Improving soil health

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E-CHAPTER FROM THIS BOOK

Biofertilizers: assessing the effects of plant growth-promoting bacteria (PGPB) or rhizobacteria (PGPR) on soil and plant health

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1 Introduction

The green revolution was driven by agricultural intensification resulting in increased productivity and incomes, but also a dependence on chemical substances in many developing countries of the world (Aeron et al., 2020). The uncontrolled application of synthetic agrochemicals imposes serious negative impacts on the environment and human and animal health, leading to a reduction in soil fertility and microbial diversity, soil pollution and environmental degradation and the development of resistance in phytopathogens and pests (Aeron et al., 2020). However, global demand for agricultural crops is increasing with yields still insufficient to face the ever-growing food demand (Timmusk et al., 2017). In this context, unsustainable agricultural intensification has often led to pollution, overexploitation of natural areas and resources, loss of soil fertility, soil erosion, salinization, runoff and in some cases desertification (IPCC, 2019, special

report; https://www.ipcc.ch/srccl/). Drought and land degradation following the salinization of soil are considerably increasing worldwide, and the ongoing climate change could amplify the negative effects of this scenario (Corwin, 2021). For these reasons, together with the increasing awareness of consumers about healthy food, sustainable agricultural practices are encouraged as alternatives to mineral fertilizers and synthetic pesticides (Brodt et al., 2011).

Sustainable agricultural management practices include the use of beneficial microorganisms, such as mycorrhizal fungi, rhizobia and other plant growth-promoting bacteria (PGPB) or rhizobacteria (PGPR), to support plant protection and nutrition and assist water conservation. Today, these beneficial microorganisms (i.e. arbuscular mycorrhizal fungi (AMF), PGPB or PGPR) are considered a key factor for managing crop productions (Schlaeppi and Bulgarelli, 2015). However, their application in agriculture is still a challenge due to inconsistent and unpredictable results, which often are context-dependent (dos Santos et al., 2020; Compant et al., 2019). There are many aspects that need to be considered for a successful implementation of AMF and PGPB/PGPR as microbial inoculants with desired outputs in different crop genotypes and upon different (and combined) stress conditions (Pascale et al., 2020). These microbial inoculants are living microorganisms that colonize the rhizosphere (i.e. the zone surrounding the roots that is directly influenced by plant root secretions) and/or the inner regions of plant tissues and promote plant growth or act as biological control agents (BCAs) against soilborne and seedborne plant pathogens (Aeron et al., 2020; Khatoon et al., 2020; Raj et al., 2020; Tsolakidou et al., 2019; Orozco-Mosqueda et al., 2018; Bhattacharyya and Jha, 2012). Additionally, understanding the effect of cropland management on soil microorganism dynamics is fundamental for designing better management practices to restore soil function in intensively managed agricultural systems (Baritz et al., 2018; http://www.fao.org/3/a-bl813e.pdf).

2 Mechanisms mediated by plant growth-promoting bacteria/rhizobacteria

Generally, about 2–5% of the total rhizospheric bacteria are PGPB/PGPR (Antoun and Prévost, 2006). Features that allow bacterial survival in the rhizosphere and plant tissue colonization are motility, chemotaxis, attachment, growth and stress resistance (Bulgarelli et al., 2013). Some PGPB/PGPR are considered biofertilizers that augment the availability of nutrients in a form that can be easily assimilated by plants, while others act as biocontrol agents or biopesticides that suppress or control plant disease (Timmusk et al., 2017). Many PGPB/PGPR can solubilize insoluble soil phosphate to release soluble phosphorus and making it available to plants. This trait is very interesting since the phosphorus content of soil is about 0.05% (w/w) but only 0.1% of this fraction is available to plants. Phosphorus

