Reduction in Trace Element Mediated Oxidative Stress towards Cropped Plants via Beneficial Microbes in Irrigated Cropping Systems: A Review

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Abstract: Summer crops grown in Australia, including rice, cotton, and sugar cane, require high volumes of water, which is applied using irrigation systems. Yields from these crops are influenced by abiotic stressors. Fluctuations in the abiotic stressors, including soil pH and trace element availability, can increase levels of reactive oxygen species (ROS) in plants leading to increased oxidative stress and subsequent reduced crop growth and yield. One potential way of reducing plant ROS production and levels in these systems is through inoculation of these crops with beneficial microbes. The ability of beneficial microbes to enhance plant growth is well characterized, and it is also clear that many of them produce antioxidant enzymes. Presented in this review are the potential modes of action for microbes to reduce abiotic stress in cropped systems.

1. Introduction

Plant stressors impact yields of both summer and winter crops, including canola, wheat, sugar cane, corn, cotton, and rice. The main abiotic plant stressors that impact crop growth include fluctuating temperatures, soil pH, salinity, soil water availability (drought), diurnal cycling changes, and availability of soil nutrients [1–12]. Summer crops grown in Australia, including rice, cotton, and sugar cane, require high volumes of water, which is applied using irrigation systems. In Australia, winter crops, including canola, wheat or maize are planted in rotation with the aforementioned summer crops and grown [13–15] using the seasonal precipitation and residual moisture from the irrigation season. Summer irrigated crops are of high economic value, producing a combined export income between $5.8–6.8 billion AUD annually [16–18], whilst their winter counterparts had an export value of $10.2 billion AUD in 2016 [19].

The irrigation strategies for these crops can either be 'high' or 'low' depending on the crop plant being cultivated, season or soil profile [6,15,20,21]. High irrigation strategies primarily refer to flood irrigation (largely water inefficient), whereas low water types include subsurface drip irrigation, sprinkler irrigation, localized irrigation, and lateral move irrigation (highly water efficient) [22,23]. Currently, flood irrigation is the main practice used in Australia for delivering consistent large volumes of water to maintain a moist soil environment that propagates crop growth [24].

Throughout the growing season, irrigated soils fluctuate between aerobic and anaerobic states based on water availability in the soil. The type of irrigation strategy will also have profound effects

on the soil temperature, soil pH, water salinity, soil water availability (water activity), light intensity, and availability of trace elements (Figure 1) [1,24]. Thus, the influence of irrigation strategies on the abiotic characteristics of agroecosystems can lead to the formation of abiotic stress towards the cropped plants [25].
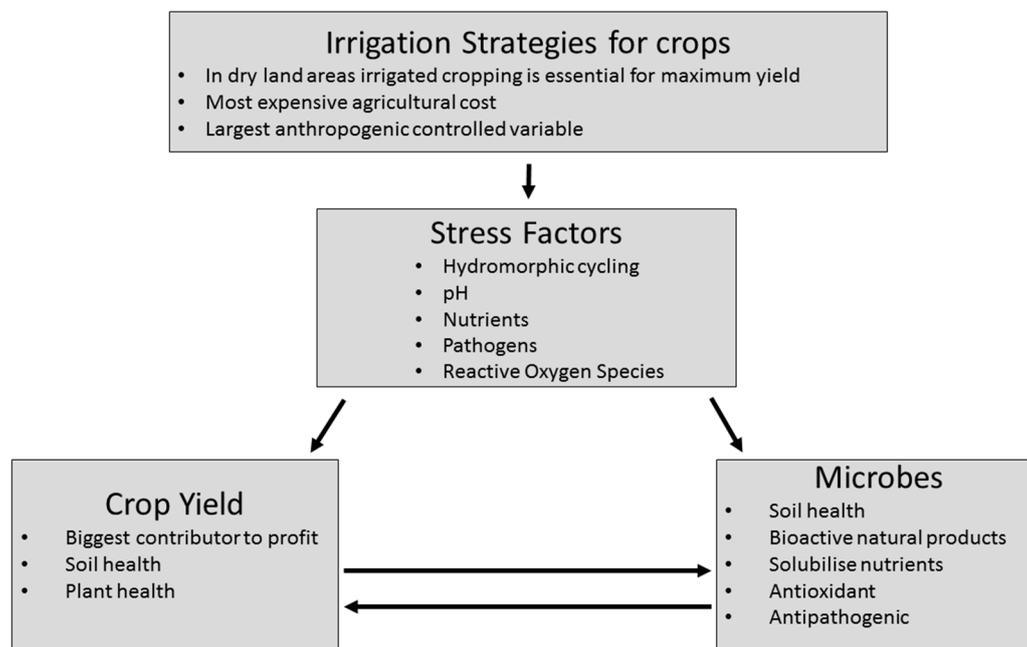
Figure 1. Irrigation strategies associated with the propagation of crops are the most expensive anthropogenically controlled variable and whilst important for maximum yield, they also have a large influence on stress formation. These stress factors include hydromorphic cycling, fluctuation in pH, nutrient availability, pathogenic attack, and ultimately reactive oxygen species formation. These stress factors influence both crop yield and microbial diversity of soils. Crop yield is the biggest contributor to profit and relies on optimal soil and plan health. Microbes in the soil can be beneficial to plants and soil health by producing bioactive compounds, solubilizing nutrients and having anti-pathogenic activity. They also have high levels of antioxidant activity, which can potentially alleviate stress towards cropped plants inflicted by soil stress factors.

