

Plant-cyanobacteria interactions: Beneficial and harmful effects of cyanobacterial bioactive compounds on soil-plant systems and subsequent risk to animal and human health

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ABSTRACT

Plant-cyanobacteria interactions occur in different ways and at many different levels, both beneficial and harmful. Plant-cyanobacteria interactions, as a beneficial symbiosis, have long been demonstrated in rice-growing areas (Poaceae) where the most efficient nitrogen-fixing cyanobacteria are present in paddies. Moreover, cyanobacteria may in turn produce and/or secrete numerous bioactive compounds that have plant growth-promoting abilities or that may make the plant more resistant to abiotic or biotic stress. In recent years, there has been a growing worldwide interest in the use of cyanobacterial biomass as biofertilizers to replace chemical fertilizers, in part to overcome increasing organic-farming demands. However, the potential presence of harmful cyanotoxins has delayed the use of such cyanobacterial biomass, which can be found in large quantities in freshwater ecosystems around the world. In this review, we describe the existing evidence for the positive benefit of plant-cyanobacteria interactions and discuss the use of cyanobacterial biomass as biofertilizers and its growing worldwide interest. Although mass cyanobacterial blooms and scums are a current and emerging threat to the degradation of ecosystems and to animal and human health, they may serve as a source of numerous bioactive compounds with multiple positive effects that could be of use as an alternative to chemical fertilizers in the context of sustainable development.

1. Introduction

Cyanobacteria, also known as blue-green algae, are one of the most diverse group of prokaryotes whose adaptive capacity along with the ability to tolerate extreme conditions makes them ubiquitous in aquatic (Kumar and Singh, 2017) and terrestrial environments (Tamaru et al., 2005). They are also found in extreme habitats such as glacial environments in polar and alpine regions (Zakhia et al., 2008). In marine and freshwater ecosystems, they are commonly found in pelagic (Elliott, 2012), benthic (Scott and Marcarelli, 2012) and symbiotic (Lesser et al., 2004) communities. Eutrophication through increased nutrient runoff from agriculture and pollution from industrial operations associated with climate change often leads to blooms of pelagic freshwater cyanobacteria, some of which can be extremely harmful (Paerl et al., 2001).

Frequent cyanobacterial blooms in these eutrophic waters produce a variety of toxins such as microcystins (MCs), anatoxin-a, cylindrospermopsins, and saxitoxins that exert further harm on ecosystems and to animal and human health (Nowruzi and Porzani, 2021; Rajabpour et al., 2019). However, the presence of these cyanotoxins in irrigation water of edible plants could inhibit their growth (Corbel et al., 2015a, 2015b, 2015c; Jubilee et al., 2010; Kos et al., 1995; Saqrane et al., 2008). Furthermore, these cyanotoxins could pose a threat to human health by indirect exposure through bioaccumulation in the tissues of irrigated plants (Bittencourt-Oliveira et al., 2014; Corbel et al., 2014; Liu et al., 2014; Nowruzi et al., 2020a,b). In addition to cyanotoxins, a few metabolites synthesized and released by cyanobacteria can also have allelopathic properties that may affect phytoplanktonic organisms and aquatic plants (Leao et al., 2009; Žak and Kosakowska,

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2016).

In soil environments, cyanobacteria are found in benthic communities (Scott and Marcarelli, 2012) and in symbiotic associations with plants (Lesser et al., 2004), the formation of which is beneficial for both the plant and its symbiont, the cyanobacterium. The latter ensures fixation of diazotrophic nitrogen into organic forms to support plant growth and the plant constitutes a unique habitat with specific physicochemical factors for its cyanobacterial partner. The most efficient nitrogen-fixing cyanobacteria present in rice-growing (Poaceae) areas include *Nostoc linckia* (Nostocaceae), *Dolichospermum variabilis* (Aphanizomenonaceae), *Aulosira fertilissima* (Nostocaceae), *Calothrix* sp. (Rivulariaceae), *Tolypothrix* sp. (Tolypothrichaceae), and *Scytonema* sp. (Scytonemataceae) (Prasad and Prasad, 2001). Moreover, cyanobacteria can produce various bioactive compounds that can influence plant growth and production (Buenaventura and Barrientos, 2019; Colla and Rouphael, 2020; Múnera-Porras et al., 2020; Sivalingam and Delfe, 2019), including gibberellins, auxins, cytokinin, ethylene and abscisic acid (Manickavelu et al., 2006; Metting and Pyne, 1986), and have been documented as improving growth and productivity in plants such as *Daucus carota* (Wake et al., 1992), *Santalum album* (Bapat et al., 1996), *Oryza sativa* (De Cano et al., 2003; Zaccaro et al., 2002) and *Lilium alexandrae* Hort (Zaccaro et al., 2006). In addition to their being plant symbionts, some species of cyanobacteria belonging to the genera *Dolichospermum* (Aphanizomenonaceae) and *Nostoc* (Nostocaceae) can also survive on the surface of soil and rocks, fixing up to 20–25 kg/ha of atmospheric nitrogen, and enrich soils in organic matter (Moore, 1969). Therefore, nitrogen-fixing cyanobacteria and plants could replace inorganic artificial fertilizers (Godlewska et al., 2019; Hegazi et al., 2010), that can cause eutrophication in aquatic ecosystems, thus limiting the proliferation of toxic cyanobacteria. Moreover, the use of dried cyanobacterial biomass as an inoculum, as opposed to introduction via irrigation, that act as biofertilizers is considered to improve soil chemical characteristics such as the mineral status of deteriorated soils (Singh et al., 2016a), including phosphorus and potassium contents, that play a major indirect role in plant growth promotion (Aly et al., 2008; Selvarani, 1983). According to a conservative estimate, the microalgal biomass market comprises about 5000 t y^{-1} (dw) equating to ca. US\$ $1.25 \times 10^9 \text{ y}^{-1}$ (Pulz and Gross, 2004). However, statistics on the cyanobacterial-based market are missing, mostly dominated by cyanobacterial specialized metabolites (Nowruzi and Porzani, 2021). Over the last 20 years, excess nitrogen inputs from agricultural fertilizers and/or domestic and industrial effluents, as well as climate change, have dramatically increased the global occurrence of cyanobacterial blooms, including cyanotoxin-containing blooms, which are active against metazoans that can affect plant health (Paerl et al., 2001). Therefore, cyanobacteria play a vital role in enhancing growth and development of plants, the mineral enrichment of soils and releasing various bioactive metabolites that protect against biotic and abiotic stress. Increasingly, evidence has accumulated on the production of bioactive compounds by cyanobacteria which can affect host plant gene expression, leading to qualitative and quantitative changes in the phytochemical composition of the latter (Liaimer et al., 2016). Although, most of these laboratory studies have been performed in greenhouses, field trials are necessary to confirm these findings.

The potential activities of compounds present in cyanobacteria are varied and can be present within and exterior to the cell (extracellular), through transportation and/or lysing of the cyanobacterial cell or filament. Cyanobacterial bioactive compounds can be harmful (cyanotoxins) or beneficial (e.g. phyto- and plant hormones). Those bioactive compounds which have activity in biological systems, can be present as pure compounds or as a component of extracts, and can have both positive or negative effects on plant growth and reproduction, with negative effects largely considered to be due to the presence of toxic compounds (e.g. cyanotoxins). Positive bioactive aspects include regulation of plant growth (phytoregulation; plant hormones), biostimulatory effects, stimulating natural processes to benefit nutrient

uptake, use and efficiency to improve crop quality or biofortification activities, whereby the nutritional quality of crops is improved through agronomic practices. Furthermore, compounds purified from or present in cyanobacterial extracts using aqueous or organic solvents may be categorized as having more than one of these properties, in addition to being beneficial or deleterious to plants. In this review, we highlight positive plant-cyanobacteria interactions with particular emphasis on the potential effects of cyanobacteria and their bioactive metabolites as natural biofertilizers of soils and as plant growth regulators. In addition, their negative effects, such as phytotoxicity and bioaccumulation of cyanotoxins in terrestrial plants, including associated health risks are highlighted.

2. Cyanobacterial bioactive compounds and their role in improving soil fertility and crop productivity

Cyanobacteria are increasingly applied as biofertilizers for improving soil and crop productivity (Singh et al., 2016b). Besides adding organic nitrogen and balancing mineral nutrition in the soil, cyanobacteria are known to synthesize and release various biologically active products such as phytohormones (auxins, gibberellins, cytokinins), polypeptides, amino acids, vitamins, polysaccharides, siderophores, and other specialized metabolites after death and decomposition (Karthikeyan et al., 2009; Maqubela et al., 2009; Nowruzi et al., 2013a; Řezanka et al., 2018; Singh et al., 2016b; Singh, 2014; Vaishampayan et al., 2001). These bioactive substances affect the expression of many genes in host plants and thus can stimulate plant growth and help fight against biotic and abiotic stress.

2.1. Cyanobacteria as biofertilizers

Filamentous cyanobacteria such as *Nostoc* and *Anabaena* (Nostocaceae) are some of the most common genera in plant growth-promoting rhizobacteria (PGPR) ((Prasanna et al., 2013a; Prasanna et al., 2016a; Saadatnia and Riahi, 2009; Singha, 2009; Swarnalakshmi et al., 2013). These diazotrophic heterocystous cyanobacteria can have good agronomic efficiency and utility regarding nutrient management of wheat (Poaceae) crops because they can create associations with vascular/non-vascular plants and produce growth-promoting substances (Karthikeyan et al., 2007). For example, the genus *Nostoc* (Nostocaceae) is present in agricultural soils and can form symbiotic relationships with gymnosperms (e.g. *cycads*; Cycadaceae) and angiosperms (e.g. *Gunnera*; Gunneraceae) (Bergman, 2002), allowing the cyanobacteria to supply the plant with nitrogen, using nitrogenases to enzymatically fix the atmospheric nitrogen as ammonia (Meeks and Elhai, 2002). The organic nitrogen forms are then assimilated by the host plant, allowing it to grow in nitrogen-deficient soils, without the need to supply expensive nitrogen fertilizers which are often a source of pollution (Li et al., 2019). Moreover, the cyanobacterial species *Anabaena variabilis* Kütz (Nostocaceae) stimulated the growth and development of two plants *Helianthus annuus* L. (Asteraceae) and *Vitis vinifera* (Vitaceae) and also intensified selected metabolic processes (Pszczółkowski et al., 2012). The use of cyanobacterial species *Anabaena* sp. (Nostocaceae) and *Calothrix* sp. (Rivulariaceae) together with the Gram-negative chemoheterotrophic bacterium *Providencia* sp. (Morganeliaceae) is a good example of the potential for biofortification of wheat (Poaceae) by increasing growth and micronutrient uptake and their translocation to grains (Rana et al., 2012, 2015).