is an essential element involved in many important metabolic pathways, such as photosynthesis, respiration, electron transport chain, biosynthesis of macromolecules and signal transduction (Khan et al., 2010). It also influences root growth, seed development and normal crop maturity (Heydari et al., 2019). Many bacterial and fungal strains, such as *Bacillus*, *Pseudomonas* or *Penicillium*, that release organic acids or phosphatases are capable to solubilize phosphorus and are, therefore, promising as PGPR (Khatoon et al., 2020; Bulgarelli et al., 2013). Apart from phosphate solubilisation (Figure 1), many other mechanisms mediated by PGPB/PGPR can lead to plant-growth promotion and improve plant tolerance/resistance to abiotic and biotic stresses (Glick, 2012), such as synthesis of hormones (abscisic acid (ABA), gibberellic acid, cytokinins and auxins) (Pérez-Flores et al., 2017; Bhattacharyya et al., 2015), nitrogen fixation (Ashraf et al., 2011), solubilization of other nutrients (Zn, K) (Vikram and Hamzehzarghani, 2008; Etesami et al., 2017; Zaheer et al., 2019), production of siderophores (Sinha and Parli, 2020; Calvo et al., 2017), ethylene (ET) control in emerging plants under stress conditions through the production of aminocyclopropane-1-carboxylate (ACC) deaminase (Ravanbakhsh et al., 2018; Glick, 2012), secretion of several molecules, including antibiotics, hydrolytic enzymes and volatile organic compounds, alleviating biotic stress effects and contributing to systemic resistance (Meena et al., 2020; Kour et al., 2019; Orozco-Mosqueda et al., 2018), production of exopolysaccharides (EPS) and biofilm formation (Dimkpa et al., 2009), heavy metal detoxification (Sharma and Archana, 2016; Tak et al., 2013; Ma et al., 2011) and pest management (Subbanna et al., 2018).

An increasing number of plants have been reported to benefit from PGPB/PGPR presence (Santos et al., 2019), including the model plant *Arabidopsis thaliana* (Lee et al., 2020) and several crops, such as winter wheat (*Triticum aestivum*) (Awan et al., 2020; Turan et al., 2012) and wheat (*Triticum durum*) (Bechtaoui et al., 2019), rice (*Oryza sativa*) (Xiao et al., 2020; Andreozzi et al., 2019;), sunflower (*Helianthus annuus*) (Ambrosini et al., 2012), rape (*Brassica napus*) (Farina et al., 2012), runner bean (*Phaseolus coccineus*) (Stefan et al., 2013) and faba bean (*Vicia faba*) (Bechtaoui et al., 2019), corn (*Zea mays*) (Batista et al., 2018; Tchuisseu Tchakounté et al., 2018; Arruda et al., 2013), soybean (*Glycine max*) (Batista et al., 2018), chickpea (*Cicer arietinum*) (Bisht et al., 2019), tomato (*Solanum lycopersicum*) (Kalam et al., 2020; Pellegrini et al., 2020), potato (*Solanum tuberosum*) (Pellegrini et al., 2020), flax (*Linum usitatissimum*) (Planchon et al., 2021), coriander (*Coriandrum sativum*) (Jiménez-Gómez, et al., 2020) and spinach (*Spinacia oleracea*) (Zafar-Ul-Hye et al., 2020). Apart from increased plant biomass, PGPR have demonstrated positive effects on total oil content and lipid composition in *G. max*, *B. napus* and *Buglossoides arvensis* that are important sources of oleic, linoleic, α-linolenic and omega-3 stearidonic acids (Jiménez et al., 2020). In addition, PGPR have been reported to improve carotenoids, tocopherols, and folate content in horseradish (*Moringa oleifera*) (Sonbarse et al, 2020).
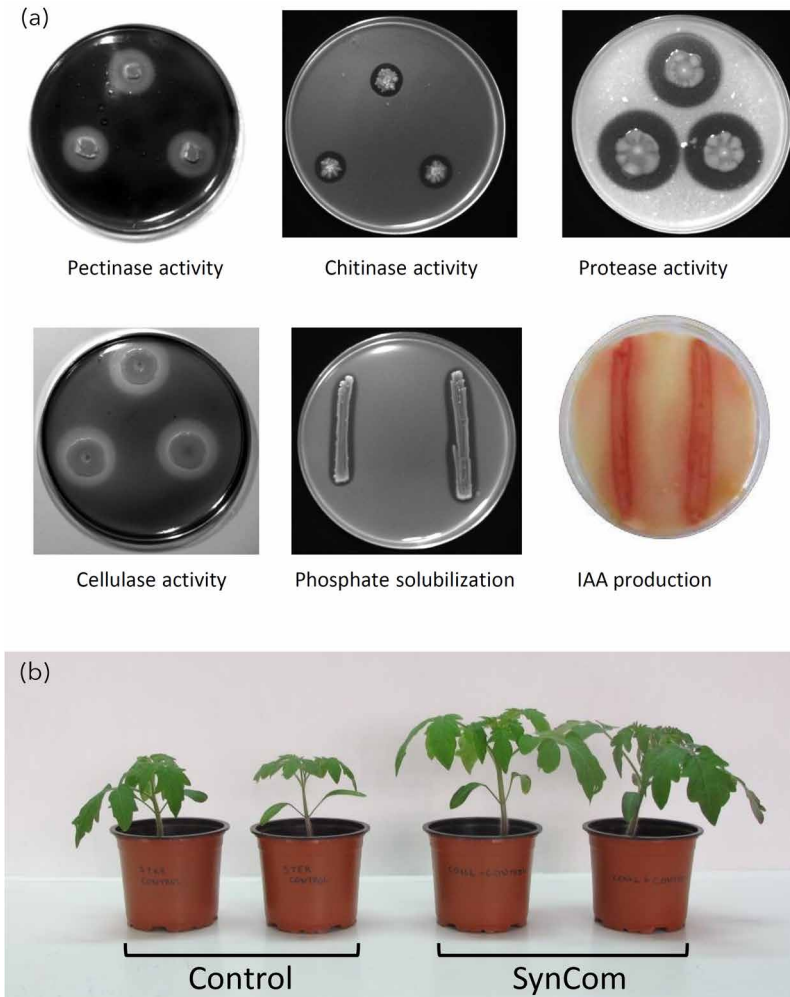
Figure 1 (a) *In vitro* screening of plant growth promotion traits; (b) Tomato plants not inoculated (left) and inoculated (right) with a microbial synthetic community (SynCom). [Photographs by I. S. Pantelides, Cyprus University of Technology].

