey *et al.,* 2005; Jaiswal *et al.,* 2010). Bicarbonate toxicity is a key constraint in sodic soils, so bicarbonate-tolerant strains have potential for bio-amelioration (Jaiswal *et al.,* 2010). The cyanobacterium *Hapalosiphon fontinalis* decreased pH, electrical conductivity, and exchangeable sodium percentage (ESP) in salinesoils (Singh &Dhar2010). White cotton mealybug numbers were also reduced by 68% after H. fontinalis treatment due to changes in physicochemical properties. This demonstrates the bio-ameliorative and biocontrol potential of cyanobacteria.

Co-cultures of cyanobacteria with other microbes have shown promise as bio-remediating inoculants for salt-affected soils (Li *et al.,* 2019). Cyanobacteria can stimulate plant responses that mitigate salinity stress and maintain ion homeostasis (Brito *et al.,* 2022). However, the priming benefits depend on the plant and cyanobacterial species as well as growth conditions (Brito *et al.,* 2022). Overall, lab and field evaluation of cyanobacterial strains native to target saline-sodic soils will be important for developing effective microbial amelioration techniques. Their safety for crops over the long-term should also be assessed. Technological advances are needed to scale up preparation of cyanobacterial inoculum to restore large, severely degraded areas (Li *et al.,* 2019).

6. BUILDING RESISTANCE TO ABIOTIC STRESSORS

Soil salinization is a significant agricultural challenge affecting approximately 20% of irrigated lands worldwide. Cyanobacteria offer a promising solution to enhance salt tolerance in crops such as rice, wheat, and millet through various mechanisms, including nitrogen fixation, the release of extracellular polysaccharides, compatible solutes, plant hormones, and antioxidative enzymes (Abbas *et al.,* 2015; Gheda & Ahmed 2015; Li et al. 2019). For instance, the inoculation of rice with halotolerant cyanobacteria like Nostoc calcicola, N. linkia, and Anabaena variabilis has been shown to increase root length, seedling growth, and grain yield under saline conditions by improving soil nitrogen content and biological activity (Hassan et al. 2018; Jan et al. 2017).

Similarly, a consortium of *Nostoc ellipsosporum* and *N. punctiforme* has demonstrated improvements in the physical structure, nutrient status, and microbial activity of salt-affected soils, leading to enhanced millet and wheat growth (Nisha et al. 2018). *Anabaena sphaerica* and *Scytonema hofmanni* contribute to salt tolerance in rice and wheat by regulating osmolytes and antioxidants through the production of exopolysaccharides and plant hormones (Kharwar *et al.,* 2022; Rodriguez et al. 2006).

In addition to salinity stress, cyanobacteria also play a vital role in enhancing drought tolerance in plants. Inoculation with Microcoleus sp. and Nostoc sp. has been shown to promote seed germination and seedling establishment, particularly in water-deficit conditions, benefiting dryland restoration efforts (Muñoz-Rojas et al. 2018). Furthermore, *Spirulina meneghiniana* and *Anabaena oryzae* have been found to increase lettuce growth under limited moisture conditions by modulating plant antioxidants and osmolytes (Ibraheem 2007).

Cyanobacteria exhibit impressive capabilities in heavy metal remediation by efficiently removing toxic heavy metals such as Cd, Cr, Cu, and Zn from contaminated soils. Species like *Anabaena variabilis, Nostoc muscorum, Aulosira fertilissima*, and *Tolypothrix tenuis* have been instrumental in reducing the levels of these metals in soils amended with coal fly ash (Kaur & Goyal 2018). *Oscillatoria* sp. and *Synechocystis* sp. have been successful in increasing wheat tolerance to Cr by decreasing bioavailable metal fractions (Faisal et al. 2005). Additionally, Spirulina platensis has been effective in restricting Cd translocation and enhancing antioxidants in maize grown in Cd-contaminated soils (Seifikalhor et al. 2019).

Another crucial application of cyanobacteria lies in pesticide detoxification, where they can degrade or sequester pesticides, including organophosphates, organochlorines, and herbicides, in both soil and water bodies, thus reducing their phytotoxicity. Fischerella sp. and Scytonema hofmanni have been known to mitigate the toxicity of methyl parathion by utilizing it as a phosphate source (Tiwari et al. 2017). Synechocystis sp. and Phormidium sp. have effectively bioabsorbed the neonicotinoid imidacloprid from soils (Aminfarzaneh & Duygu 2010). Furthermore, the inoculation of Spirulina platensis has induced protective amino acids in bean plants, counteracting the effects of the herbicide fusilade (Osman et al. 2016).