Other heterocystous and non-heterocystous cyanobacterial genera such as *Cylindrospermum* (Nostocaceae), *Synechococcus* (Synechococaceae), *Aulosira* (Nostocaceae), *Scytonema* (Scytonemataceae), *Gloeotrichia* (Gloeotrichiaceae), *Tolypothrix* (Tolypothrichaceae), *Wetliellopsis* (Hapalosiphonaceae), *Spirulina* (Spirulinaceae), *Calothrix* (Rivulariaceae), *Phormidium*, *Plectonema*, and *Oscillatoria* (Oscillatoriaceae) have also been used as biofertilizers (Manjunath et al., 2011; Osman et al., 2010; Prasanna et al., 2016b; Singha, 2009; Verma et al., 2016). For

example, an extract of the cyanobacterium *Aulosira fertilissima* (Nostocaceae) induced the development of rice (Poaceae) with a growth pattern more or less similar to that of seedlings treated with algae filtrate (Singh and Trehan, 1973). Since this pioneering finding, many studies have been carried out on cyanobacterial extracts concerning their biofertilization potential on seed germination and the growth of roots, seedlings and plants. Aqueous extracts of *Pseudanabaena* sp. WSU1 (Pseudanabaenaceae), *Phormidium* sp. WSU2, *Oscillatoria* sp. WSU5, *Phormidium* sp. WSU6, *Oscillatoria* sp. WSU9 (Oscillatoriaceae), *Geitlerinema* sp. WSU3 (Coleofasciculaceae), *Arthrospira* sp. WSU4, (Oscillatoriaceae), *Lyngbya* sp. WSU7, *Gloeocapsa* sp. WSU8, (Oscillatoriaceae), *Spirulina* sp. WSU10 (Spirulinaceae) and *Calothrix* sp. WSU11 (Rivulariaceae) were evaluated at three different concentrations (1%, 2%, and 3%) on seed germination of *Zea mays* L. (Poaceae). The results showed that only the non-heterocytous cyanobacterial extracts of *Pseudanabaena* sp. (Pseudanabaenaceae) at 1%, *Phormidium* sp. (Oscillatoriaceae) at 2%, *Geitlerinema* sp. at 2%, *Lyngbya* sp. (Oscillatoriaceae) at 3%, *Spirulina* sp. (Spirulinaceae) at 2% concentration and the extract of heterocytous *Calothrix* sp. (Rivulariaceae) at 3% concentration induced significantly higher effects on morphological and biochemical parameters of *Zea mays* (Poaceae) compared to control (Sivalingam and Delfe). Furthermore, Sivalingam and Batiri (2020) evaluated aqueous extracts of *Pseudanabaena galeata* KA1 (Pseudanabaenaceae), *Oscillatoria perornata* KA2 (Oscillatoriaceae), *Phormidium acutum* KA3 (Oscillatoriaceae), *Rivularia* sp. KA4 (Rivulariaceae) and *Lyngbya* sp. KA5 (Oscillatoriaceae) on seed germination of wheat (*T. aestivum*; Poaceae). They found that the aqueous extract of *Rivularia* sp. (Rivulariaceae) at 3% showed a significant effect on seed germination, suggesting that this cyanobacterial species could be used either in dried form or as an aqueous liquid extract for the pretreatment of wheat (Poaceae) seeds and/or as a biofertilizer for growing wheat (Sivalingam and Batiri, 2020). The pretreatment of seeds of *Cicer arietinum* (Fabaceae), *Oryza sativa* and *Triticum aestivum* (Poaceae) with extracts of cyanobacteria at low temperature could shorten the life cycle of these plants and be an effective way to manage crops and produce plants of great agricultural importance more quickly and of better quality (Khushwaha and Banerjee, 2015). The cultivation of radish (*Raphanus sativus*; Brassicaceae) was tested with *Spirulina platensis* (Spirulinaceae) filtrate (applied for seed soaking and for foliar spray) and homogenate (used for seed coating), examining length, wet mass, multi-elemental composition and the greenness index of the radish leaves. The compounds present in *Spirulina* (Spirulinaceae) increased plant growth relative to control and a commercial product (Godlewska et al., 2019). Furthermore, filtrates from *Spirulina* (Spirulinaceae) can promote the accumulation of substances essential for the growth of *Amaranthus gangeticus* (Amaranthaceae), *Phaseolus aureus* (Fabaceae) and tomatoes (Solanaceae) (Anitha et al., 2016). Mutale-Joan et al. (2020) evaluated the bio-stimulant effect of 18 crude bio-extracts obtained from microalgae and cyanobacteria on tomato plant growth, chlorophyll content, nutrient uptake and metabolite profiles (Mutale-Joan et al., 2020). They found that treated plants recorded a higher accumulation of palmitic and stearic acids, which could indicate a stimulation of *de novo* lipid synthesis. Similarly, extracts of *Microcystis aeruginosa* (Microcystaceae), *Anabaena* sp. (Nostocaceae) and *Chlorella* sp. (Chlorellaceae) were evaluated on germination, growth, and metabolic activity of corn seedlings (Grzesik and Romanowska-Duda, 2014; Grzesik et al., 2017). Cyanobacterial extracts increased the number of germinated grains, as well as the dynamics, germination and growth of seedlings. In addition, chlorophyll content, net photosynthesis, transpiration, stomatal conductance, intercellular CO₂ concentration, acid and alkaline phosphatase activities, RNase and total dehydrogenase were increased, with faster elongation of roots and leaves and increased fresh and dry biomass. When date palm was cultivated in a growing medium supplemented with an extract of *Oscillatoria tenuis* (Oscillatoriaceae), root development increased significantly compared to the growing medium without the cyanobacterial extract (Ibrahim et al., 2020). Moreover,

evaluation of extracts from the cyanobacterium *Calothrix elenkinii* (Rivulariaceae) on the growth of rice (Poaceae) showed significant increases in plant growth, nitrogenase activity, and indole acetic acid production, along with activities of hydrolytic and defense enzymes (Priya et al., 2015; Ranjan et al., 2016).

2.2. Cyanobacterial bioactive compounds as signaling molecules and their effects against biotic and abiotic stress

2.2.1. Signaling molecules: phytohormones

Several cyanobacterial species, including *Dolichospermum variabilis*, *Nostoc muscorum*, *Aulosira fertilissima* (Nostocaceae), and *Tolypothrix tenuis* (Tolypothrichaceae) are known to release extracellular bioactive substances, which act as signaling molecules, promoting plant growth and producing similar responses to phytohormones such as IAA (indole-3-acetic acid), cytokinin, gibberellin, ethylene, jasmonic acid or abscisic acids (Singh, 2014). These phytohormones contribute to the co-ordination of diverse physiological processes in plants, including the regulation of seed germination, stimulation of root growth and branching, seedling growth, inflorescence, and fruit ripening (Bareke, 2018). They promote plant resistance to environmental factors and induce or suppress the expression of genes and the synthesis of enzymes, pigments, and metabolites (Singh, 2014). For example, the extracellular filtrate from a cyanobacterial *Phormidium* sp. (Oscillatoriaceae) culture was tested on tobacco seeds (Solanaceae) and enhanced seed germination and multiple root formation, a characteristic feature of auxins (Boopathi et al., 2013). Cultivation of a cytokinin and IAA-producing endophytic *Nostoc* strain (Nostocaceae) isolated from rice roots with wheat and rice seedlings (Poaceae) under glass house conditions showed an increase in shoot length, root length and grain weight (Hussain et al., 2013, 2015). Presoaking seeds of rice, wheat (Poaceae) and other plants in an extract of *P. foveolarum* (Oscillatoriaceae) containing a gibberellin-like substance enhanced growth, yield and protein content of these plants (Gupta and Agarwal, 1973). The addition of *Oscillatoria acuminata* (Oscillatoriaceae) extracellular products enhanced shoot elongation and root production in the cotton plant *Gossypium hirsutum* L. (Gurusaravanan et al., 2013). Cytokinin- and auxin-secreting cyanobacterial strains such as *Calothrix* sp. (Rivulariaceae) and *Phormidium animale* (Oscillatoriaceae) were evaluated for stimulating plant growth under axenic, as well as field conditions. A positive correlation between cyanobacterial hormones and plant growth parameters such as shoot length, root length, spike length, and weight of seeds was observed (Hussain and Hasnain, 2011; Mazhar et al., 2013; Renuka et al., 2018). Moreover, the cyanobacterial *Aphanothece* sp. MBDU 515 (Aphanotheceaceae) extracellular product (CEP) containing the phytohormone IAA was evaluated on the growth of two economically important plants *Arachis hypogaea* (Leguminosae) and *Moringa oleifera* (Moringaceae). The results showed that the effects of CEP were comparable to the commercial phytohormones BAP and IBA, suggesting that CEP may be used for industrial micropropagation in place of commercially available phytohormones (Gayathri et al., 2015).

2.2.2. Biotic and abiotic stress

2.2.2.1. Salt tolerance.

Plant growth and the yield of plants and crops can be significantly affected by salt accumulation in arid or sub-arid soils (Mathur et al., 2007) (Fig. 1). Therefore, cyanobacteria, which are usually considered tolerant of salt stress, as they can colonize salt-affected soils naturally, could play a role in the rehabilitation of these soils (Apte and Bhagwat, 1989; De Philippis and Vincenzini, 1998; Nikkinen et al., 2012; Pandhal et al., 2009; Singh and Dhar, 2010). El-Sheek et al. (2018) found that using *Nostoc calcicola*, *Anabaena variabilis*, and *Nostoc linckia* (Nostocaceae) as a biofertilizer for rice (Poaceae) plants in saline soils induced both an increase of plant growth and a decrease of soil electrical conductivity (El-Sheek et al., 2018). Arora

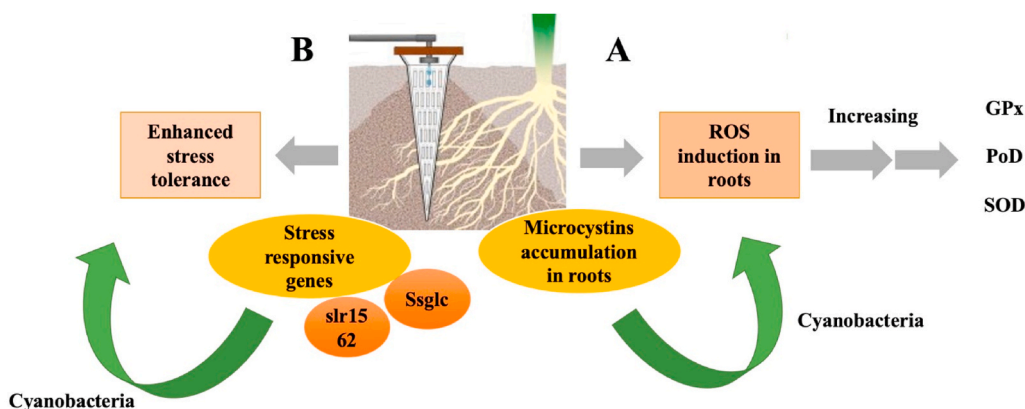


Fig. 1. Cyanobacterial active compounds induce negative, (A) ROS and enzyme activities such as superoxide dismutase (SOD), glutathione peroxidase (GPx), peroxidase (POD); and positive effects (B) expression of stress responsive genes (SsGlc and slr1562) that can have a positive effect on increasing plants' stress tolerance.

et al. (2010) measured the impact of exopolysaccharides (EPS) from four cyanobacteria (*Nostoc calcicola*, *Nostoc spongiaeformae*, *Nostoc linckia* and *Nostoc muscorum*; Nostocaceae) on salt stress tolerance and germination of wheat, corn and rice (Poaceae) seeds. They showed that the salts promoted the biosynthesis of EPS, which in turn had considerable potential to extract Na^+ ions from water in the surrounding environment, considerably promoting seed germination in all three cultures (Arora et al., 2010). In another study, El-Gamal et al., 2008 used *Anabaena variabilis* and *Nostoc linckia* (Nostocaceae) to test salt stress and showed improvement in the growth conditions of some salt-stressed plant seedlings. The presence of *A. Variabilis* (Nostocaceae) resulted in a significant increase in shoot and root volume, as well as a significant reduction in the proline content of seedlings of beans (Fabaceae), zea and barley (Poaceae) grown under salt stress. In contrast, *N. linckia* (Nostocaceae) induced a massive decrease in the proline content of zea and barley (Poaceae) seedlings, although the chlorophyll content increased in the two seedling plants as opposed to the control (El-Gamal et al., 2008). Co-cultivation of rice (Poaceae) seedlings with a cyanobacterial species *Scytonema hofmanni* (Scytonemaceae) under salt stress showed a positive impact on the growth of this plant (Rodríguez et al., 2006), with the authors suggesting that extracellular products of *S. hofmanni* (Scytonemaceae) completely or partially reversed the growth effects induced by NaCl, in addition to biochemical alterations of the rice plants (Poaceae) such as 5-aminolevulinic acid dehydratase activity, total free porphyrin and pigment content. Cyanobacterial extracts also seemed to offset deficiencies in plant phytohormones, and thus may be used to promote development in salt-affected crops. High salt concentrations were shown to induce an increase in abscisic acid content, which plays an important role in the biochemical and physiological activity of plant tissues and usually causes inhibition of growth and development under salt stress conditions (Montero et al., 1997). Therefore, treatment with an extract of cyanobacteria could neutralize excess abscisic acid, reducing alterations in the ratios of plant growth regulators. In fact, Haroun and Hussein (2003) showed a decrease in abscisic acid content and an increase in IAA, gibberellic acid and cytokinin content in *Lupinus termis* (Leguminosae) after application of a cyanobacterial extract. Multiple cyanobacteria-based approaches have been proposed as a potentially powerful biotechnological tool for generating cultures tolerant to multiple stresses including salt stress (Apte and Bhagwat, 1989; Nikkinen et al., 2012; Pandhal et al., 2009). For example, Coba de la Peña et al. (2010) examined whether the expression of the flavodoxin gene from the cyanobacterial species *Anabaena variabilis* (Nostocaceae) in the plant model *Medicago truncatula* (Fabaceae), could directly improve salt stress tolerance and maintain nitrogen fixation in the plant under saline conditions. Expression of flavodoxin did not confer salt tolerance to the whole plant, but the