PGPR have also been known to mediate biotic stress tolerance in plants through the production of antimicrobial compounds and the induction of plant defence responses. Ali et al. (2020) recently isolated bacteria from maize, rice, wheat, potato, sunflower and soybean rhizosphere and verified the antifungal activity against *Fusarium oxysporum*, *Fusarium moniliforme*, *Rhizoctonia solani*, *Colletotrichum gloeosporioides*, *Colletotrichum falcatum*, *Aspergillus niger* and *Aspergillus flavus*. The PGPR showing the highest antagonistic activity belonged to *Pseudomonas* and *Bacillus* species (Ali et al., 2020). The same

genera have also suppressed *Phytophthora capsic*i infections in chilli pepper (Hyder et al., 2020). Multiple strains of *Bacillus* spp. together with a strain of *Stenotrophomonas rhizophila* were also effective in reducing *Meloidogyne incognita* population density and improving turfgrass root growth (Groover et al., 2020). In addition, *Bacillus amyloliquefaciens* strain S1 exhibited high *in vitro* antagonistic activity against *Clavibacter michiganensis* ssp. *michiganensis,* suggesting its possible employment in controlling bacterial canker in tomato plants (Gautam et al., 2019).

Following a transcriptomics approach, Gamez et al. (2019) highlighted that PGPR inoculation in banana (*Musa acuminata* Colla) cv. Williams resulted in differential expression of genes related to growth promotion and regulation of specific functions (flowering, photosynthesis, glucose catabolism and root growth) as well as genes involved in plant defence. Jiang et al. (2019) also demonstrated that the watermelon gene expression profile was altered in the presence of a *Bacillus* strain in combination with *F. oxysporum* f. sp. *niveum*. The *Bacillus* strain enhanced plant disease resistance against the pathogen through activation of defence-related genes and phytohormone signal factors (Jiang et al., 2019). Recently, Bertani et al. (2021) showed the expression of rice genes involved in ET and auxin pathways together with genes coding for a metallothionein-like protein and a multiple stress-responsive zinc-finger protein when the plants are inoculated with *Pseudomonas chlororaphis* ST9.

3 Tolerance to abiotic stresses

Over the past years, several studies indicated that PGPB/PGPR inoculation can induce plant tolerance against different abiotic stresses (Alagna et al., 2020; Gamalero et al., 2020; Sangiorgio et al., 2020; Meena et al., 2017). Nevertheless, the level of tolerance depends on the microbial capability to induce the expression of stress-responsive transcription factors in plants as well as the production of enzymes involved in the detoxification of reactive oxygen species (ROS), synthesizing proline and EPS and biomass stabilization (Aeron et al., 2020).