Trace element availability is an abiotic stressor that directly impacts growth and yield of cropped plants and is influenced by irrigation strategy [26]. Trace elements are found in small concentrations (mg/kg^{-1} or less) in the environment and include: copper (Cu), cobalt (Co), zinc (Zn), iron (Fe), nickel (Ni), manganese (Mn), vanadium (V), selenium (Se), and molybdenum (Mo). These are essential as they act as cofactors for enzymatic activities and other metabolic processes in plants [27]. Irrigation affects trace element availability by solubilizing these metals, changing soil pH, changing soil transformation rate, and subsequent redox changes associated with soil compounds [6,28].

Differences in trace element availability are observed between flooded soils and dry soils, and it is known that Zn solubility differs greatly between flooded anaerobic soils compared to aerobic dry conditions [29]. This change in trace element solubility has become a major concern for the production of rice crops as cultivation practices change. As irrigated soils dry out and become aerobic, associated pH and redox changes render some trace elements unavailable—referred to as 'nutrient lock out' [27,30,31]. Moreover, the bioavailability of non-essential heavy metals, including arsenic (As), cadmium (Cd) and mercury (Hg), is also affected by changes in anaerobic/aerobic cycling, and these metals are typically more toxic at much lower concentrations compared to essential trace elements [27].

Metal levels in soil can range from less than 1 ppm (0.0001%), through to 100,000 ppm (10%) or higher in extreme cases [32,33]. Fluctuations of metal levels in the environment alters their availability to the biota. Generally for higher plants, the deficiency limit of essential metals, such as Cu, Mn,

Ni, and Zn required for normal cellular functioning and growth is: 20–30 mg/kg, 200–5300 mg/kg, 10–50 mg/kg and 100–300 mg/kg, respectively [34]. When concentrations of these metals exceed these trace-levels they start to reduce cellular metabolism leading to toxicity, and in the most drastic case the death of the plant [21,23].

For most uncontaminated soils, the levels of trace metals Co, Cu, Mn, Ni, and Zn are in the ranges of 0.08–29 µg/L, 0.5–135 µg/L, 25–8000 µg/L, 0.2–150 µg/L and 0.1–750 µg/L, respectively [35]. Optimal levels of trace elements such as Fe, Mn, Cu, and Zn are required for both catalase and superoxide dismutase antioxidant activity [36]. These enzymes break down both H_2O_2 and superoxide that forms from oxidative stress, respectively. When levels of free metals become too high, rather than act as co-factors, these metals become cytotoxic and cause damage to plants through the influence of physiological changes that result in ROS formation and eventual oxidative damage towards plants [37]. However, sub-optimal levels of trace elements can lead to oxidative stress being unregulated, as the activity of enzymes that break-down ROS (e.g., catalase) may be inhibited without the metal ion co-factors, leading to the loss of homeostatic control of ROS [38].