reactive nitrogen fixation function in plants expressing flavodoxin was preserved under salt stress, suggesting that flavodoxin caused minor but essential improvements in the enzymatic behaviors involved in the redox balance of the nodule that could be responsible for the positive nitrogen binding effect. Furthermore, the expression of flavodoxin can be considered a possible method to increase the symbiotic efficiency of legumes under saline tension, and possibly other environmental stresses (Coba de la Peña et al., 2010). In addition, a *Synechocystis* (Merismopediaceae) gene called SsGlc encoding a β -1,4-glucanase-like protein (SsGlc) has been shown to function in salt stress tolerance and therefore could be used to improve salt tolerance in plants. Rady et al. (2018) examined the effect of cyanobacteria, with or without glutathione and ascorbic acid (AsA), and their variations on morphological, physiological, metabolic and enzymatic activity status in specific bean plants grown on salt-stressed soil. They found that all single or combined (cyanobacteria, AsA, or GSH) applications greatly improved plant length, number and area of leaves, plant fresh and dry weights, yield parameters and photosynthetic leaf pigments, and the photochemical performance of specific bean plants. Furthermore, for all the applications mentioned above, relative water quality, membrane stability index, soluble sugar content, proline, AsA, GSH, N, P and K^+ ion content, and superoxide dismutase, catalase, and guaiacol peroxidase activities were substantially increased. In comparison, electrolytes and the Na^+ ion concentration decreased dramatically (Rady et al., 2018).

2.2.2.2. Antimicrobial activities. Cyanobacteria are considered a major source of natural antimicrobial (Burja et al., 2001; Nowruzi et al., 2020a, b; Safavi et al., 2019), and antiprotozoal (Simmons et al., 2008) compounds. For example, Mikhail et al. (2016) examined *in vitro* antibacterial activity of filtrates of three cyanobacterial species, *Nostoc muscorum* (Nostocaceae), *Spirulina platensis* (Spirulinaceae), and *Anabaena flos-aquae* (Nostocaceae), on the growth of *Ralstonia solanacearum* (Ralstoniaceae), a Gram-negative soil bacterium, which colonizes the xylem, causing bacterial rot or vascular bacteriosis in many host plants, such as tomatoes and potatoes (Solanaceae). The three cyanobacterial filtrates exhibited antibacterial activity against *R. solanacearum* (Solanaceae), with the filtrate of *A. flos-aquae* (Nostocaceae) being the most active. In addition to antibacterial activity, the application of the cyanobacterial filtrates improved plant growth and induced an increase in photosynthetic pigments (chlorophyll-a, -b and carotenoids), ascorbic acid, total phenols and proline as well as the NPK and Na^+ contents in the treated plants (Mikhail et al., 2016). Recently, Aldayel and El Semy (2020) evaluated the effect of UV-B treatment on extracts from four-cyanobacterial species *Synechococcus* sp. (Synechococcaceae), *Oscillatoria* sp. (Oscillatoriaceae), *Synechocystis* sp. (Merismopediaceae) and *Phormidium* sp. (Oscillatoriaceae) against the plant pathogenic

bacteria, *Erwinia* sp. (Erwiniaceae), *Pseudomonas* sp. (Pseudomonadaaceae), and *Bacillus* sp. (Bacillaceae). The results showed that the extracts were more active after UV exposure, suggesting a novel approach in enhancing antibacterial activity of cyanobacterial extracts (Aldayel and El Semary, 2020).

Concerning antifungal activities, Kim (2006) reported that different cyanobacterial genera such as *Oscillatoria* (Oscillatoriaceae), *Anabaena*, *Nostoc* (Nostocaceae), *Nodularia* (Aphanizomenonaceae) and *Calothrix* (Rivulariaceae) significantly inhibited the growth of two-necrotrophic pathogenic fungi, *Alternaria alternata* (Pleosporaceae) and *Botrytis cinerea* (Sclerotiniaceae), which cause gray mold and black mold respectively and result in worldwide losses of horticultural crops (Kim, 2006). The antifungal potential of extracellular cyanobacterial media from *Anabaena subcylindrica*, *Nostoc muscorum* (Nostocaceae) and *Oscillatoria angusta* (Oscillatoriaceae) was evaluated on various pathogenic fungi isolated from different organs (leaves, stems and roots) of the faba bean (Fabaceae) and significantly inhibited fungal growth isolated from the three plant parts (Abo-Shady et al., 2007). Moreover, cyanobacterial extracts have been reported to reduce the occurrence of *Botrytis cinerea* (Sclerotiniaceae) on strawberries and *Erysiphe polygoni* (Erysiphaceae) responsible for powdery mildew on turnips and damping-off in tomato seedlings (Solanaceae), as well as reducing saprophytes such as *Chaetomium globosum* (Chaetomiaceae), *Cunninghamella blakesleeana* (Cunninghamellaceae) and *Aspergillus oryzae* (Trichocomaceae) and plant pathogens such as *Rhizoctonia solani* (Ceratobasidiaceae) and *Sclerotinia sclerotium* (Sclerotiniaceae) (Kulik, 1995). Methanolic extracts of *Nostoc commune* FK-103 (Nostocaceae) and *Oscillatoria tenuis* FK-109 (Oscillatoriaceae) showed antifungal activities against *Phytophthora capsici* (Pythiaceae), an oomycete plant pathogen that causes blight and fruit rot of peppers and other important commercial crops. A methanolic extract of *Nostoc commune* FK-103 (Nostocaceae) inhibited the growth of *Rhizopus stolonifer* (Mucoraceae), a fungus responsible for soft and liquid rots on various fruits and vegetables (strawberries (Rosaceae), grapes (Vitaceae), tomatoes (Solanaceae)) as well as black mold, commonly observed on the surface of bread and other starchy foods (Kim, 2006). Manjunath et al. (2010) investigated the biocidal effectiveness of *Calothrix elenkenii* (Rivulariaceae) fungicidal compounds toward damping-off infection in three vegetable crops-tomato, chili, and brinjal (Solanaceae), and results revealed that the *Calothrix elenkenii* (Rivulariaceae) ethyl acetate extract was successful against the fungi examined (Manjunath et al., 2010). Chaudhary et al. (2012) reported that two-cyanobacterial species *Anabaena variabilis* and *A. oscillarioides* (Nostocaceae) prevented damping off infection in tomato seedlings (Solanaceae) threatened by a fungal consortium including *Pythium debaryanum* (Pythiaceae), *Fusarium oxysporum lycopersici*, *Fusarium moniliforme* (Nectriaceae), and *Rhizoctonia solani* (Ceratobasidiaceae). Moreover, Roberti et al. (2016) reported that an extract of *Anabaena* sp. (Nostocaceae) showed considerable inhibitory activity against the plant pathogen *Podosphaera xanthii* (Erysiphaceae), responsible for powdery mildew on cucurbits such as zucchini (*Cucurbita pepo* (Cucurbitaceae)) cotyledons (Roberti et al., 2016). The use of extracellular media from *Oscillatoria* sp. (Oscillatoriaceae) and *Nostoc muscorum* (Nostocaceae) can regulate the purple blotch disease of onion induced by *Alternaria porri* (Pleosporaceae) (Abdel-Hafez et al., 2015). As part of the biological control of *Fusarium oxysporum* f. sp. lycopersici (FOL) (Nectriaceae), a xylem-colonizing fungus that has long been known to cause wilt on tomato (Solanaceae), Alwathnani and Perveen (2012) reported that the methanolic extract of two cyanobacterial species *Nostoc linckia* (Nostocaceae) and *Phormidium autumnale* (Oscillatoriaceae) exhibited moderate inhibitory activity against the growth of this fungus (Alwathnani and Perveen, 2012). However, Kim and Kim (2008) showed that extracts of the cyanobacterium *Nostoc commune* FK-103 (Nostocaceae) inhibited *in vitro* and *in vivo* growth and sporulation of the tomato-wilt (Solanaceae) pathogen in tomato (Solanaceae) seeds. Moreover, the antifungal potential of cyanobacteria on the tomato-wilt (Solanaceae) pathogen was also evaluated with extracts of two other species of cyanobacteria,

Anabaena variabilis and *A. laxa* (Nostocaceae). The results showed that this new type of biological control was effective and allowed both reduction of disease intensity alongside increased growth/production of tomato (Solanaceae) crops affected by *Fusarium* wilt (Nectriaceae) (Prasanna et al., 2013b).

2.2.2.3. *Disease resistance.* Given the harmful effects of agrochemicals such as fertilizers and pesticides on soils and aquatic environments, in recent years studies have focused on alternatives to these chemicals. Cyanobacteria and their extracts could be an attractive strategy within a sustainable agricultural framework (Saxena, 2014; Singh, 2014) as they may be a source of both biofertilizers (Chittora et al., 2020; Singh et al., 2016b) and bioactive compounds for disease control in plants (Gonçalves, 2021). Biocontrol agents derived from cyanobacteria can modify the physiological and biochemical reactions of the host plant leading to the synthesis or supply of defense chemicals against pathogens such as antioxidants. Such changes can lead to increased plant growth, enhanced yields and quality of products.

To our knowledge, the pioneering study of the use of cyanobacteria in the control of plant diseases was reported by de Caire et al. (1979), studying the effect of extracts from a nitrogen-fixing cyanobacterium *N. muscorum* (Nostocaceae) on the growth of millet (*Panicum miliaceum* L. (Poaceae)) seedlings. They showed that the cyanobacterial extract prevented the appearance of damping-off in millet seedlings. Later, the cyanobacterial biological control mechanism against plant diseases was studied in tomato (Solanaceae) plants infected with *Fusarium* (Nectriaceae) wilt and which were treated with two cyanobacterial species, *Anabaena variabilis* and *A. laxa* (Nostocaceae) (Prasanna et al., 2013a). The results showed that the activity of defense enzymes such as phenylalanine ammonia lyase, polyphenol oxidase and enzymatic activity related to pathogenesis, including the activity of chitinase and β -1,3 glucanase, was higher in the roots of tomato (Solanaceae) plants treated with cyanobacterial extracts compared to controls (Prasanna et al., 2013a).

The transfection of cyanobacterial flavodoxin genes, coding for a final electron acceptor protein of the photosynthetic electron transport chain, in tobacco plants (Solanaceae) resulted in an overall antioxidant benefit, restoration of the distribution of electrons, and cellular homeostasis contributing to generalized stress tolerance (Cabello et al., 2014; Giró et al., 2011; Lodeyro et al., 2012; Zurbriggen et al., 2008, 2010). Tognetti et al. (2006) reported that tobacco plants (Solanaceae) expressing plastid-targeted Fld in chloroplasts improved resistance to numerous stress factors, including redox-cycling herbicides, intense temperatures, excessive irradiation, water scarcity, and UV radiation. In addition, oxidant accumulation and oxidative inactivation of thioredoxin-dependent plastid enzymes were also reduced in stressed plants expressing Fld, indicating that the formation of the tolerant phenotype was based on the successful interaction of this flavoprotein with the host's Fd-dependent oxidoreductive pathways, most notably, reduction of thioredoxine (Tognetti et al., 2006). Moreover, Li et al. (2017) studied the use of cyanobacterial flavodoxin genes in improving the response of plant stress to creeping bentgrass (*Agrostis stolonifera* L. (Poaceae)), showing that Fld overexpression altered the growth and production of plants. Transgenic plants exhibited dramatically improved performance under oxidative, drought and heat stress, as well as nitrogen (N) starvation associated with higher water retention and cell membrane integrity than controls of the wild variety (Li et al., 2017). In addition, in Fld-expressing transgenic plants, the expression of other stress-related genes was also impacted such as heat shock protein gene expression, production of more reduced thioredoxin, elevated nitrogen accumulation and total chlorophyll content, as well as up-regulation of nitrite reductase and N transporter genes. Some cyanobacterial species such as *Synechocystis* sp. (Merismopediaceae), *Synechococcus* sp. (Synechococcaceae) and *Aphanothece halophytica* (Aphanothecaceae) can produce and accumulate glycinebetaine (GB). The use of exogenous GB and genetically engineered GB biosynthesis has the ability to improve

plant resistance to abiotic stress as evidenced by [Chen and Murata \(2008\)](#) who showed that GB-accumulating transgenic plant reproductive organs displayed an increased resistance to abiotic stress.