Salt stress is one of the major threats to agriculture, negatively affecting crop yield and growth (Shrivastava and Kumar, 2015). It induces osmotic and ionic stress in plants, causing nutritional imbalance, morphological damages, less photosynthetic capacity and death (Ahmad et al., 2013). Unfortunately, high salinity areas are increasing every year, and agriculture has therefore to manage salt stress maintaining a sufficient crop production to satisfy food demand (Panwar et al., 2016). PGPR can alleviate the negative effects of salt by incrementing seed germination rate and leaf area, improving chlorophyll and protein content, increasing plant growth, productivity, and nutrient availability, delaying leaf senescence and enhancing tolerance to stresses

(Saghafi et al., 2019; Habib et al., 2016). PGPR ameliorate salt stress tolerance through several mechanisms, for example, accumulation of osmolytes operating in ion homeostasis, improvement of nutrient uptake (N, P, K, Zn and Si), production of ACC deaminase, indole acetic acid (IAA), sideropheres and EPS, and alteration of the antioxidant defence system (Saghafi et al., 2019 and reference therein). Upadhyay and Singh (2015) have demonstrated that salt-tolerant PGPR improved both growth and dry mass of wheat grown in pots, as well as root dry weight and shoot biomass in field conditions. Palaniyandi et al. (2014) demonstrated that inoculation of tomato plants with *Streptomyces* sp. strain PGPA39A under salt stress increased plant biomass and chlorophyll content, while leaf proline content decreased. In another study, it was shown that strains belonging to *Streptomyces* ameliorated salt stress tolerance in *Stevia* crops (Tolba et al., 2019). Panwar et al. (2016) suggested that using a combination of two PGPR (bacterial strains belonging to genus *Pantoea* and *Enterococcus*) on mung bean (*Vigna radiate*) plants resulted in enhanced growth and yield, a reduced Na$^+$ concentration, less membrane damage and more antioxidants, such as ascorbic acid and glutathione, under salt stress. In the study of Khan et al. (2019), isolation and application of halotolerant PGPR on soybean plants grown under salt stress resulted in an increase in the antioxidant level, K$^+$ uptake, plant growth attributes and chlorophyll content and a reduction of the Na$^+$ ion concentration and the ABA level. Recently, Galicia-Campos et al. (2020) showed that the use of PGPR strains improved stress tolerance and water use efficiency in olive plants grown under saline stress.

Drought can also have a negative impact on crops causing significant yield reductions (Zhang et al., 2009; Breitkreuz et al., 2019). Many crops, including rice and winter wheat, need irrigation with big quantities of water in order to grow and produce acceptable yields. The research carried out by Zhang et al. (2020) showed that the association of rice roots with *Enterobacter aerogenes* is involved in rhizosheath (i.e. the layer of soil around the root containing a mixture of exudates, mucilage and exopolymers, which increases the wettability and water use efficiency of the root system) formation under moderate soil drying. It has been proposed that root-bacteria associations substantially contribute to this process by mechanisms that involve the ET response, considering that an ACC deaminase-deficient mutant of *E. aerogenes* failed to enhance rice rhizosheath formation. Breitkreuz et al. (2019) showed the positive role of *Phyllobacterium* in phosphate solubilization in rhizosphere under drought conditions. Brilli et al. (2019) demonstrated that tomato plants inoculated with *Pseudomonas chlororaphis* subsp. *aureofaciens* strain M71 have more proline and an improved antioxidant activity under mild water stress, thus reducing ROS presence and enhancing stress tolerance. The presence of the M71 strain also had an impact on stomatal closure, increasing ABA level in leaves and

improving water use efficiency and biomass in water-stressed plants (Brilli et al., 2019). Rolli et al. (2015) demonstrated that PGPB have the ability to increase grapevine root biomass in field conditions under drought stress, while Saleem et al. (2018) showed that two PGPR strains improve velvet bean growth under drought conditions, by reducing ET production through ACC deaminase activity, which acts on the ET precursor ACC. Rubin et al. (2017) using a meta-analysis reported that PGPR can contribute to drought amelioration and water conservation, increasing shoot biomass and yield, especially under drought conditions.