2. Physiological and Biochemical Impacts of Oxidative Stress towards Cropped Plants

The two primary ways abiotic stressors cause oxidative stress towards plants is either by creating imbalance in the metabolic pathways or a reduction in the efficiency of antioxidant enzymes [39–41].

Abiotic stressors can reduce growth and metabolism by increasing unmoderated production of free-radicals, such as reactive oxygen species (ROS) [3,4,42]. Free radicals that form after exposure to these abiotic stressors, such as OH^-, are capable of damaging the heterocyclic bases and the sugar-phosphate backbone of DNA. Other ROS, including $H^.$ free radicals and free electrons, react with the double bonds in DNA [43]. Free radicals can damage lipids and other cellular components by oxidizing them (via attack of paired electrons), and are directly linked to a reduction in cellular viability leading to oxidative stress [2,44]. On a farming scale, the impacts of oxidative stress on crops can potentially result in large losses of biomass, yield, reduced seed vigor, reduced germination efficiency, improper plant development, loss of plant viability and ultimately, reduced economic benefit to the grower [1,45,46].

Most abiotic stressors inflict oxidative damage towards cropped plants by inducing the overproduction of free radicals as part of essential metabolic processes, including photosynthesis. These abiotic stressors can include shifts in diurnal cycling, where a cropped plant is exposed to fluctuating light intensities [47], and drought conditions in soils where osmotic stress impacts the crop [48].

During photosynthesis, when exposed to high levels of light, the electron transport chain becomes over-reduced and harmful ROS species are produced [49]. Similarly, fluctuations in temperature lead to stress development in plants. Low temperature stress reduces seed vigor, growth, and metabolic activity [50], whilst high temperature exposure in plants results in leaf membrane degradation and lipid peroxidase damage linked to increased ROS activity, as observed in *Jatropha curcas* (Nettlespurge) [51]. Variances in water availability lead to osmotic stress (the reduction in turgor and water potential of plants), sufficient to disrupt normal metabolism and induce desiccation of plant tissues [52,53]. In *Brassica napus* L. (canola) leaves, growth reducing oxidative damage caused by reduced water availability has been observed to occur at around −1.5 MPa. This is due to increased lipid peroxidation, reduced phospholipid and galactolipid content of leaf cells, and altered leaf structure [54].

Trace element availability has varying effects on oxidative stress in cropped plants and is the abiotic stressor that has the highest influence on antioxidant enzyme activity. The bioavailability of trace elements for cropped plants are heavily influenced by soil factors including: soil pH, soil organic matter (SOM) content, and Mn/Fe oxyhydroxide presence [55], indicating that irrigation and soil properties are ultimately the drivers of trace element induced oxidative stress towards cropped plants.

3. The Impact of Trace Element Availability on the Induction of Oxidative Stress in Cropped Plants

The availability of metals fluctuates between anaerobic (high moisture) conditions and aerobic (low moisture) conditions. Increased metal solubility leads to higher levels of bioavailable metals in soils leading to potentially growth-inhibiting toxicity in plants. Low metal solubility results in nutrient lockout of some trace elements, inhibiting plant growth and exacerbating other stressors on the crops [1,24,31]. The tendency for flood irrigation to solubilize more metals than in drier soil conditions is suspected to be due to increasing overall soil pH, increasing metal precipitation with chemical compounds such as sulphides and increased concentrations of Fe oxides [6].

Increasing heavy metal availability is also of concern to crop health and this fluctuates with irrigation strategy. Under flooded irrigation conditions, AS bioavailability increases, which in turn can lead to higher uptake of As by plants resulting in reduced plant growth or even death. Likewise, the use of sprinkler irrigation has shown to reduce concentrations of As in the soil; however, it has been shown to increase concentrations of Cd [21,23].