The cyanobacterium *Nostoc calcicola* (Nostocaceae) increased the resistance of *Glycine max* cv. soybean ([Fabaceae](#)) cultivars to the cowpea aphid (*Aphis craccivora* Koch (Aphididae)), a serious pest of leguminous crops, not only by the regulation of the generation and effects of O_2^- and H_2O_2 , but also by increasing the activity of SOD, CAT and GPx in soybean leaves ([Fabaceae](#)) ([Mai et al., 2017](#)) ([Fig. 1](#)). [Essa et al. \(2015\)](#) reported that cyanobacterial extracts of *Anabaena oryzae*, *Nostoc ellipso-sporum* (Nostocaceae) and *Synechococcus* sp. (Synechococcaceae), significantly induced the activity of antioxidant enzymes such as catalase, peroxidase and polyphenol oxidase in *Sorghum durra* (Poaceae) and *Helianthus annuus* (Asteraceae) plants, helping to improve seed germination and seedling development. The colonization of the root rhizosphere of rice (*Oryza sativa* (Poaceae)) by various cyanobacterial species including *Anabaena oryzae*, *Anabaena doliolum* (Nostocaceae), *Phormidium delicate* (Oscillatoriaceae), *Calothrix geitonos* (Rivulariaceae), *Hapalosiphon intricatus* (Hapalosiphonaceae), *Aulosira fertilissima* (Nostocaceae), *Tolypothrix tenuis* (Tolypothrichaceae), *Oscillatoria acuta* (Oscillatoriaceae) and *Plectonema boryanum* (Oscillatoriaceae), resulted in the growth of the plant and its resistance to stress by enhancing the activity of peroxidase and phenylalanine ammoniolyase and total phenolic content ([Singh et al., 2011](#)). A summary of the positive effects of cyanobacteria and their compounds is given in [Table 1](#).

3. Cyanotoxins and their impacts on plant, animal and human health

Although research is understanding the production of biologically active cyanobacterial compounds in e.g. rice paddies and their effects on food crops, much of this has used cultures and strains isolated from environmental collections. Therefore, further research is necessary to understand the implications of inoculating agricultural land with cyanobacteria. Besides biologically active substances, which affect soils and promote plant growth, many cyanobacterial species can release cyanotoxins such as hepatotoxins (microcystins, nodularins and cylindrospermopsins) and neurotoxins (anatoxin-a, saxitoxins and beta-N-methylamino-L-alanine) that can inhibit seed germination, root and plant growth ([Buratti et al., 2017](#); [Corbel et al., 2014](#); [Merel et al., 2013](#); [Niamien-Ebrottie et al., 2015](#); [Nowruzi and Lorenzi, 2021a, b](#)).

Cyanobacterial neurotoxins are grouped into three main families: anatoxin-a, guanitoxin (anatoxin-a(S)) and saxitoxins (STXs). Anatoxin-a and homoanatoxin-a are potent postsynaptic depolarizing neuromuscular blocking agents that mimicking the action of acetylcholine and guanitoxin inhibits acetylcholinesterase activity ([Campos et al., 2006](#)). The maximum reported concentration of anatoxin-a, the first cyanobacterial toxin to be structurally elucidated, was 1444 $\mu\text{g/L}$ ([Lovin and Brooks, 2020](#)). Anatoxin-a and guanitoxin are considered to be specific to cyanobacteria, whereas STXs are also synthesized by some marine dinoflagellates and are associated with paralytic shellfish poisoning ([Suarez-Isla, 2015](#)). STXs exert their toxic effects by binding with high affinity to voltage-gated sodium channels ([Zhang et al., 2013](#)). STXs are also capable of interfering with potassium and calcium-mediated ion channels. In the case of potassium channels, saxitoxins bind at the channel site, requiring stronger membrane depolarisation to open the channel ([Cusick and Sayler, 2013](#)), resulting in an overall reduction of potassium conductance across membranes. STXs act on calcium channels in a manner similar to but not as efficient as for sodium channels ([Cusick and Sayler, 2013](#)). The maximum recorded cyanobacterial STX concentration (3800 $\mu\text{g/L}$) was recently observed during a bloom episode of *Dolichospermum lemmermannii* (Aphanizomenonaceae) in the Angara River, Russia ([Grachev et al., 2018](#)). β -N-methylamino-L-alanine (BMAA) is a non-protein amino acid with neurotoxic effects, having originally been isolated from seeds of *Cycas micronesica* Hill (Cycadaceae) ([Vega and Bell, 1967](#); [Vega et al., 1968](#)). Further, it has been found

to be produced by almost all cyanobacteria; including the genus *Nostoc* (Nostocaceae), which lives symbiotically in plant roots ([Cox et al., 2005](#); [Mello et al., 2018](#)), but also in Nebraska reservoirs, USA at 24.5 $\mu\text{g/L}$ ([Al-Sammak et al., 2014](#)). BMAA is considered to be an excitotoxin and acts in mammals as a glutamate agonist at AMPA, kainate and NMDA receptors ([Chiu et al., 2011](#)).

Several reports indicate that blooms formed by hepatotoxin-producing cyanobacteria are more widespread than neurotoxin-producing blooms ([Almuhtaram et al., 2018](#); [Bláhová et al., 2007, 2008](#); [Chénais, 2021](#); [Jaiswal et al., 2008](#); [Metcalf and Codd, 2020](#); [Zanchett and Oliveira-Filho, 2013](#)). The cyclic heptapeptide hepatotoxic microcystins are the most common and diverse group of cyanotoxins with 279 variants characterized ([Bouaïcha et al., 2019](#)). They have been frequently reported worldwide ([Carmichael, 1994](#); [Falconer et al., 1994](#)) with concentrations in aquatic ecosystems ranging from 1 to 29,000 $\mu\text{g/L}$ ([Corbel et al., 2014](#)). They are potent and specific inhibitors of protein phosphatases ([Bouaïcha et al., 2019](#)), involved in several physiological and molecular processes in plants ([Sheen, 1993](#); [Takeda et al., 1994](#)). These hepatotoxins are also known to induce oxidative stress in mammalian and plant cells ([Bouaïcha and Maatouk, 2004](#); [Campos and Vasconcelos, 2010](#); [Pappas et al., 2020](#)). However, nodularins, cyclic pentapeptides with similar mechanisms of action to microcystins are not as prevalent in the environment ([Chen et al., 2013](#)), with a maximum environmental concentration of 220 $\mu\text{g/L}$ recorded ([McGregor et al., 2012](#)). The alkaloid cytotoxin cylindrospermopsin has been found in surface freshwaters at concentrations ranging from non-detectable up to 126 $\mu\text{g/L}$ ([Messineo et al., 2009](#)). This alkaloid hepatotoxin is known to act as an inhibitor of protein synthesis in mammal and plant cells ([Frosio et al., 2008](#); [Metcalf et al., 2004](#)).

In view of the specific activities via receptors and enzymes present in the animal realm, some cyanotoxins may be expected to have harmful effects on plants. In addition to the toxic effects of cyanotoxins to plants, when exposed through spraying, irrigation or watering, these cyanotoxins may accumulate in different tissues and grains of crop plants, and thus cause adverse health effects to humans and animals that consume them.

3.1. Phytotoxicity of cyanotoxins

Water quality is a key environmental issue in the agricultural sector. However, surface water used to irrigate food crops, vegetables and plants is often taken directly from public supply reservoirs without treatment, and sometimes may be contaminated with high concentrations of cyanotoxins. In addition, the presence of cyanotoxins can have negative effects on growth processes of cultivated plants at several levels: seed germination, root development and growth, seedling and adult plant growth, potentially leading to significant economic losses, manifested by a reduction in productivity and crop yield. Furthermore, cyanotoxins can also be absorbed and bioaccumulated by vegetables and plant crops and therefore may have a significant impact on food quality and pose a possible threat to human and animal health ([Bouaïcha and Corbel, 2016](#); [Machado et al., 2017](#); [Redouane et al., 2021](#)). Concerning this cyanotoxin-plant interaction, MCs are the most intensively studied compounds as pure standards or as MC-containing crude cyanobacterial extracts and their effect on agricultural plants was recently reviewed ([Zhang et al., 2021](#)). However, information concerning other groups of cyanotoxins remains limited.

3.1.1. Effects on seed germination and root and seedling growth

Microcystins are water-soluble molecules, and their cyclic structure provides them with high chemical stability and a half-life in soils estimated to be between 6 and 17.8 days ([Chen et al., 2006](#)). [Corbel et al. \(2014\)](#) examined the fate and availability of these toxins in an agriculture soil using radiolabelled microcystin-LR (^{14}C -MC-LR). Results showed that the $^{14}\text{CO}_2$ from the degradation of ^{14}C -MC-LR amounted to 11% of total ^{14}C initial input; 74–80% of ^{14}C -MC-LR occurred in

Table 1
Positive effects of cyanobacterial bioactive compounds.

(a) Cyanobacteria as biofertilizers				
Cyanobacterial species	Plant species	Effect on plant	Effective agent	References
<i>Nostoc</i> sp.	Cycads; <i>Gunnera</i>	Symbiotic relationships; Reduction of atmospheric molecular nitrogen to ammonia via nitrogenases	Cyanobacterial extract	Bergman (2002)
<i>Aulosiva fertilissima</i>	rice seedlings	↑ shoots Length	Not found	Singh and Trehan (1973)
<i>Pseudanabaena</i> sp. WSU1	<i>Zea mays</i> L. (maize) seeds	↑ morphological and biochemical parameters	Not found	Sivalingam and Delfe (2019)
<i>Phormidium</i> sp. WSU2				
<i>Geitlerinema</i> sp. WSU3				
<i>Arthrospira</i> sp. WSU4				
<i>Oscillatoria</i> sp. WSU5				
<i>Phormidium</i> sp. WSU6				
<i>Lyngbya</i> sp. WSU7				
<i>Gloeocapsa</i> sp. WSU8				
<i>Oscillatoria</i> sp. WSU9				
<i>Spirulina</i> sp. WSU10				
<i>Calothrix</i> sp. WSU11				
<i>Anabaena variabilis</i>	<i>Helianthus annuus</i> L., <i>Vitis vinifera</i> L.	↑ growth and development of plants, metabolic processes	Not found	Pszczółkowski et al. (2012)
<i>Anabaena</i> sp.	Wheat	↑ plant growth, yield, micronutrient uptake and translocation	Not found	Rana et al. (2012, 2015)
<i>Calothrix</i> sp.				
<i>Anabaena</i> sp.				
<i>Pseudanabaena galeata</i> KA1	wheat (<i>T. aestivum</i>)	The results indicated that only the aqueous extract of <i>Rivularia</i> sp. at 3% shows a significant effect on the seed germination	Cyanobacterial extract	Sivalingam and Batiri (2020)
<i>Oscillatoria perornata</i> KA2				
<i>Phormidium acutum</i> KA3				
<i>Rivularia</i> sp. KA4				
<i>Lyngbya</i> sp. KA5				
<i>Spirulina platensis</i>	radish (<i>Raphanus sativus</i>)	↑ plant duration;	Cyanobacterial extract	(Osman et al., 2016).
<i>Spirulina platensis</i>	<i>Amaranthus gangeticus</i> , <i>Phaseolus aureus</i> and tomatoes	promote the accumulation of substances essential for the growth	Cyanobacterial extract	Anitha et al. (2016)
<i>Aphanothece</i> sp.	Tomato	↑ accumulation of palmitic and stearic acids in stimulating <i>de novo</i> lipid synthesis	Crude Bio-Extracts (CBEs)	Mutale-Joan et al. (2020)
<i>Microcystis aeruginosa</i>	corn seedlings	↑ number of the germinated grains, dynamics, germination and accelerated growth of seedlings	Cyanobacterial extract	(Grzesik and Romanowska-Duda, 2014; Grzesik et al., 2017)
<i>Anabaena</i> sp.				
<i>Chlorella</i> sp.				
<i>Oscillatoria tenuis</i>	date palm	↑ root development	Cyanobacterial extract	Ibrahim et al. (2020)
<i>Calothrix elenkinii</i>	Rice	↑ plant growth, nitrogenase activity, indole acetic acid production, activities of hydrolytic and defense enzymes	Not found	(Priya et al., 2015; Ranjan et al., 2016)
(b) Phytohormones as as signalling molecules				
Cyanobacterial species	Plant species	Effect on plant	Effective agent	References
<i>Phormidium</i> sp.	tobacco seeds	↑ seed germination and multiple root formation	auxins	Boopathi et al. (2013)
<i>Nostoc</i> sp.	rice roots	↑ shoot length, root length and weight of grain	cytokinin and IAA,	Hussain et al. (2013)
<i>Phormidium foveolarum</i>	Rice, wheat	↑ growth, yield, and development of secondary root, shoot and protein content	Gibberellin	Gupta and Agarwal (1973).
<i>Oscillatoria acuminata</i>	<i>Gossypium hirsutum</i> L (cotton)	↑ growth, shoot elongation	Not found	Gurusaravanan et al. (2013)
<i>Calothrix</i> sp.	Wheat	↑ shoot length, root length, spike length, and weight of seeds	cytokinin and auxin	
<i>Phormidium animale</i>				(Hussain and Hasnain, 2011; Mazhar et al., 2013; Renuka et al., 2018)
<i>Aphanothece</i> sp.		↑ shoot and root lengths		Gayathri et al. (2015)