Application of PGPR in combination with salicylic acid (SA) on maize plants (Khan et al., 2020) resulted in significant increases in nutrients content (Ca, K, Mg, Zn and Fe) in the shoots and the rhizosphere of plants and alleviated the adverse effects of low moisture stress of soil. Previously, Khan and Bano (2019) showed that the combination of PGPR and SA on wheat under drought stress led to a significant increase in leaf protein and sugar contents and higher chlorophyll content, chlorophyll fluorescence and performance index (Khan and Bano, 2019), suggesting the adoption of a mixed approach including both biological and chemical priming (Alagna et al., 2020).

In natural conditions, abiotic stresses can occur simultaneously, for example, salinity and phosphorous deficiency. It has been demonstrated that, under phosphate (Pi) limitation and salt stress, PGPR can support plant growth in plant genotype- and bacterial strain-dependent way (Tchuisseu Tchakounté et al., 2018). Osmotic stress and limitation of resources can also affect ornamental plants. It was shown that inoculation of petunia with *Pseudomonas* strains increased plant biomass and flowers number (Nordstedt et al., 2019). A study by Liu et al. (2019) focused on the physiological features and growth of North China red elder (*Sambucus williamsii*) under drought stress and in the presence of PGPR. *Acinetobacter calcoaceticus* X128 significantly increased stomatal conductance (Liu et al., 2019). The bacterium was able to increase cytokinins levels in the leaves that promote the stomatal opening, mitigating the inhibition of the photosynthetic rate in arid locations (Liu et al., 2019). In addition, the application of the PGPR strain might increase the permeability of roots to water or improve the transport of ions into the xylem, with an intensification of ABA transport, resulting in a decrease or complete closure in the stomatal opening (Liu et al., 2019). Generally, PGPR inoculation under drought conditions improved the adaptability of red elder plants to the arid environment by affecting phytohormones content in plants (Liu et al., 2019).

4 Beneficial effects against biotic stresses

The use of PGPB/PGPR is an eco-friendly tool that can be used for biocontrol of plant pathogens either by suppressing pathogenic microorganisms directly

or by improving plant defence against pathogens (Lugtenberg and Kamilova, 2009). Controlling plant diseases by microorganisms is a complex process involving the biocontrol agent, the pathogen and the host, but also the indigenous microorganisms of the rhizosphere, other native macrobiota and the plant growth substrate. To act efficiently, the biocontrol microbe should remain active under varying conditions, such as temperature, moisture, pH and other soil properties.

Various mechanisms have been reported to be involved in biocontrol. The production of antibiotics and other antimicrobial metabolites is considered as a primary mechanism of biocontrol by PGPB and PGPR and is the most effective antagonistic activity to suppress phytopathogens. Diffusible antibiotics produced like phenazines, rhamnolipids, cyclic lipopeptides, zwittermycin A, kanosamine, oomycin A, ecomycins, butyrolactones and volatiles, such as hydrogen cyanide, ammonia, 2,3-butanediol and other blends of aldehydes, alcohols, ketones and sulphides, are known to possess antimicrobial and growth-promoting activities (Kai et al., 2009; Fernando et al, 2005). These compounds are toxic towards phytopathogens at concentrations depending on the compound and the target. Modes of action are not fully understood for many antimicrobial metabolites yet. In fungal pathogens, they may affect the cell membrane and zoospores (biosurfactants), inhibit the respiratory electron transport (phenazines, pyrrolnitrin) or cytochrome c oxidases and other metalloenzymes (hydrogen cyanide) (Raaijmakers, et al., 2006; Haas and Défago, 2005).

Another important mechanism in biocontrol is the production of hydrolytic enzymes by PGPB/PGPR directed against plant pathogens. Many biocontrol agents synthesize and secrete catabolic enzymes that can contribute to the suppression of phytopathogens through the hydrolysis of fungal cell wall components, such as cellulose, chitin, β-glucans and proteins (Abdullah et al., 2008; Dunne et al., 1997; Chernin et al., 1995). Production of β-1,3-glucanase by *Streptomyces* and *Paenibacillus* strains was shown to have an inhibitory effect on *F. oxysporum*, while *Bacillus cepacia* with glucanase activity showed inhibitory effect on many soilborne pathogens, including *Rhizoctonia solani*, *Sclerotium rolfsii* and *Pythium ultimum* (Compant et al., 2005). Several microorganisms were reported to show chitinolytic activity, including many *Bacillus, Streptomyces*, *Serratia* and *Pseudomonas* strains (Tsolakidou et al., 2019; Felse and Panda, 2000;). Co-cultivation of *Rhizoctonia solani* with the chitinolytic *Serratia marcescens* B2 strain led to several abnormalities of the mycelia (e.g. swelling, curling or bursting), suggesting degradation of the hyphal cell wall or hyphal cell death. Moreover, the application of *Serratia marcescens* B2 strain on cyclamen plants suppressed the diseases caused by *Rhizoctonia solani* and *F. oxysporum* f. sp. *cyclaminis* (Someya et al., 2000). Chitinases and cellulases are also involved in predation and parasitism, the major biocontrol mechanism