Innovative approaches are emerging, such as plant genetic engineering using cyanobacterial genes, to develop stress-resilient crops. For example, transforming poplar with a heat shock protein

(HSP70) gene from the halotolerant *Aphanothece halophytica* has resulted in increased tolerance to salinity, drought, and extreme temperatures (Takabe et al. 2008). Similarly, Arabidopsis lines expressing a water stress protein (WSPA1) from Nostoc commune have exhibited improved performance under saline conditions (Ai et al. 2014). Overexpression of Anabaena flavodoxin genes has enhanced tolerance against drought, heat, salinity, and oxidative stress in tobacco, creeping bentgrass, and alfalfa by modulating antioxidants and stress proteins (Tognetti et al. 2006; Li et al. 2017; Coba de la Peña et al. 2010).

7. BUILDING RESISTANCE TO BIOTIC STRESSORS

Cyanobacteria offer valuable properties for agricultural applications, including antibacterial activity against crop pathogens like *Pseudomonas aeruginosa*, *Ralstonia solanacearum*, and *R. syzygii*. For instance, research has shown that Spirulina platensis, *Nostoc sp*., and *Stigonema sp*. filtrates can inhibit the growth of *P. aeruginosa* by releasing bioactive substances such as fatty acids, norharmane, and 4,4'-dihydroxybiphenyl (Abedin & Taha 2008; Catarina Guedes et al. 2011; Volk & Furkert 2006). Cell extracts of *Anabaena flos-aquae* have also demonstrated potent antibacterial effects against the potato brown rot pathogen *R. solanacearum* (Mikhail et al. 2016). Moreover, indigenous rhizospheric cyanobacteria isolated from chili fields have shown promising biocontrol capabilities against chili bacterial wilt caused by *R. syzygii* (Yanti et al. 2019).

Cyanobacteria are also known for their antifungal properties, as they produce secondary metabolites, enzymes, and volatiles that combat phytopathogens like Fusarium, Alternaria, Aspergillus, and Botrytis in various crops, including rice, tomato, lupine, and maize. Methanolic extracts of *Nostoc commune*, for example, effectively inhibit the mycelial growth of these fungi (Kim 2006). Anabaena variabilis has been found to reduce Fusarium wilt in tomatoes by releasing antifungal fatty acids and lipopeptides (Chaudhary et al. 2012). Additionally, cyanobacteria produce chitinase enzymes that suppress fungi like *Fusarium oxysporum* and *Macrophomina phaseolina* (Gupta et al. 2012; Afify & Ashour 2018). They also stimulate plant systemic resistance against foliar fungal pathogens by priming defense enzyme activity (Attia et al. 2017).

Furthermore, cyanobacteria exhibit nematicidal activity through cell-free extracts, effectively targeting plant-parasitic nematodes like Meloidogyne, Heterodera, and Rotylenchulus species by inhibiting mobility, egg hatching, and juvenile mortality (Holajjer et al. 2012; Chandel 2009). They enhance host plant tolerance by triggering systemic resistance pathways mediated by salicylic acid and jasmonic acid signaling (Sharaf et al. 2016).

In terms of pest control, cyanobacterial strains produce insecticidal metabolites toxic to crop pests such as cotton bollworm, Colorado potato beetle, and rice stem borer. Crude extracts of Nostoc sp. have demonstrated larvicidal activity against cotton bollworm *Helicoverpa armigera* (Biondi et al. 2004). Toxins derived from *Anabaena variabilis* and *Synechococcus leopoliensis* have been found to inhibit the feeding behavior of the Colorado potato beetle *Leptinotarsa decemlineata* on potato foliage (Gol'din 2012). Additionally, *Anabaena oryzae*, *A. cylindrica*, and *Nostoc muscorum* have shown field control of rice whorl maggot and stem borer by inducing systemic resistance against insects (Yanni & Abdallah 1990).