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Table 1 (continued)

(a) Cyanobacteria as biofertilizers				
Cyanobacterial species	Plant species	Effect on plant	Effective agent	References
<i>Cylindrospermum muscicola</i> <i>Anabaena oryzae</i>	<i>Arachis hypogaea</i> and <i>Moringa oleifera</i> <i>Lupinus termis</i>	Decrease of abscisic acid content and a rise in the production of IAA, gibberellic acid and cytokinin in <i>Lupinus termis</i>	Indole-3-acetic acid Not found	Haroun and Hussein (2003).
(c) Salt tolerance				
Cyanobacterial species	Plant species	Effect on plant	Effective agent	References
<i>Nostoc calcicola</i>	Rice	Induction of plant growth and a decrease of soil electrical conductivity in saline soil	Cyanobacterial extract	El-Sheek et al. (2018)
<i>Anabaena variabilis</i> <i>Nostoc linckia</i> <i>Nostoc calcicola</i>	wheat, corn and rice seeds	↑ promotion of EPS biosynthesis and seed germination	exopolysaccharides (EPS)	Arora et al. (2010)
<i>Nostoc spongiaeformae</i> <i>Nostoc linckia</i> <i>Nostoc muscorum</i> <i>Anabaena variabilis</i>	beans, zea and barley	↑ shoot and root volume and reduction in the proline content of seedlings of beans, zea and barley grown under salt stress	Cyanobacterial extract	El-Gamal et al. (2008)
<i>Nostoc linckia</i> <i>Scytonema hofmanni</i>	Rice seedlings	Positive impact on growth under salt stress	Gibberellin-like substances	Rodríguez et al. (2006)
<i>Scytonema hofmanni</i>	Rice	↑ development in salt-affected crops ↑ abscisic acid content	Cyanobacterial extract	Montero et al. (1997)
<i>Anabaena variabilis</i>	<i>Medicago truncatula</i>	Improvement of salt stress tolerance and maintaining nitrogen fixation in the plant under saline conditions	flavodoxin	Coba de la Peña et al. (2010)
Soil cyanobacteria	<i>Phaseolus vulgaris</i> L. (bean plants)	Improvement of plant length, number and area of leaves, plant fresh and dry weights, yield parameters and photosynthetic leaf pigments, and photochemical performance	Crude extract, Glutathione and ascorbic acid (AsA)	Rady et al. (2018)
<i>Anabaena variabilis</i>	Model legume <i>Medicago truncatula</i>	Preservation of reactive nitrogen-fixing function in flavodoxin-expressing plants, Improvements of abiotic enzymatic behaviors	Flavodoxin	Coba de la Peña et al. (2010)
(d) Antimicrobial activities				
Cyanobacterial species	Plant species	Effect on plant	Effective agent	References
<i>Nostoc muscorum</i>	Radish	Inhibitory activity against <i>R. solanacearum</i> growth	Not Found	Mikhail et al. (2016)
<i>Spirulina platensis</i> <i>Anabaena flos-aquae</i> <i>Synechococcus</i> sp.	plant pathogenic bacteria, <i>Erwinia</i> sp., <i>Pseudomonas</i> sp., and <i>Bacillus</i> sp	Enhancing antibacterial activity	Cyanobacterial extract	Aldayel and El Semary (2020)
<i>Oscillatoria</i> sp. <i>Synechocystis</i> sp. <i>Phormidium</i> sp. <i>Oscillatoria</i>	<i>Capsicum annuum</i> L. (<i>hot pepper</i>)	Fungicidal activity	Methanolic extract of <i>Nostoc commune</i> and cyanobacterial filtrates	Kim (2006)
<i>Anabaena</i> <i>Nostoc</i> <i>Nodularia</i> <i>Calothrix</i> <i>Anabaena subcylindrica</i>	leaves, stems and roots of the faba bean	Inhibiting the growth of pathogenic fungi isolated from the three plant organs	Cyanobacterial extract	Abo-Shady et al. (2007)
<i>Nostoc muscorum</i> <i>Oscillatoria angusta</i> <i>Calothrix elenkenii</i>	Crops-tomato, chilli, and brinjal	Fungicidal activity	Ethyl acetate	Manjunath et al. (2010)
<i>Anabaena variabilis</i>	Tomato seedlings	Fungicidal activity	Not Found	(Chaudhary et al., 2012)
<i>A. oscillarioides</i> <i>Anabaena</i> sp.	<i>Cucurbita pepo</i> cotyledons (zucchini)	Inhibitory effect	Not Found	Roberti et al. (2016)
<i>Anabaena oryzae</i> , <i>Arthrospira</i> sp. <i>Nostoc minutum</i> <i>N. muscorum</i> <i>Oscillatoria</i> sp. <i>Nostoc linckia</i>	Onion	Regulation of violet blotch disease of floral onion stalks (<i>Alternaria porri</i>)	Not Found	Abdel-Hafez et al. (2015)
<i>Phormidium autumnale</i> <i>Nostoc commune</i> FK-103	Tomato	Inhibitory effect against <i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i> (FOL)	Methanol	Alwathnani and Perveen (2012)
	Tomato plant	Fungicidal activity	Not Found	

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Table 1 (continued)

(a) Cyanobacteria as biofertilizers				
Cyanobacterial species	Plant species	Effect on plant	Effective agent	References
<i>Anabaena variabilis</i>	Tomato plant	Inhibition of <i>Fusarium</i> wilt	Not Found	Kim and Kim (2008) Prasanna et al. (2013b) Kulik (1995)
<i>Lyngbya majuscula</i>	Strawberries and tomato seedlings	Reduction of <i>Botrytis cinerea</i> , <i>Erysiphe polygoni</i> , <i>Chaetomium globosum</i> , <i>Cunninghamella blakesleeana</i> , <i>Aspergillus oryzae</i> , <i>Rhizoctonia solani</i> and <i>Sclerotinia sclerotium</i> occurrence	Cyanobacterial extract	
(e) Disease resistance				
Cyanobacterial species	Plant species	Effect on plant	Effective agent	References
<i>Nostoc muscorum</i>	<i>Panicum miliaceum</i> L.	Prevention of the appearance of damping off in millet seedlings	Cyanobacterial extract	de Caire et al. (1979)
<i>Anabaena variabilis</i>	Tomato	↑ phenylalanine ammonia lyase, polyphenol oxidase	Cyanobacterial extract	Prasanna et al. (2013a).
<i>A. laxa</i> <i>Synechocystis</i>	<i>Nicotiana tabacum</i> (Tobacco)	Improvement resistance to numerous stress factors, including redox-cycling herbicides, intense temperatures, excessive irradiation, water scarcity, and UV radiation	flavodoxins (Flds)	Tognetti et al. (2006)
Cyanobacteria <i>Synechocystis</i>	<i>Agrostis stolonifera</i> L Various plants	Improved performance under oxidative, drought and heat stress Improvement of plant resistance to abiotic stress	Flavodoxin Glycinebetaine (GB)	Li et al. (2017) Chen and Murata (2008)
<i>Synechococcus</i> <i>Aphanothece</i> <i>halophytica</i>				
<i>Nostoc calcicola</i>	Soybean (<i>Glycine max</i> (L.) Merr. cv. Nam Dan)	Improvement of defense responses via antioxidant defense systems	Not found	Mai et al. (2017)
<i>Anabaena oryzae</i>	<i>Sorghum durra</i>	↑ Seed germination, improvement in antioxidant enzyme activity, root initiation, cell division and cell enlargement	Gibberellins, N-acetyl-D-glucosamine, Linalool, Dihydroxyphenyl glycol, Niacinamide	Essa et al. (2015)
<i>Nostoc ellipsosporum</i> <i>Synechococcus</i> sp.				
<i>Helianthus annuus</i> <i>Anabaena oryzae</i>	<i>Oryza sativa</i> (rice)	↑ Plant growth (shoot, root volume, and biomass), improvement of plant resistance to abiotic stress	Crude extract	Singh et al. (2011)
<i>Anabaena doliolum</i> <i>Phormidium delicata</i> <i>Calothrix geitonos</i> <i>Hapalosiphon intricatus</i> <i>Aulosira fertilissima</i> <i>Tolypothrix tenuis</i> <i>Oscillatoria acuta</i> <i>Plectonema boryanum</i>				

extractable fractions and only less than 14% of ^{14}C -MC-LR was adsorbed on soil particles. This finding showed that more than two thirds of the MC-LR present in irrigation water remained bioavailable in the soil and could thus have effects on seed germination and root and seedling growth, as well as its transfer to and accumulation in different tissues of the plant. Consequently, the seeds sown in the soil potentially constitute the first stage of contact with cyanotoxins present in irrigation water. However, to our knowledge the majority of studies on the impact of cyanotoxins on seed germination have been performed *in vitro* in a soil-free system. Generally, after sterilization by washing with sodium hypochlorite solution for 1 min, seeds were deposited in Petri dishes and covered with filter paper moistened with solutions of pure cyanotoxin standards or extracts of cyanobacterial cells containing cyanotoxins. The Petri dishes were then maintained in the dark for 1 week at 25 °C and after this period, the germination rate was calculated and the length of seedling radicles measured. Under these conditions, several studies reported that MCs were associated with inhibition of germination and growth of several agricultural and forage plants (Crush et al., 2008; El Khaloufi et al., 2011; Saqrane and Oudra, 2009). Kurki-Helasma and

Meriluoto (1998) showed that MC-RR at a concentration of 5 µg/ml significantly reduced seed germination of *Sinapsis alba* (Brassicaceae). Furthermore, Pflugmacher et al. (2006) reported that germination of alfalfa seeds was inhibited by both purified MCs and anatoxin-a and by a crude extract from a cyanobacterial bloom containing these toxins. More recently, EL-Sheekh et al. (2013) reported that a *M. aeruginosa* (Microcystaceae) crude extract containing 200, 300 and 500 µg/ml MC equivalents induced a reduction in germination of maize seeds (Poaceae) by 23, 33 and 47%, respectively; while a high concentration of 800 µg/ml completely inhibited the germination of seeds after 4 days of growth. Seeds of two varieties of tomatoes (Solanaceae) (MicroTom and Saint-Pierre), wheat (*T. aestivum* (Poaceae)) and lettuce (*L. sativa* var. Les capitata (Asteraceae)) were exposed to a MC-containing crude *M. aeruginosa* (Microcystaceae) extract (0–20 mg MC-LR eq./L) for 7 days, resulting in inhibition of germination for only the wheat seeds (Poaceae), with an EC₅₀ of 11 mg eq. MC-LR/L (Corbel et al., 2015c). Similarly, Saqrane et al. (2008) showed that an aqueous cyanobacterial extract containing MC-LR induced a significant inhibition of seed germination in another species of wheat (*T. durum* (Poaceae)) with an

EC₅₀ of 11 mg eq. MC-LR/L and El Khalloufi et al. (2012) reported that a cyanobacterial extract containing 16 mg eq. MC-LR/L significantly reduced (40%) seed germination of another tomato species (*Lycopersicon esculentum* (Solanaceae)). In addition, Saqrane et al. (2008) reported that the effect of a cyanobacterial extract at different concentrations of MCs (0–12 mg/L) on seed germination rates of *Lens esculenta* (Fabaceae), *Zea mays*, *Triticum durum* (Poaceae) and *Pisum sativum* (Fabaceae) was dose dependent and significantly different between species, in agreement with Chen et al. (2004) showing that rice seeds (Poaceae) are more resistant to MCs than rapeseeds.