used by *Trichoderma* and *Gliocladium* species (Harman et al., 2004a). This form of antagonism affects various fungal pathogens, such as *Sclerotinia*, *Rhizoctonia*, *Verticillium* and *Gaeumannomyces* (Harman et al., 2004b), and involves tropic growth of the BCA towards the target organism, coiling and dissolution of the pathogen's cell wall or membrane through enzymatic activity (Djonović et al., 2006; Woo et al., 2006; Zeilinger et al., 1999).

Apart from the mechanisms where a BCA produces substances with direct inhibitory effect for phytopathogens, it is possible for some PGPB/PGPR to outcompete the phytopathogens, either for space at the root surface or for nutrients, especially those secreted by the roots. This competition excludes pathogens by the physical occupation of binding sites on the root or by the depletion of food. Competition can take place for organic compounds necessary for pathogen proliferation and subsequent root colonization and for micronutrients that are essential for the growth and activity of the pathogen (Raaijmakers et al., 2009). Biocontrol based on competition for micronutrients has long been recognized, especially for nutrients that are not readily available for plants and microorganisms. Iron is a characteristic example of a micronutrient that is extremely limited in soils, and its availability depends on soil pH. In oxidized soils, iron is in the ferric form that is insoluble in water (Lindsay, 1979), and its concentration is too low to support the growth of microorganisms. To survive, microorganisms produce and secrete high-affinity chelators called siderophores (Neilands, 1995). Siderophore-producing PGPB/PGPR show increased efficiency in iron uptake making iron unavailable to pathogens and thus preventing their proliferation around the root, especially in soils with high pH (Kumar et al., 2015). Competition for iron as well as competition for carbon is an important mode of action of many biocontrol agents (Alabouvette et al., 2006; Lemanceau et al., 1992).

Besides functioning as BCAs, several PGPB and PGPR can induce a systemic response in the plant, leading to the activation of plant defence mechanisms against a wide range of phytopathogens (Pieterse et al., 2014). This form of resistance is referred to as induced systemic resistance (ISR) and is described as an enhanced defence capability of the plant against multiple pathogens (Conrath et al., 2015). ISR is induced by non-pathogenic PGPR, PGPB and fungi and can reduce the activity of pathogenic microorganisms via a complex system mediated by jasmonic acid (JA) and ET signalling (Pieterse et al., 2014; Van Loon, 1997). In contrast to classical biological control, in which the BCA is active against one or a few pathogens, ISR is effective against a broad spectrum of pathogens (Hariprasad et al., 2014). Several cell surface components and compounds produced by PGPR/PGPB can trigger ISR, including lipopolysaccharides and flagella, (Pieterse et al., 2003; Haas and Défago; 2005), siderophores (Meziane et al., 2005), volatiles (Ryu et al., 2004), hydrogen cyanide (HCN) (Defago et al., 1990), diacetylphloroglucinol (DAPG) (Weller et al., 2007) and cyclic lipopeptide

surfactants (Ongena et al., 2007). The first reports of ISR were published back in 1991 and provided evidence that certain PGPR strains can stimulate the plant immune system and promote plant health (Alström, 1991; Van Peer et al., 1991; Wei et al., 1991). Since then, many studies have reported the ability of non-pathogenic microorganisms to trigger ISR including bacteria (e.g. *Pseudomonas*, *Serratia*, *Bacillus*), fungi (*F. oxysporum*, *Trichoderma*, *Piriformospora indica*) and symbiotic AMF (Pieterse et al., 2014). Enhancement in the plant's defence capability by ISR involves the activation of many biochemical pathways leading to fortification of structural barriers, such as thickened cell walls, suberization and deposition of lignin and callose (Raj et al., 2012; Benhamou et al., 1998). The phenomenon of ISR is also associated with increased expression of defence-related enzymes, such as phenylalanine ammonia lyases, peroxidases, lipoxygenases, polyphenol oxidases and synthesis of antimicrobial compounds, such as pathogenesis-related proteins, phytoalexins, phenolic compounds and cell wall peroxidases (Stringlis et al., 2018; van Loon et al., 1998; Zdor and Anderson, 1992; van Peer et al., 1991; Mauch et al., 1988).