The mode of action for free metal mediated oxidative stress towards living organisms arises from chemical reactions that catalyze metabolic products into ROS. For example, the Haber-Weiss reaction is the catalysis of superoxide and hydrogen peroxide to harmful hydroxyl radicals by transition metals, mostly Fe and Cu [56]. It incorporates the Fenton reaction, which occurs when Fe^{2+} or Cu^+ reacts with hydrogen peroxide (e.g., produced in the mitochondrion as a cellular respiration by-product) into harmful hydroxyl radicals [57]. The Fenton reaction can be exacerbated when organisms are under Cu stress. Whilst Cu is a cofactor for SOD, higher SOD activity leads to higher levels of H_2O_2 being produced. This particular situation has been observed in some bacterial species including *Staphylococcus aureus* [58], *Mycobacterium tuberculosis* [59], and *Pseudomonas aeruginosa* [60].

For plants, the major source of Cu^+ is found in the roots, whilst Fe^{2+} and Mn^{2+} are primarily found in shoots, where they are heavily involved in photosynthesis [61]. Excessive Cu^+ levels in the soil can lead to localized Fenton reactions within the root walls, forming toxic hydroxyl radicals, causing chlorosis and ultimately reducing biomass [61]. Similarly, excessive soil Fe^{2+} or Mn^{2+} levels may lead to an imbalance in photosynthetic enzyme activity, resulting in an excessive production of hydroxyl radicals and subsequent photoinhibition [61].

Some bacterial species have been shown to combat free metal oxidative stress by substituting enzymes that require Fe^{2+} as a cofactor for homologues that have no requirement for it. For example, *Streptococcus pyogenes* has been demonstrated to substitute an Fe-containing ribonucleotide reductase (RNR) enzyme for an Fe-free homologue for DNA synthesis. Similarly, *E. coli* has been shown to be able to use Mn^{2+} as a substitute for Fe^{2+}, as a cofactor for its RNR enzyme [62].

Excessive levels of other free transition metals, including Cd, Co, Ni, and Zn are also known to cause stress challenges towards cropped plants. In *Spinacia oleracea* L. (spinach), 500 μM treatments of spinach for 10 days with each metal resulted in chlorosis and reduced the activity of CAT. Excess Cd, Co, and Ni also saw an increase in lipid peroxidation [63]. High concentrations of Zn, Co, Ni, and Cd have been shown to significantly interfere with physiological and genetic Fe homeostasis mechanisms, mimicking Fe-deficiency in plants such as *A. thaliana* [64]. The subsequent metal toxicity and Fe-deficiency reduces root elongation and growth, shoot weight, and chlorophyll content of leaves [64]. Excessive levels of Cu, Co, and Ni can also lead to oxidative stress by causing cytotoxicity and injury to plants through the production of ROS, and subsequent oxidative damage [37].

In contrast, a lack of trace element availability reduces metabolic function, as many enzymes and cellular processes require particular trace elements to maintain optimal activity for growth, reproduction, and defense [65]. In particular, plants can become susceptible to oxidative stress if particular trace elements become unavailable, as antioxidant defense mechanisms require these to function, such as Fe or Mn for catalases (CATs), or both Cu and Zn for superoxide dismutases (SODs) [66–68].

Ultimately, plant cells must have protection against free radical damage, balancing ROS production to allow for healthy growth whilst maintaining respiration and energy production [69]. To combat the challenges to growth and survival presented by abiotic stress, they have several antioxidant mechanisms in place, including CAT, SOD, ascorbate peroxidase, glutathione, and phytochelatins to reduce the production of ROS [51,69]. These enzymes act to reduce the accumulation of ROS and their activity is tightly regulated [51,69]. For example, in *Jatropha curcas* (Nettlespurge), antioxidant enzyme activity increases under heat stress to match increased H_2O_2 production, and the ability to limit ROS activity is linked to efficient detection and increased expression of genes in response to the stressor [51].

4. Plant Antioxidant Defenses against Oxidative Stress Challenges

Catalase enzymes oxidize H_2O_2 and are the most characterized antioxidant proteins [70,71]. In plants, two types of catalases exist, monofunctional catalases and bifunctional catalase-peroxidases [70,72]. In *Arabidopsis thaliana*, a small gene family encodes three CAT proteins, known as Cat1, Cat2, and Cat3, and this is typical of most plants, including *B. napus* (canola) [73]. The Cat1 enzyme is predominantly found in vascular tissue, Cat2 is largely found in leaf tissue and is primarily expressed in the morning period, and Cat3 is primarily abundant in seedlings and heavily involved in removing H_2O_2 from glyoxysomes, acting primarily in the evening period [74].