The low sensitivity of seeds from certain plant species to MC-containing cyanobacterial extracts or pure MC variants could be due to the impermeability of the pericarp, which does not allow the passage of cyanotoxins through its rigid shell. However, after germination, the emerging radicle could be much more sensitive to cyanotoxins even at very low concentrations. In fact, Sanevas et al. (2006) studied the phytotoxic behavior of a crude extract of the cyanobacterium *Hapalosiphon* sp. (Hapalosiphonaceae) on the initial growth and cell division of many plant species. While the extract did not influence the germination rates of the plants, root and shoot development was considerably reduced, indicating that roots were more sensitive to the extract than shoots (Sanevas et al., 2006). Furthermore, Corbel et al. (2015c) reported that although a *M. aeruginosa* (Microcystaceae) extract containing MCs at 0.1 mg/L had no significant effects on the germination of seeds of two tomato (Solanaceae) varieties (MicroTom and Saint-Pierre) and lettuce *L. sativa* var. Capitata (Asteraceae), significant effects were observed on the growth and morphology of radicles of these plants. In contrast, in the same study the authors reported that no significant differences compared to the control were observed either with low or high concentrations of MCs on the emergence of sprouted wheat (Poaceae) radicles. However, Pflugmacher et al. (2007) reported that the root length of the germinated seed of wheat *T. aestivum* (Poaceae), was inhibited by 44% using a crude cyanobacterial extract containing 5×10^{-4} mg eq. MC-LR/L. Chen et al. (2012) reported that a cyanobacterial extract containing high concentrations (>2 mg/L) of MC-LR affected rice (Poaceae) root morphogenesis by inhibiting root elongation, crown root formation, and lateral root development from primordia. However, in an earlier study they reported that lower MC-LR concentrations (0–0.2 mg/L) did not affect rice (Poaceae) root growth. Márta et al. (2003) reported that MCs had a pronounced inhibitory effect on the number of primary roots, epicotyl length and lateral root formation of white mustard seedlings. These alterations in root architecture and development could be attributed to the activity of MCs on cytoskeletal elements such as microtubule (MTs) and microfilament (MFs) organization and inhibition of mitosis (Máthé and Vasas, 2013; Máthé et al., 2013). This organization is strongly dependent on protein phosphorylation/dephosphorylation and on the synthesis of certain regulatory proteins like microtubule-associated proteins (Hamada, 2007; Yokota et al., 2000). Therefore, inhibition of protein phosphatase activities by MCs and protein synthesis by CYN are likely to interfere with several plant mechanisms, leading to stimulation or inhibition of development and growth of primary and lateral plant roots. Several studies reported that pure MC congeners and MC-containing crude cyanobacterial extracts exert a characteristic dose-dependent effect on the development and growth of primary and lateral plant roots. They stimulate the growth of these roots at low doses of MCs or with short exposure times, versus inhibition of growth at higher doses (Máthé et al., 2013). For example, Corbel et al. (2015) reported that after 7 days exposure to a *M. aeruginosa* (Microcystaceae) extract containing 0.05 mg eq. MC-LR/L, the length of the radicles of tomatoes (Solanaceae; Saint-Pierre) increased significantly by 125% when compared to the control. However, at the highest concentration (20 mg eq. MC-LR/L) they decreased significantly below the control value. This dualistic response is presumably related to the following mechanism: At low concentrations, partial inhibition of ser/thr protein phosphatases (PP1 and PP2A) induces the maintenance of phosphorylation state of certain

mitogen activated protein kinases (MAPKs), activating them and causing stimulation of root cell growth. However, a severe inhibition of PP1 and PP2A at high concentrations of MCs will induce a general disturbance of cell functionality that leads to root cell death.

Considering the importance of primary and secondary roots in, among other things, the absorption of water and nutrients necessary for the first stage of plant development, their growth inhibition by cyanotoxins could subsequently induce alterations of growth, development, anatomy, cell structure and physiological/biochemical processes and health of the plants. Following exposure to a MC-containing crude *Microcystis aeruginosa* (Microcystaceae) extract, a reduction in the amount of roots and fronds, chlorophyll (a+b) concentrations and acid phosphatase activity were observed in the aquatic plant *Spirodela oligorhiza* (Lemnaceae) (Romanowska-Duda et al., 2002). In addition, cyanotoxins can also modulate absorption and content of plant minerals as exposure of lettuce (Asteraceae) to MC-containing crude cyanobacterial extracts induced an increase in macro-mineral (Ca, Mg, P, K, Na) content of roots (El Khalloufi et al., 2012; Lahrouni et al., 2013; Saqrane and Oudra, 2009). Exposure of *Lactuca sativa* (Asteraceae) and *V. faba* (Fabaceae) to MC-containing crude cyanobacterial extracts induced a decrease in the mineral content of the leaves (Lahrouni et al., 2013). In contrast to MCs, pure CYN caused an increase in micro-mineral (Fe, Mn, Cu, Zn, Mo) and macro-mineral (Ca, Mg, P, K, Na) contents in the leaves of lettuce (Asteraceae) (Freitas et al., 2015).

3.1.2. Inhibition of plant photosynthesis

Cyanotoxins present in irrigation waters can enter agricultural soils and result in severe negative impacts on crops from the perspective of histology, cytology, physiology and morphology, decreasing growth and yield. Plant growth is mainly influenced by four factors: light, water, temperature and nutrients. These are essential for plant growth, in particular photosynthesis, whereby light energy is used to transform simple molecules into organic substances that circulate between the leaves and the rest of the plant, being used for e.g. growth and stored in fruits and roots. Of the cyanotoxins present in irrigation and spray waters, MCs are of growing concern worldwide due to their ubiquity, stability and high toxicity, and their ability to disrupt the mechanisms of photosynthesis in agricultural plants and inhibit growth. To our knowledge, Siegl et al. (1990) reported for the first time that MCs can decrease the efficiency of photosynthesis through inhibition of light-dependent sucrose synthesis when MC-LR was administered to spinach (Amaranthaceae) leaves via the transpiration stream (Siegl et al., 1990). Since this pioneering work, several studies have confirmed this in other model and agricultural plants (Abe et al., 1996; do Carmo Bittencourt-Oliveira et al., 2016; Saqrane and Oudra, 2009). Increased net photosynthetic output, stomatal conductance, transpiration from the leaf tissue, and concentration of intercellular CO₂ were observed in lettuce (Asteraceae) exposed to various concentrations of MCs (do Carmo Bittencourt-Oliveira et al., 2016). Saqrane et al. (2009) showed a decrease of chlorophyll concentrations in *Z. mays* (Poaceae) and *L. esculenta* (Asteraceae) leaves after chronic exposure by irrigation for 30-days to 4.2 and 2.1 mg eq. MC/L, respectively. Similar results were obtained following exposure of tomato (Solanaceae) plants to 22 mg eq. MC/L (El Khalloufi et al., 2012). Corbel et al. (2015a, b, c) reported that chronic irrigation of tomato (Solanaceae) plants for a period of 90 days with lower MC concentrations (5–100 µg eq. MC-LR/L) did not induce a modification of chlorophyll-a and b concentrations or disturbed photosynthetic metabolism. However, in a study performed by Gutiérrez-Praena et al. (2014) in which tomato (Solanaceae) plants were exposed to MCs at 100 µg L⁻¹, modulations were detected in the function of various proteins related to ATP synthesis, carbon fixation, photosynthesis and carbohydrate metabolism that appear to be linked with an observed decrease in photosynthetic efficiency (Gutiérrez-Praena et al., 2014). Azevedo et al. (2014) observed a decrease in the expression of some proteins involved in photosynthesis in rice (Poaceae) plants exposed to 13 µg MCs/L. The contradictory results obtained in these

different studies may be associated with differences in the MC concentrations used and the MC congeners present in the crude cyanobacterial extract (Azevedo et al., 2014).

In contrast to MCs, very little information is available concerning the effect of nodularins (NOD) on plant photosynthesis. For example, Lehtimäki et al. (2011) reported that a NOD-containing crude extract of *Nodularia spumigena* (Aphanizomenonaceae) inhibited growth and bleached the leaves of Spinach (*Spinachia oleracea* (Amaranthaceae)); however, it did not disturb photosynthetic performance or the structure of the photosynthetic machinery in the chloroplast thylakoid membrane of this plant (Lehtimäki et al., 2011). Although CYN is a protein synthesis inhibitor, one study reported a significant increase in the abundance of proteins involved in photosynthesis in lettuce (Asteraceae) plants exposed to this toxin (Freitas et al., 2015). However, for neurotoxins (anatoxin-a and saxitoxins) there are few data on their phytotoxicity and particularly their effects on plant photosynthesis. The only study described in the literature is that relating to anatoxin-a showing reductions in the efficiency of photosynthesis and an increase in cation leakage in *Lemna trisulca* (Lemnaceae) (Kaminski et al., 2016).

3.1.3. Induction of oxidative stress

In various plants, MCs induce oxidative stress through the increased formation of reactive oxygen species (ROS) and/or depletion of non-enzymatic antioxidant glutathione (GSH) levels, which contribute to the major mechanism of their phytotoxicity (Corbel et al., 2014). In order to combat the adverse effects of these ROS and to assure their survival, plants develop antioxidant protection systems consisting of essential antioxidant enzymes such as superoxide dismutase (SOD), glutathione peroxidase (GPx) and peroxidase (POD), in addition to the synthesis of the non-enzymatic antioxidant glutathione (GSH) (Fig. 1) (Babica et al., 2006). Exposure of *Arabidopsis thaliana* (Brassicaceae) cells to MC-LR at 5 mg/L induced lipid peroxidation, decreases in glutathione (GSH) content and increases in superoxide dismutase (SOD) and catalase (CAT) activities (Yin et al., 2005). Similarly, exposure to pure MC congeners or MC-containing crude cyanobacterial extracts induced lipid peroxidation in both roots and shoots of several agricultural plants (*Pisum sativum*, *Cicer arietinum*, *Vigna radiata*, *Phaseolus vulgaris*, *Glycine max*, *M. sativa*, *Lens culinaris* (Fabaceae), *T. aestivum* and *Zea mays* (Poaceae)) (Peuthert et al., 2007). Exposure of *Lepidium sativum* (Brassicaceae) seedlings to pure microcystin-LR as well as to a MC-containing crude cyanobacterial extract induced an increase in lipid peroxidation, α - and β -tocopherols and antioxidant enzyme (glutathione peroxidase, glutathione S-transferase and glutathione reductase) activities (Stüven and Pflugmacher, 2007). El Khalloufi et al. (2013) reported that POD, PPO and CAT activities were highly increased in leaves, stems, and nodules of alfalfa (*Medicago sativa* (Fabaceae)) plants exposed to a MC-containing crude *Microcystis* sp. extract (Microcystaceae). Concerning NODs, although they present a similar structure and mechanism of action as MCs, there is relatively little knowledge on their effects on plants (El Khalloufi et al., 2013). NOD-containing crude *Nodularia spumigena* (Aphanizomenonaceae) extracts induced oxidative stress in spinach (Amaranthaceae) by modulating ROS levels and changing levels of enzymes involved in scavenging of reactive oxygen species (ROS), in addition to increasing α -tocopherol, an important non-enzymatic antioxidant (Lehtimäki et al., 2011; Shunmugam et al., 2013).