5 Interaction between plant growth-promoting bacteria/ rhizobacteria and arbuscular mycorrhizal fungi

The rhizosphere harbours a diverse community of microorganisms, such as bacteria and fungi that can interact with the plant, influencing plant growth, nutrition and health and protecting them from biotic and abiotic stresses in agro-ecosystems and in natural ecosystems (Philippot et al., 2013). AMF are one among the soilborne fungi that form symbiotic interactions with the majority of terrestrial plants. AMF are actively involved in the uptake of water and nutrients (such as phosphorus, nitrogen, zinc, copper, etc.) and increase resistance or tolerance of plants to biotic and abiotic stresses (Balestrini and Lumini, 2018).

AMF may interact synergistically with PGPR, leading to enhanced plant growth compared to single inoculation with either of them (Nanjundappa et al., 2019).

The review of Nanjundappa et al. (2019) focusing on the interaction between AMF and *Bacillus* concluded that combined inoculation leads to enhanced growth of plants, such as *Medicago sativa* (Medina et al., 2003), *Lactuca sativa* (Adriana et al., 2007), *Calendula officinalis* (Flores et al., 2007), *Artemisia annua* (Awasthi et al., 2011), *Pelargonium graveolens* (Alam et al., 2011), and *Cucumis sativus* (Rabab, 2014) as compared to single inoculation with either of them. Cely et al. (2016) also demonstrated that AMF and PGPR increased wood yield of *Schizolobium parahyba* var. *amazonicum* with respect to a fertilizer addition. Recently, Rocha et al. (2020) confirmed by field trials the positive role of co-presence of *Pseudomonas libanensis* and multiple AM fungal isolates of *Rhizophagus irregularis* in cowpea (*Vigna unguiculata*).

The plants showed increased shoot dry weight, pods and seeds per plant and grain yield (Rocha et al., 2020). In another study, a consortium of PGPR-rhizobia-AMF affected positively fava bean and wheat, improving shoot and root dry weight, leaf number, productivity and sugar, protein N, P, Ca, K and Na content (Raklami et al., 2019). Bona et al. (2015, 2017) demonstrated that the AMF-bacterium combined application can also affect fruit crop quality and nutritional value of strawberry and tomato (increased sugar content, fruit size, quantity and flowers) in conditions of reduced chemical inputs. The interaction between fungi and bacteria can also protect plants, by inducing systemic resistance to soilborne pathogens (Nanjundappa et al., 2019). For example, Jaizme-Vega et al. (2006) demonstrated a reduction of *Meloidogyne* infestation in AMF-PGPR-inoculated papaya plants, while Phirke et al. (2008) showed reduced *Fusarium* wilt in addition to improved yield in mycorrhized banana inoculated with rhizobacteria. The co-presence of AMF and PGPB/PGPR also improved tolerance to drought and salt stress in *Lactuca sativa* (Vivas et al., 2003), *Retama sphaerocarpa* (Marulanda et al., 46), *Z. mays* (Armada et al., 2015), *Trifolium repens* (Ortiz et al., 2015), *Lavandula dentate* (Armada et al., 2016) and *Acacia gerrardii* (Hashem et al., 2016). Recently, Inculet et al. (2019) demonstrated that inoculation of an irrigated tomato cultivar with AMF, PGPR and *Trichoderma*-based products increased plant length, fruit number, yield and quality traits based on lycopene and polyphenol content. Mannino et al. (2020), using different microbial inocula based on AM fungi or PGPR tolerant to salt, demonstrated that the tomato responses to water limitation depended on the inoculum composition. Balestrini et al. (2017) showed that the response of grapevine changed in the presence of a mixed inoculum composed by bacterial and fungal consortium compared to that with an inoculum based on *Funneliformis mosseae* only. Thus, the strategy of using a combination of AMF and PGPR in agricultural practice may improve soil health management, aiding nutrient solubilization and uptake and reduce the necessary fertilizer quantity. Nevertheless, more field studies are needed in order to verify the successful performance of the combined inoculations under real conditions (Nanjundappa et al., 2019).