Some abiotic stressors reduce the efficiency of antioxidant enzymes. Saline soils induce stress towards cropped plants and lead to oxidative damage by reducing the activity of antioxidant enzymes. This occurs when the cellular balance of Na^+ and K^+ is disrupted [75], allowing for unregulated production and accumulation of ROS in plant tissues. Soil pH can influence the sensitivity of cells to ROS under either low or high pH conditions by changing bioavailability of trace metals, meaning they are either more or less available for uptake by plants [76]. Altered soil pH has been shown to limit bioavailability of trace elements, including Zn and Cu, which are essential for SOD activity in most plants [69,77]. Ultimately, low soil nutrients indirectly result in oxidative damage to plant cells, as the activity of enzymes that break-down ROS may be inhibited without the metal ion co-factors, hence allowing ROS to accumulate to deleterious levels [38].

High trace metal solubility is also detrimental to crop growth. Plants produce a glutathione (GSH, organic acid antioxidant that plays a role in reducing the impact of endogenous and exogenous ROS) [78], in response to elevated trace metal stress [37]. Plant phytochelatins work with GSH to chelate the metals to reduce toxicity impact. Glutathione then reduces H_2O_2 produced as a result of heavy metal exposure [37,78].

Whilst plants have antioxidant defense systems to deal with abiotic stress challenges, these systems are often limited in their ability to combat abiotic stress in broad-acre cropping systems. This is due to water and nutrient scarcity, as well as increasing temperatures due to climate change [79]. A potential way to promote crop plant stress tolerance is to utilize bacterial inoculants with high abiotic stressor tolerance, which may be able to provide a protective benefit for cropped plants [80].

5. Can Bacterial Antioxidant Activity Reduce Oxidative Stress towards Cropped Plants?

Plant growth promoting bacteria (PGPB) are microbes that form part of the plant holobiont [81]. They are found in the rhizosphere (the region of soil directly surrounding the roots), and are able to enhance plant growth through increased nutrient availability, production of plant growth hormones, and by providing protection from pathogens [81–83]. Well characterized bacterial plant growth promotion activities include: Nitrogen (N) fixation [84], 1-Aminocyclicpropane-1-carboxylase (ACC) deaminase activity (reduction of ethylene induced stress signaling) [85], increased phosphate solubilization [86], indole-3-acetic acid production (IAA—cell elongation and cell growth factor) [87], and pathogen suppression [81].

Bacteria have their own antioxidant enzymes for dealing with oxidative stress. Bacterial catalases, like those of plants, are also classified as monofunctional (HPII) or bifunctional (HPI) catalases,

as well as a third group of Mn-catalases [70]. The common catalase enzymes in bacteria are KatA, KatB, KatC, KatE, KatG, and KatM [70,88]. Bifunctional catalases (HPI) are generally activated when initially challenged by oxidative stress, whereas monofunctional catalases (HPII) are utilized as the cells grow into stationary phase [70]. Some soil bacteria, including *Pseudomonas fluorescens*, have high antioxidant and CAT activity, potentially being able to remove excess H_2O_2 from the rhizosphere, produced during photosynthesis by plants or from abiotic stressors [89,90].

Mn-Catalases lack a heme prosthetic group and instead contain a dimanganese cluster [70]. These catalases are known to be important in reducing stress associated with abiotic stress factors, including Fe deficiency, microaerophilic environments, temperature fluctuation, high saline environments, desiccant conditions, and exposure to chemicals such as cyanide [91,92]. Cyanobacteria from the genus *Anabaena* (known rice biofertilizers) have been shown to tolerate oxidative stress induced by high levels of salt and desiccation via their KatB Mn-CAT enzyme [92].