CYNs also induced oxidative stress in plants, probably through their effects on the metabolic CYP450 system (Beyer et al., 2009; Máthé and Vasas, 2013; Máthé et al., 2013; Prieto et al., 2011). This included modulation of enzymatic antioxidant activities as has been demonstrated for POD and SOD in shoots of the terrestrial white mustard plant seedlings and two aquatic plants, *Egeria densa* (Hydrocharitaceae) and *Lemna minor* (Lemnaceae) (Flores-Rojas and Esterhuizen, 2020; Flores-Rojas et al., 2015). Freitas et al. (2015) also reported that CYN induced an increase of the GST activity in the roots of lettuce (Asteraceae) which was time and dose dependent. However, following exposure to 100 μ g CYN/L for 5 days GPx activity was significantly

decreased in the roots and leaves (Freitas et al., 2015).

The phytotoxicity of neurotoxins remains limited. BMAA altered POD and CAT activity in aquatic mosses and ferns (Contardo-Jara et al., 2014) and increased ROS levels in *C. demersum* (Ceratophyllaceae) (Esterhuizen-Londt et al., 2011). However, no alterations were observed for terrestrial crops (Esterhuizen-Londt and Pflugmacher, 2019). Anatoxin-a induced oxidative stress in plants by increasing ROS levels, lipid peroxidation, and antioxidant enzyme activities both in aquatic plants *Lemna minor* (Lemnaceae) and *C. demersum* (Ceratophyllaceae) (Ha and Pflugmacher, 2013a, b; Mitrovic et al., 2004) and in the terrestrial plant alfalfa (*Medicago sativa* (Fabaceae)) seedlings (Pflugmacher et al., 2006). Furthermore, anatoxin-a exposure induced an increase of peroxidase activity in the aquatic plant *Lemna minor* (Lemnaceae) (Mitrovic et al., 2004) and carotenoid content in *C. demersum* (Ceratophyllaceae), which is a typical plant stress response (Ha and Pflugmacher, 2013b). A summary of the negative effects of cyanobacteria and their toxins on plants is given in Table 2.

3.2. Transfer of cyanotoxins in crops and impacts on human and animal health

3.2.1. Bioaccumulation of cyanotoxins in crops

For aquatic plants that naturally co-exist with toxic cyanobacteria, several laboratory and field studies have shown that they can bioaccumulate cyanotoxins (Al-Sammak et al., 2014; Esterhuizen-Londt et al., 2011; Kaminski et al., 2016; Mitrovic et al., 2004; Nowruzi et al., 2012, 2013b, 2018; Pflugmacher et al., 2001; Romero-Oliva et al., 2014; Saqrane and Oudra, 2009; Xiao et al., 2009). For example, exposure of the aquatic plant *Ceratophyllum demersum* (Ceratophyllaceae) to ¹⁴C-labelled MC-LR demonstrated that 11.2% of the applied toxin was bioaccumulated in the plant (Pflugmacher et al., 1999). Similarly, agricultural crop plants, irrigated with surface waters containing toxic cyanobacterial blooms, also accumulated cyanotoxins in their leaves, roots and other organs (Corbel et al., 2014; Lahrouni et al., 2016; Lee et al., 2017; Pindihama and Gitari, 2017; Saqrane et al., 2008; Saqrane and Oudra, 2009; Zamyadi et al., 2012). Waters used to irrigate crop plants are often taken directly from reservoirs and used without treatment, potentially contaminated with high concentrations of MCs (Corbel et al., 2014; Giannuzzi et al., 2011; Liu et al., 2011; Nasri et al., 2008). Unfortunately, these high concentrations of MCs can be absorbed and bioaccumulated by these plant crops and can therefore pose a possible threat to human and animal health (Bouaïcha and Corbel, 2016; Hereman and Bittencourt-Oliveira, 2012; Machado et al., 2017; Mohamed and Al Shehri, 2009; Redouane et al., 2021). Corbel et al. (2014) studied in a soil-plant system the fate of radiolabeled MC-LR (¹⁴C-MC-LR) in agricultural salty sand soil and its potential transfer to tomato (*Solanaceae*) seedlings. Their results showed that this MC congener underwent a low microbial mineralization and remained mobile in the soil column in large quantities (74–80% in aqueous soil extracts) and accumulated at up to 6 μ g/g in fresh tomato (*Solanaceae*) seedlings. Exposure of lettuce (Asteraceae) seedlings for 15 days by spraying their leaves with water containing different concentrations of a crude extract of *M. aeruginosa* (Microcystaceae) (0–13 μ g eq. MC-LR/L) showed bioaccumulation of MCs, reaching 158.35 μ g/kg (do Carmo Bittencourt-Oliveira et al., 2016). Recently, Cao et al. (2018) evaluated the bioaccumulation of MCs in a soil-plant (rice (Poaceae) and lettuce (Asteraceae)) system irrigated for 120 days with MC-containing water from Taihu Lake (China). They showed that in the soil-lettuce system, high concentrations of MCs were detected in roots and leaves with values reaching 424 and 183 μ g/kg, respectively. However, in the soil-rice system, the highest concentration of MCs (1504 μ g/kg) was detected in roots, whereas in grains it was extremely low (5.2 μ g/kg). Crop plants can also accumulate CYN present in irrigation waters (Cao et al., 2018), such as with *Brassica* species (*B. oleracea* var. *sabellica* and *B. juncea* (Brassicaceae)). When exposed in a hydroponic system using a CYN-containing cyanobacterial extract or with purified CYN, CYN

Table 2
Negative effects of cyanobacterial bioactive compounds.

(a) Effects on seed germination and root and seedling growth				
Cyanobacterial species	Plant species	Effect on plant	Effective agent	References
<i>Microcystis</i> sp.	<i>Sinapis alba</i>	Inhibition of germination and growth	MC-RR	Kurki-Helasma and Meriluoto (1998)
<i>Microcystis aeruginosa</i>	<i>Medicago sativa</i> (alfalfa)	Inhibition of germination, root development, oxidative disruption	Microcystin, anatoxin-a	Pflugmacher et al. (2006)
<i>Microcystis aeruginosa</i>	maize seeds	Reduction of germination	Microcystin	El Sheekh et al. (2013)
<i>Microcystis aeruginosa</i>	Tomatoes, wheat (<i>T. aestivum</i>) and lettuce (<i>L. sativa</i> var. <i>Les capitata</i>)	Inhibition of seed germination	Microcystin	Corbel et al. (2015).
<i>Microcystis aeruginosa</i>	<i>Lycopersicon esculentum</i> (tomato)	↓ Germination, Inhibition of <i>L. esculentum</i> development and efficiency, adverse effects on the operation of Photosystem II, Tissue necrosis of leaves ↑ Na ⁺ , K ⁺ , and Ca ²⁺ nutrients	Microcystin	El Khalloufi et al. (2012)
<i>Microcystis aeruginosa</i>	<i>Pisum sativum</i> , <i>Lens esculenta</i> , <i>Zea mays</i> , and <i>Triticum durum</i>	↓ Germination, duration of plant epicotyls, root length, and a net inhibition of lateral root development	Microcystin	Saqrane et al. (2008)
<i>Hapalosiphon</i> sp.	<i>Triticum aestivum</i> (wheat), <i>Allium cepa</i> (onion)	↓ root and shoot development, mitotic index of root cells (onion), number of cells in prophase, metaphase, anaphase, and telophase	Not found	Sanevas et al. (2006)
<i>Microcystis aeruginosa</i> <i>Aphanizomenon flos-aquae</i>	<i>Spinacia oleracea</i> (spinach)	Growth inhibition, chlorosis, inducing oxidative stress,	Microcystin-LR	Pflugmacher et al. (2007)
<i>Microcystis</i> sp.	Rice	Inhibiting root elongation, crown root formation, and lateral root development from primordia	MC-LR	Chen et al. (2012)
<i>Microcystis aeruginosa</i>	<i>Brassica napus</i> L. (rape), <i>Oryza sativa</i> L. (rice)	Growth and development inhibition	Microcystin	Chen et al. (2004)
<i>Microcystis</i> sp.	white mustard seedlings	Inhibitory effect on number of primary roots, epicotyl length and the lateral root formation	Microcystin	Márta et al. (2003)
<i>Microcystis</i> sp.	<i>Sinapis alba</i> L.	Growth stimulation at low doses of MCs or at shorter exposure times and growth inhibition at higher doses	Microcystin	(Máthé and Vasas, 2013; Máthé et al., 2013)
<i>Microcystis aeruginosa</i>	<i>Spirodela oligorrhiza</i> (water plant)	↓ Frond mass, chlorophyll concentration (a+b), and acid phosphatase activity	Microcystin	Romanowska-Duda et al. (2002)
<i>Microcystis aeruginosa</i>	<i>Lactuca sativa</i> and <i>V. faba</i>	Induction of decrease in the mineral content in the leaves	Microcystin	Lahrouni et al. (2013)
<i>Microcystis aeruginosa</i> <i>Cylindrospermopsis raciborskii</i>	<i>Lactuca sativa</i> L. (lettuce plants)	↑ GST activity in roots ↓ GPx activity in roots and leaves	Microcystin-LR, cylindrospermopsin (CYN)	Freitas et al. (2015)
(b) Inhibition of plant photosynthesis				
Cyanobacterial species	Plant species	Effect on plant	Effective agent	References
<i>Microcystis</i> sp.	spinach leaves	Decrease the efficiency of photosynthesis by showing an inhibition of light-dependent sucrose synthesis	Microcystin	Siegl et al. (1990)
<i>Microcystis aeruginosa</i>	Lettuce	↑ Photosynthetic output, stomatal conductance, transpiration of the leaf tissue, concentration of intercellular CO ₂ , superoxide dismutase, catalase, and peroxidase activities	Microcystin	do Carmo Bittencourt-Oliveira et al. (2016)
<i>Microcystis aeruginosa</i>	Tomato	Decrease in photosynthetic efficiency via modulation of various proteins related to ATP synthesis, carbon fixation, photosynthesis and carbohydrate metabolism	Microcystin	Gutiérrez-Praena et al. (2014)
<i>Microcystis aeruginosa</i>	Rice	Decrease in the expression of some proteins involved in photosynthesis	Microcystin	Azevedo et al. (2014)
<i>Nodularia spumigena</i>	Spinach (<i>Spinachia oleracea</i>)	Inhibit growth and bleached spinach leaves	Nodularin	Lehtimäki et al. (2011)
<i>Dolichospermum flos-aquae</i>	<i>Lemna trisulca</i>	Reductions in the efficiency of photosynthesis and increase of cation leakage in <i>Lemna trisulca</i>	Anatoxins and saxitoxins	Kaminski et al. (2016)
(c) Induction of oxidative stress in plants				
Cyanobacterial species	Plant species	Effect on plant	Effective agent	References
<i>Microcystis aeruginosa</i>	<i>Arabidopsis thaliana</i>	↓ Glutathione (GSH) levels ↑ Superoxide dismutase and catalase activities	Microcystin-RR	Yin et al. (2005)
<i>Microcystis aeruginosa</i> <i>Microcystis aeruginosa</i>	Alfalfa and wheat roots <i>Lepidium sativum</i> seedlings	Inducing cell injury ↑ concentrations of a- and b-tocopherols, glutathione peroxidase, glutathione S-transferase and glutathione reductase	Microcystin-LR, -LF and -LR Microcystin	Peuthert et al. (2007) Stüven and Pflugmacher (2007)
<i>Microcystis aeruginosa</i>	<i>Medicago sativa</i> seedlings	↓ Photosynthetic pigments ↑ POD, PPO and CAT activities	Microcystin	El Khalloufi et al. (2013)
<i>Microcystis aeruginosa</i>				

(continued on next page)

Table 2 (continued)