Lastly, cyanobacterial genes have been employed in plant genetic engineering to create transgenic plants with enhanced resistance to biotic stress. For example, rice lines expressing insecticidal Bacillus thuringiensis cry genes, along with promoters and 5'-UTRs from *Anabaena sp*., have exhibited improved resistance against lepidopteran pests (Datta et al. 1998). Similarly, the expression of osmotin, a PR-5 family protein from the halotolerant *Aphanothece halophytica,* has conferred transgenic tobacco with resistance to fungal pathogens such as *Phytophthora parasitica, Alternaria alternata*, and *Botrytis cinerea* (Safdar *et al.,* 2013)

8. ANTIMICROBIAL METABOLITES FOR PLANT DISEASE CONTROL

Cyanobacteria produce a diverse array of bioactive metabolites that can inhibit fungal and bacterial phytopathogens (Kulik, 1995). Crude extracts prepared from cyanobacteria using various organic solvents have shown antifungal activity against *Aspergillus, Fusarium, Sclerotinia, Rhizoctonia, Pythium* and other pathogens (Righini *et al.,* 2022). Cyanobacterial strains such as *Anabaena, Nostoc, Hapalosiphon, Scytonema, Tolypothrix,* and *Fischerella* produce antifungal alkaloids, lipopeptides, polyketides, and other compounds (Demay *et al.,* 2019;Swain *et al.,* 2017; Svirčev *et al.,* 2016).

The antifungal metabolites from cyanobacteria act through mechanisms such as disruption of membrane integrity, inhibition of respiration, interference with cell division, and deprivation of nutrients. These multiple modes of action can prevent development of resistance in fungal pathogens (Shishido *et al.,* 2015). Cyanobacteria also have antibacterial properties attributed to peptides, fatty acids, and phenolic compounds which disrupt membranes, inhibit enzymes, and interfere with metabolism in bacteria (Alsenani *et al.,* 2020).

Application of live cyanobacterial cells or their extracts can induce systemic resistance against pathogens in plants. *Anabaena* extracts triggered defense enzyme activity in zucchini leaves, leading to reduced powdery mildew severity (Roberti *et al.,* 2015). Foliar sprays of *Nostoc piscinale* and *Anabaena variabilis* suppressed rice sheath blight caused by *Rhizoctonia solani* via induced phytohormones and antifungal metabolites (Zhou *et al.,* 2020). Combining biocontrol traits with N_2-fixing ability gives multifunctional benefits to these bio-inoculants (Bao *et al.,* 2021).

However, cyanobacteria can also produce toxins which may limit their utilization for plant disease control. The cyanotoxins microcystins and nodularin are potential public health hazards if they accumulate in produce or leach into water sources (Nowruzi *et al.,* 2021). Further studies are needed under field conditions along with safety and risk assessments before widespread adoption of cyanobacteria as biofungicides or antibacterials.

9. INFLUENCE ON CEREAL CROP YIELDS

Cyanobacteria have a long history of use in rice paddy agriculture to enhance soil fertility, provide fixed nitrogen, and ultimately increase yields. In early studies, cyanobacterial inoculation was found to increase rice grain weight and the number of productive tillers per plant (Shukla & Gupta, 1967; Singh, 1961). These positive effects result largely from biological nitrogen fixation by heterocystous genera like Nostoc and Anabaena.

Modern research has focused on integrating cyanobacteria into integrated nutrient management systems for rice. *Anabaena azotica* was able to substitute 30-50% of urea nitrogen without compromising grain yields when applied along with 50% of the recommended mineral fertilizer (Zhang *et al.,* 2021). The cyanobacteria provided between 22-39 kg ha^{-1} of nitrogen based on the substitution rate.

Cyanobacteria also influence rice yield components like tillers per hill and filled grains per panicle (Begum *et al.,* 2011). Inoculation with *Nostoc muscorum* increased tiller production, grains per panicle, and straw yield of rice over uninoculated controls (Abou Elatta *et al.,* 2019). Combining cyanobacteria with plant growth-promoting bacteria can further improve yield attributes and productivity (Prasanna *et al.,* 2008). Seed biopriming with cyanobacteria shows potential to enhance germination, seedling vigor and subsequent growth and yields of rice (Sharma *et al.,* 2020).

Cyanobacteria supply growth-promoting substances and mobilize nutrients like zinc in the rhizosphere, which translate to better crop performance (Prasanna *et al.,* 2015). However, the effectiveness varies based on the cyanobacterial strain, plant genotype, and environmental conditions (Sharma *et al.,* 2020).