Bacterial CAT enzymes serve to reduce ROS accumulation associated with stressors rather than mediating, as both stressor reducers and intracellular signaling molecules (as seen in plants) [70]. The root nodule bacterium *Sinorhizobium meliloti* utilizes KatA, KatB, and KatC to cope with the production of H_2O_2 generated by bacterial N-fixation [89]. In *S. meliloti*, KatA activity primarily increases in response to exogenous H_2O_2 exposure, whilst KatC activity increases in response to abiotic heat and salinity stress [89]. The KatB enzyme is constitutively expressed throughout the whole growth period of the bacteria as an initial defense against oxidative stress [89]. In addition to reducing oxidative stress, *S. meliloti* utilizes catalase and other antioxidants to form symbioses with legumes, including *Medicago sativa* (alfalfa) [93], as part of the symbiosis process requiring the breakdown of plant produced H_2O_2 for nodule organogenesis [93].

Bacterial inoculants have also been shown to increase the antioxidant activity of plants when exposed to drought stress. Leaves of *Lactuca sativa* L. (Lettuce) were inoculated with *Pseudomonas mendocina* Palleroni, and either the mycorrhizal fungi *Glomus intraradices* or *Glomus mosseae*, or alone. The highest amount of CAT activity was observed in the *P. mendocina*-inoculated plants grown under severe stress conditions. Under moderate drought conditions, total peroxidase and CAT activity increased with bacterial and fungal inoculation, whilst SOD activity decreased [94], suggesting that these beneficial microbes could be used to alleviate oxidative stress in the lettuce.

While many soil microbes have the potential to enhance plant growth using antioxidants, some plant pathogens exploit their antioxidant systems during infection. Plants will use ROS as defense mechanisms to stop a pathogen from successful infection, often by releasing H_2O_2 into the environment or using oxidative burst [40,95,96]. For the proteobacterium *Xanthomonas citri*, enhanced production of KatG allows it to deal with the challenge of oxidative burst by citrus plants during infection of leaves [97]. It also allows for protection from UV radiation and subsequent biofilm formation [97]. Interestingly, KatG also confers resistance to microbicidal H_2O_2, and promotes virulence of *Actinobacter* spp. towards humans [98], suggesting that this bifunctional KatG enzyme may have a specialized role in defense and virulence for bacterial species [70,97,98]. As a bifunctional catalase, KatG has been shown to interact with other substrates such as guaiacol [70], and in *M. tuberculosis* infection in mammals, it is able to inactivate the anti-tuberculosis drug isoniazid [99].

Plants need to balance ROS production to allow for healthy growth, whilst maintaining respiration and energy production [69]. When grown under ideal conditions or moderately stressful conditions, plants reduce levels of ROS through CAT, SOD, ascorbate peroxidase, glutathione, and phytochelatin activity [51,69]. Under constant high stress from either insufficient nutrient availability or over exposure to high levels, these plants systems become insufficient and plant growth and prosperity is lost with plant death being the final outcome. One of the potential ways oxidative stress in cropped plants could be reduced is through inoculating plants with a beneficial microbe, which has the capacity to produce high levels of peroxidase/catalase enzymes that may directly reduce the oxidative stress in the plants through their interactions. Bacteria can also be highly capable of solubilizing nutrients from their environment and making them available through their production of siderophores. In nutrient scarce

conditions, some rhizospheral bacteria produce siderophores that chelate Fe previously unavailable for plant uptake, and deliver them to plants enabling both plant and bacteria to thrive [100,101].

Many bacteria are highly adept at tolerating fluctuation in trace metal availability. For example, in the model system *Nostoc punctiforme*, the highest non-toxic levels of trace elemental tolerance for Co, Cu, Mn, Ni, and Zn were determined to be 2 μM, 0.5 μM, 500 μM, 1 μM, and 18 μM, respectively [102]. However, for most bacterial cells, total intracellular trace metal levels are observed in the millimolar range (10^{-3}). Despite intracellular levels being very high, levels of trace metals that promote active uptake and efflux channels are usually in the femtomolar range (10^{-15}). Bacterial cells are able to combat the stress challenges presented by high concentrations of metals, such as Zn or Mn, by regulating efflux transporters embedded in the cytoplasmic membrane, hence excluding the metals from the intracellular environment and overcoming potential toxicity effects [103].