(a) Effects on seed germination and root and seedling growth				
Cyanobacterial species	Plant species	Effect on plant	Effective agent	References
	<i>Lemna minor</i> and <i>C. demersum</i> , alfalfa (<i>Medicago sativa</i>) seedlings	Induction of oxidative stress in plants by increasing ROS levels, lipid peroxidation, and antioxidant enzymes activities	Anatoxins BMAA	(Ha and Pflugmacher, 2013a, b; Mitrovic et al., 2004)
(d) Bioaccumulation of cyanotoxins in crops				
Cyanobacterial species	Plant species	Effect on plant	Effective agent	References
<i>Microcystis aeruginosa</i>	<i>Ceratophyllum demersum</i>	↑ Microsomal GST activity (above 0.12 µg/L), soluble GST activity (above 0.5 µg/L) ↓ Microsomal GST activity (above 1.0 µg/L)	Microcystin-LR	Pflugmacher et al. (1999)
<i>Microcystis aeruginosa</i>	tomato seedlings	MC's congener underwent a low microbial mineralization and remained mobile in the soil column in large quantities (74–80% in aqueous soil extracts) and accumulated up to 6 µg/g in fresh tomato seedlings	MC-LR (¹⁴ C-MC-LR)	Corbel et al. (2014)
<i>Microcystis aeruginosa</i>	rice and lettuce	High concentrations of MCs were detected in roots and leaves with values reaching 424 and 183 µg/kg	Microcystin, CYN	Cao et al. (2018)
<i>Cylindrospermopsis</i> sp. <i>Aphanizomenon</i> sp.	<i>Brassica</i> species (<i>B. oleracea</i> var. <i>sabellica</i> and <i>B. juncea</i>)	Accumulation of toxin in leaves with levels ranging from 18 to 35 µg/kg	CYN	Kittler et al. (2012)
Not found	alfalfa (<i>Medicago sativa</i>) seedlings	Both NPAAAs significantly inhibited root growth of this plant	Non-protein amino acids (NPAAAs) L-β-N-methylamino-L-alanine (BMAA) and its structural isomer L-2,4-diaminobutyric acid (DAB)	Samardzic et al. (2021)

*↑ = increase, ↓ = decrease.

accumulated in the leaves at between 18 and 35 µg/kg. Likewise, absorption of the cyanobacterial neurotoxin, β-N-methylamino-L-alanine (BMAA), in cultivated plants was also observed (Kittler et al., 2012). Irrigating *Triticum aestivum* (Poaceae) seedlings for 28 days with water contaminated with 100 µg/L BMAA resulted in absorption of this neurotoxin in roots and shoots, and its incorporation and bioaccumulation in proteins (Contardo-Jara et al., 2014). Recently, Samardzic et al. (2021) investigated the toxicity of the cyanobacterial non-protein amino acids (NPAAAs), L-β-N-methylamino-alanine (BMAA) and its structural isomer L-2,4-diaminobutyric acid (DAB), in the forage crop plant alfalfa (*Medicago sativa* (Fabaceae)) seedlings, which were exposed to NPAA-containing media for four days. Both NPAAAs significantly inhibited root growth of this plant. Consequently, all previously mentioned studies clearly show that cyanotoxins might be taken-up into crop plants from contaminated irrigation waters and enter the food chain. This may represent a supplementary exposure pathway for these toxins and therefore create risks to human and animal health (Samardzic et al., 2021).

3.2.2. Impacts on human and animal health

People may be exposed to cyanotoxins through multiple routes: drinking water, inhalation and dermal contact during recreational activities, hemodialysis, consumption of cyanobacterial dietary supplements as well as contaminated vegetables and fruits irrigated with water containing cyanotoxins and aquatic organisms from contaminated waters (reviewed in (Corbel et al., 2014; Drobac et al., 2013)). While the drinking water route is well known, human exposure through plant crops needs to be further investigated due to frequent reports of cyanotoxins in these plants (Cao et al., 2018; Corbel et al., 2014; Drobac et al., 2013; Llana-Ruiz-Cabello et al., 2019; Machado et al., 2017). To protect consumers from the adverse effects of MCs, the WHO has suggested a Tolerable Daily Intake (TDI) of 0.04 µg/kg body weight (bw). Unfortunately, until now, there have been no guidelines on the regulation of cyanotoxins in edible plants; although the recent European Food and Safety Authority (EFSA) report on cyanotoxins in food pointed out that the accumulation of MC in edible plant crops may exceed the WHO-TDI guideline (Testai et al., 2016). However, there is a limited number of epidemiological studies focusing on this route of exposure. One study investigating cyanotoxin-plant associated human health

effects examined the incidence of amyotrophic lateral sclerosis/Parkinson dementia complex (ALS/PDC) in the population of Guam in the Pacific (USA), linked to the consumption of cycad seeds (Cycadaceae) contaminated by the neurotoxin, β-methylamino-L-alanine (BMAA) (Banack et al., 2006). This neurotoxin is produced by a cyanobacterial species of the genus *Nostoc* (Nostocaceae) living in symbiosis in the roots of this plant (Banack and Cox, 2003). Dobrac et al. (2017) examined the bioaccumulation of MCs in leaves and pepper fruits of *Capsicum annuum* (Solanaceae), irrigated with water containing MCs for a period of 3 months. Data from this study showed that MCs did not accumulate in leaves, but could accumulate in fruits at concentrations reaching the acceptable WHO-TDI guideline (Drobac et al., 2017). In contrast, Cao et al. (2018) reported that consumption of rice (*Oryza sativa* L. (Poaceae)) irrigated for 120 days with water from a lake contaminated with MCs (5.22 µg/L) posed no human health threat. However, when the same water was used for irrigating of lettuce (*Lactuca sativa* L. (Asteraceae)) for 60 days, the estimated daily intake (EDI) values of MCs following consumption of this plant by adults and children could have reached the WHO-TDI guideline (Cao et al., 2018). Several studies have shown that in plants, cyanotoxins, especially MCs, accumulate mostly within the roots, leaves and stems, but much less in fruits (reviewed in (Machado et al., 2017)). Consequently, tissues that accumulate cyanotoxins such as roots, stems and leaves and which may not be edible by humans but are eaten by herbivorous animals could pose a health problem for the latter. In addition, it is important to underline that BMAA can occur not only as a free amino acid, but also in a protein-associated form in plant tissues (Contardo-Jara et al., 2014; Esterhuizen-Londt et al., 2011; Murch et al., 2004). Furthermore, several studies have shown as much as 60–90% of the total MCs contained within the tomato (Solanaceae) tissues are covalently bound (Corbel et al., 2016). Therefore, BMAA- or MC-associated proteins may act as reservoirs for these toxins, potentially being transferred between different trophic levels of food webs. Recently, Samardzic et al. (2021) reported that β-N-methylamino-L-alanine (BMAA) and its structural isomer L-2,4-diaminobutyric acid (DAB) were detected in free and protein-bound fractions, with higher concentrations in free fractions from alfalfa (*Medicago sativa* (Fabaceae)) roots and seedlings (Samardzic et al., 2021).

4. Plant bioactive compounds as promising ecological tools to control toxic cyanobacterial blooms

Various biological and chemical technologies have been proposed and used to prevent cyanobacterial blooms in freshwater reservoirs. For example, in order to control cyanobacterial proliferation in some dams, phytoplanktivorous fish such as Chinese silver carp (*H. molitrix*) and common carp (*Cyprinus carpio*) (Cyprinidae) have been introduced (Jia et al., 2014). Although this biological control has given some satisfactory results in controlling the massive development of toxic cyanobacteria, several studies have shown that these fish species can bioaccumulate high concentrations of cyanotoxins and could pose a health risk to consumers (Drobac et al., 2013). Moreover, chemical algacides such as copper sulfate ($\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$) have been used for decades to control noxious phytoplankton in surface waters (Millie et al., 1995). However, while it is possible to control algae by this algacide in small reservoirs, it is difficult to control their growth in large lakes, where tons of copper sulfate may be needed to affect algal blooms. In addition, the application of copper sulfate often results in negative side effects, including the potential release of cyanotoxins (Zamyadi et al., 2020) as well as effects on other non-harmful algae and aquatic plants, which are necessary for biodiversity in aquatic ecosystems (Baek et al., 2014).

Therefore, the use of new alternative methods, which are environmentally friendly and economically and technologically feasible, to prevent toxic cyanobacterial blooms and reduce health risks has become a priority. In recent years, the use of natural products isolated from aquatic and terrestrial plants has received more attention and is now considered an alternative to chemical agents to control the development of toxic cyanobacteria (Li et al., 2016; Tazart et al., 2019; Zerrifi et al., 2020). For example, aromatic and medicinal plants are known to produce a wide range of bioactive compounds that can affect the growth and development of toxic microalgae (Mohamed, 2017). Pakdel et al. (2013) demonstrated that extracts of *Chara australis* (Characeae) inhibited the growth of the filamentous cyanobacterium *Dolichospermum variabilis* (Aphanizomenonaceae) but without toxicity to the green alga *Scenedesmus quadricauda* (Scenedesmaceae) (Pakdel et al., 2013). Wang et al. (2014) showed that extracts of two emerging plants *Typha latifolia* (Typhaceae) and *Arundo donax* (Poaceae) at a concentration of 50 $\mu\text{g}/\text{mL}$ inhibited the growth of *Microcystis aeruginosa* (Microcystaceae) by more than 40% (Wang et al., 2014). Furthermore, Wang et al. (2015) showed that essential oils (EOs) from different macrophytes such as *Potamogeton cristatus*, *Potamogeton maackianus*, *Potamogeton lucens* (Potamogetonaceae), *Vallisneria spirulosa* (Hydrocharitaceae), *Ceratophyllum demersum* (Ceratophyllaceae) and *Hydrilla verticillata* (Hydrocharitaceae), inhibited the growth of *Microcystis aeruginosa* (Microcystaceae) at rates of more than 30% (Wang et al., 2015). Recently, Zerrifi et al. (2020) reported that EOs extracted from *Thymus broussonetii* (Lamiaceae) present a most promising and eco-friendly alternative approach for controlling *Microcystis aeruginosa* (Microcystaceae) in aquatic ecosystems.

5. Conclusions and future directions

Cyanobacteria can be very effective in enriching the nutritional status of the soil by improving the bioavailability of organic carbon, nitrogen and phosphorus for plants and in controlling pests and diseases that can ultimately lead to deterioration in product quality and reduced harvests. Plant-cyanobacteria interactions as a beneficial symbiosis have long been highlighted in rice-growing areas where the most efficient nitrogen-fixing cyanobacteria are present. More recently, the positive effects observed with bioactive compounds of cyanobacteria on growth of various crop plants have reinforced the idea concerning their exploitation as biofertilizers to replace chemical fertilizers as well as to satisfy increasing organic-farming demands. However, this interest has been hampered by the negative effects linked to the phytotoxicity of

cyanotoxins and their transfer and accumulation in various crop plant tissues. However, the presence of cyanotoxins in cyanobacterial biomass or in irrigation water at environmental concentrations may also have multiple positive effects on plant growth, disease resistance or tolerance towards abiotic stresses. Corbel et al. (2015a, b, c) reported that in a plant–soil system, cyanobacterial extracts containing realistic environmental concentrations of MCs significantly increased the dry weight of the aerial part of the tomato *Solanum lycopersicum* (Solanaceae) (MicroTom variety) and the nitrification potential of the soil with an increase in *amoA* gene abundance corresponding to the ammonia-oxidizing bacterial community. Moreover, MCs are known to inhibit the growth of metazoans, which pose a possible danger to plant health (Paerl et al., 2001).

Thus, cyanobacterial biomass can be used to improve the quality of soils and to positively change growth capacities of plants and make them more resistant to biotic and abiotic stresses that will likely occur more often with climate change. Although our knowledge of how plants react positively and negatively to the effects of cyanobacterial bioactive compounds has increased in recent years, most of this evidence is produced in the laboratory on model plants and in hydroponic systems. Therefore, there is an urgent need to address certain key issues such as the benefit risk balance of exploiting toxic or non-toxic cyanobacterial biomass in the open field in order to assess the fate and stability of the various compounds of cyanobacteria in agricultural soils and to achieve the objective for safe agriculture and environmental sustainability. In addition, cyanobacteria used as inoculums in agriculture may also require analysis to determine whether toxic compounds may be present. Furthermore, to improve their utility in agriculture, cyanobacteria can be genetically modified to potentially increase their growth (Volkman and Gorbushina, 2006; Volkman et al., 2006) or attenuate their capacity to biosynthesize cyanotoxins (Dittmann et al., 1997).

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