While cyanobacteria contribute to soil fertility and plant nutrition, their ability to decrease incidence of diseases like bacterial leaf blight and sheath blight also contributes to enhanced productivity in rice systems (Bao *et al.,* 2021). Both biofertilization and biocontrol traits make them well-suited to sustainable agriculture approaches. However, maintaining cultures and scaling production remain challenges for widespread application to cereal crops like rice and wheat.

10. TERRESTRIAL CARBON SEQUESTRATION

Cyanobacteria contribute to terrestrial carbon cycling through oxygenic photosynthesis, carbon fixation, and incorporation into soil organic matter. Their natural abundance in agricultural soils and ability to fix CO_2 make cyanobacteria potential organisms for enhancing soil carbon sequestration. The filamentous morphology of many cyanobacteria also aids in soil particle aggregation, which physically protects organic carbon from decomposition (Chen *et al.,* 2014). Incorporation of cyanobacterial biomass directly contributes carbon to the soil, while their oxygenic photosynthesis creates aerobic conditions that slow C mineralization by heterotrophs (Rajeev *et al.,* 2013). Cyanobacteria grown on agricultural waste substrates can provide a carbon-negative source of biofertilizer (Chatterjee *et al.,* 2017). Photosynthetic activity further reduces CO_2 levels in the rhizosphere, thus the cyanobacteria act as a carbon sink (Sheikh *et al.,* 2018).

Biological soil crusts rich in cyanobacteria increase total organic carbon and carbon sequestration rates in arid soils (Li *et al.,* 2022). While non-photosynthetic bacteria dominate the rhizosphere, cyanobacteria occupy soil microsites at the surface where they contribute significantly to C fixation (Zhang *et al.,* 2018). Their Carbon inputs are protected from decomposition by soil aggregates (Darrouzet-Nardi *et al.,* 2015).

Cyanobacteria genetically engineered to overexpress inorganic carbon uptake systems could further optimize CO_2 sequestration in soils (Gupta *et al.,* 2013). However, there are still challenges translating laboratory studies to effective field application for enhancing soil C storage. Maintaining cyanobacterial inoculants in soils requires adequate light, moisture, temperature, and nutrients. Better understanding synergies between cyanobacteria, plants and heterotrophic microbes that accelerate soil Carbon sequestration is also needed (Gao *et al.,* 2021).

11. PROGRESS AND LIMITATIONS

Algalization refers to the application of algae or cyanobacteria as inoculants to improve soil health and plant growth. Cyanobacteria have a long history of use as algalizers in flooded rice systems to provide biofertilization. Traditional practice in parts of Asia involves inoculating rice paddies with native cyanobacteria from genera such as *Nostoc, Anabaena, Aulosira*, and *Tolypothrix* (Prasanna& Nayak2007).

Cyanobacterial inoculation forms algal mats on the water surface that can contribute 25-30 kg N ha−1 and increase rice yields 10-24% (De, 1939; Singh, 1961). Coating rice seeds with cyanobacteria before sowing stimulates germination, plant growth, and grain yield (Taubaev *et al.,* 1970). The exopolysaccharides of cyanobacteria also improve soil structure and fertility (Renuka *et al.,* 2018). However, the efficacy of cyanobacteria-based algalization depends on species selection, rice cultivar, temperature, water, soil nutrients, and other conditions (Yanni, 1991; Vaishampayan *et al.,* 1998). Contamination, limited shelf life of inoculum, and variability in field performance currently constrain more widespread adoption (Herrmann& Lesueur, 2013). Scaling up production of cyanobacteria is challenging compared to fungal and bacterial biofertilizers.

Targeted uses of cyanobacterial algalizers show potential improvements in area such as salt-affected soils, degraded drylands, and cold deserts (Thomas, 1977; Singh& Dhar2010). Cyanobacteria inoculation was found to increase soil organic carbon, total nitrogen, and aggregation in the desert soils (Muñoz-Rojas *et al.,* 2018; Román *et al.,* 2018). However, field testing is still limited. Cyanobacteria also face competition from other microorganisms in the rhizosphere. Integrating cyanobacteria with plant growth-promoting bacteria or fungi may improve colonization and effectiveness (Nain *et al.,* 2010; Orozco-Mosqueda *et al.,* 2018). Further innovations are needed to make algalization an affordable and reliable means of improving soil health and crop yields.