Although the bacteria increase the availability of metals to plants when they have limited access to them, they can help the plants meet their requirement to have ideal functioning of their own systems and enzymes—such as the aforementioned ROS reduction systems (CAT, SOD, ascorbate peroxidase, glutathione, and phytochelatin) listed above. In environments with toxic levels of trace elements, rhizospheral bacteria can protect plant roots from stress by acidifying, chelating, precipitating, complexing, or inducing redox reactions that reduce toxicity of those metals [104]. Under high environmental metal conditions, bacteria present in the soil may provide a buffering effect; where the metals will bind with high affinity to the bacteria cells (predominantly by charge with the cell walls) potentially reducing their direct availability to plants, therefore indirectly reducing oxidative stress towards cropped plants [102,105].

Bacteria isolated from heavy metal polluted environments have been shown to reduce toxic impacts of metals and even enhance plant growth. The Cu-resistant bacterium *Providencia vermicola* has been shown to protect lentils from oxidative damage when exposed to high Cu soil levels—both by reducing Cu uptake by the plants and production of indole acetic acid and siderophores [106]. Moreover, *P. vermicola* was able to increase root and shoot length, dry weight, and leaf size area of the lentils [106] compared to a negative control. In another study, two Zn-resistant *Rhizobium leguminosarum* strains were able to enhance growth of *Trifolium repens* (white clover) in high Zn conditions [107].

In nutrient scarce conditions, some rhizospheral bacteria produce siderophores that chelate Fe previously unavailable for plant uptake and deliver them to plants, enabling both plant and bacteria to thrive [100,101]. The PGPB isolate *Chrysiobacterium* spp. C138 (previously isolated from an *O. sativa* rhizosphere) has been shown to enhance Fe uptake in Fe-starved *Solanum lycopersicum* L. (tomato) [108]. Similarly, inoculation of maize seeds with siderophore-producing *Pseudomonas* spp. strains lead to increases in root and shoot growth, and hence larger dry weights [109]. Chemical chelators such as ethylenediaminetetraacetic acid (EDTA) are currently used to deliver trace elements to cropped plants with varying success [110]. Prolonged use is known to lead to ecotoxicological effects, as EDTA also increases the bioavailability of dangerous heavy metals in soils [111]. Ethylenediaminetetraacetic acid has also been shown to cause leaf necrotic lesions in *Brassica rapa* (Chinese cabbage), and to reduce root symbiosis with arbuscular mycorrhiza in *Trifolium pratense* (red clover) [111].

Bacterial metabolites have already been utilized for applications, including in cosmetics, as semiconductor components; and in dairy, food, and textile industries [91]. However, their use in an agricultural context as a stress reducing agent for cropped plants is relatively unexplored. Understanding the modes of action for microbial oxidative stress reduction towards cropped plants and modulating trace element availability is essential. In other instances, microbes previously identified to be plant growth promoting can induce oxidative stress towards plants in different growth systems. For instance, the *P. fluorescens* isolate DUS1-27 was previously shown to enhance *B. napus* L. (canola) growth in soil based systems; however, when grown in a hydroponic system with the plants, an oxidative stress response is observed [112]. This highlights the importance of understanding the modes of action for microbial antioxidant mediated stress reduction in plants, as changes in environment can negatively alter microbe associated molecular patterns. Importantly,

this highlights that expanding their use requires: (1) Understanding and characterization of how these bacteria reduce oxidative stress towards plants, and (2) confirmation as to which of these are relevant under field-based conditions.

Overall, abiotic stressors including soil temperature, moisture, Ph, and trace metal availability, all play a role in inducing oxidative stress towards irrigated cropped plants in the form of ROS. Ultimately, fluctuating trace metal availability can increase ROS production leading to increased levels of free radicals, such as hydroxyl radicals being formed. ROS imbalance in cropped plants not only reduces growth, but also reduces crop yields. The ability of beneficial microbes to enhance plant growth is well characterized and it is also clear that many of them have a high tolerance for trace metal fluctuations in the environment. Therefore, their characteristics and modes of action to reduce abiotic stress in cropped systems is worthy of further exploration to determine their potential to increase overall soil health and cropping sustainability, as well as to reduce input costs and increase yields.

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