12. FUTURE PROSPECTS FOR AGRICULTURAL APPLICATIONS

Cyanobacteria have potential to enhance agricultural sustainability and soil resilience through pathways like carbon sequestration, nitrogen fixation, and bioremediation. However, much remains unknown regarding their taxonomy, phylogeny, genomics, and ecology in soil systems (Hirose *et al.,* 2021). Advancing fundamental knowledge should be a priority for directing applied research and biotechnological innovations (Shih *et al.,* 2013). Culture-independent techniques have revealed new cyanobacterial clades and expanded phylogenetic diversity (Di Rienzi *et al.,* 2013; Soo *et al.,* 2017). Further sampling of under-studied environments combined with genomes and metagenomes will likely uncover novel cyanobacteria relevant to agriculture (Lumian *et al.,* 2022). The stressful conditions cyanobacteria endure in soils and their adaptions merit more study (Gr *et al.,* 2021).

Elucidating Cyanobacteria -plant-microbe interactions is also crucial (Rodríguez *et al.,* 2022). Cyanobacteria influence soil microbiomes through organic matter input, oxygenation, nutrient alterations, and bioactive compounds (Gupta *et al.,* 2021; Nowruzi *et al.,* 2021). However, we have limited knowledge of these complex dynamics in the rhizosphere and effects on plant health (Rodríguez *et al.,* 2022). Potential negative impacts like cyanotoxins or competition with crops require investigation (Nowruzi *et al.,* 2021). Advances in cultivation techniques, formulation, stabilization, and delivery systems are essential for translating laboratory research into effective cyanobacterial inoculants. Most agricultural applications have involved commonly studied genera, while bioprospecting novel strains may reveal enhanced traits. Finally, stakeholders like farmers, industries, policymakers, and consumers should be engaged to develop integrated, scalable solutions using cyanobacteria to sustain food production and ecosystem services (Vigani *et al.,* 2015).

13. CYANOBACTERIAL APPLICATIONS IN THE PHYTOREMEDIATION OF CONTAMINATED FIELDS

Cyanobacteria exhibit inherent tolerance mechanisms that enable their survival in environments contaminated with heavy metals and organic pollutants, rendering them promising candidates for phytoremediation processes (Thevarajah *et al.,* 2022). These microorganisms possess the capacity to accumulate heavy metals such as Cd, Cr, Ni, Zn, As, and Pb via extracellular sequestration, efflux systems, and intracellular chelation (Mehta & Gaur, 2005). Noteworthy genera like *Phormidium, Microcoleus, Nostoc, Anabaena,* and *Oscillatoria* have demonstrated resistance to chromium and significant bioremediation potential (Yadav *et al.,* 2021).

In the realm of organic pollutant degradation, specific strains of cyanobacteria have undergone genetic modification to facilitate the breakdown of pollutants. Solvent-tolerant species like *Synechocystis* and *Synechococcus* have been engineered to degrade organic contaminants (Kuritz & Wolk, 1995). A synergistic approach involves integrating metal-resistant cyanobacteria with aquatic plants in wetland systems, offering a viable strategy for the phytoremediation of metal-contaminated water bodies (Li *et al.,* 2020).

Furthermore, cyanobacteria-derived bio-surfactants, such as microcolin, exhibit promise in solubilizing and degrading petroleum hydrocarbons, thereby serving a crucial role in oil spill bioremediation efforts (Najafi *et al.,* 2010). Despite their diverse detoxification capabilities, comprehensive large-scale field studies are imperative to fully comprehend the efficacy and feasibility of utilizing cyanobacteria for phytoremediation purposes. Ongoing advancements in genetic engineering and synthetic biology hold the potential to further enhance the biodegradation capacities of cyanobacteria.

14. CONCLUSION

Cyanobacteria offer immense opportunities to improve agricultural sustainability through bio-fertilization, bioremediation, disease control, and carbon sequestration. However, knowledge gaps around genetics, plant-microbe interactions, and soil ecology must be addressed to direct applied research. Advancing cultivation techniques and field delivery methods is vital for developing effective cyanobacterial inoculants. With innovations in biotechnology and soil management, cyanobacteria could reduce agrochemical reliance, improve stress resilience, restore degraded lands, and sustain productivity. However, effectiveness varies based on strain, plant species, and agro-climatic conditions. Realizing their potential requires cross-disciplinary engagement and locally-adapted solutions to strengthen climate resilience, soil health, and productivity. Further research on genetics, plant interactions, field performance, stress mechanisms and formulations can help utilize cyanobacteria's full potential for sustainable agriculture.

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