The study of Todeschini et al. (2018) highlighted the importance of selecting the optimal combination of AMF and PGPR to positively influence physiological parameters, yield and quality in strawberry. The results of this study showed that application of the AMF affected the parameters associated with the plant vegetative portion, while application of the bacterium affected the fruit yield and quality. Interestingly, the volatile profile and elemental composition of the strawberry fruit were affected by the presence of a specific fungal–bacterial combination (Todeschini et al., 2018). This study showed for the first time that different soil microorganisms are able to influence the fruit concentration of some elements and/or volatiles (Todeschini et al., 2018).

Previous studies tested the ability of *Pseudomonas fluorescens* PGPR strains to form biofilm on mycorrhized and non- mycorrhized roots and on extraradical mycelium of an AM fungus (Bianciotto et al., 2001a, b). The nonmucoid wild-type strain *Pseudomonas fluorescens* CHA0 adhered very little on all surfaces, whereas two mucoid strains with increased production of acidic extracellular polysaccharides formed a dense and patchy bacterial layer on the roots and fungal structures (Bianciotto et al., 2001a). The results of this study suggest that increased adhesive properties of PGPR may lead to more stable interactions in mixed inocula and the rhizosphere. In another study, the bacterial components possibly involved in the attachment of two other PGPR (*Azospirillum* and *Rhizobium*) to AM roots and AM fungal structures were evaluated; mutants affected in EPS were tested in *in vitro* adhesion assays and shown to be strongly impaired in the attachment to both types of surfaces as well as to quartz fibres (Bianciotto et al., 2001b). Anchoring of PGPR to AMF seems to be a significant trait for a stable fungus–bacteria association that would improve the development of mixed inocula.

6 Conclusion and future trends in research

PGPB/PGPR can be promising economical and healthy alternatives to chemical fertilizers, antibiotics, herbicides, pesticides, with their abilities to improve agro-ecological sustainability. However, it is important to realize that PGPR showing a positive effect on a plant species may not have the same effect on others (Raj et al., 2020; Zeller et al., 2007). As explained by Timm et al. (2016), not all the microbes present in the soil have positive functions, so it is important to understand which microbial species should be employed to maximize plant growth, development and health (Xiao et al., 2020; Yuan et al., 2016; Mueller and Sachs, 2015). Recently, Finkel et al. (2020) demonstrated that a single bacterial genus in a complex microbiome modulates root growth. Interestingly, Guerrieri et al. (2020) suggested that using a consortium of native PGPR strains may represent a suitable solution in sustainable agriculture, to guarantee crop yield and quality, reducing the chemical input application. Apart from the studies on the efficacy of microbial inoculants on plants, their potential risks to other plants, animals, and humans must also be evaluated (Martínez-Hidalgo et al., 2019). Also, isolation, purification and characterization of microorganisms from saline habitats and inoculation of agricultural plants with them could be a successful strategy to increase tolerance and productivity of the plants grown under stress conditions (Saghafi et al., 2019). Escudero-Martinez and Bulgarelli (2019) highlighted that the genetic diversity of the crop microbiota is reduced compared to that of wild plants and that in combination with the application of human inputs, the agroecosystem resilience and sustainability to various stressors (e.g. climate change) is undermined. It is, therefore, desirable to carry

out genetic mapping analyses, crossing interfertile wild and modern varieties, to discover host traits putatively influencing the recruitment and maintenance of the microbiota (Perez-Jaramillo et al., 2016; Schlaeppi and Bulgarelli, 2015). A concept named 'breeding for the plant microbiota' based on the development of plant varieties able to recruit specific microbial taxa may result in future crops that are less dependent on external inputs to produce acceptable yields (Escudero-Martinez and Bulgarelli, 2019; Bulgarelli et al., 2013; Wissuwa et al., 2009). Moreover, the prospect of using microbial mixtures as inoculants that can positively affect plant performance is gaining research interest. A substantial number of studies suggests that complex microbial consortia provide plants with increased growth and health as compared to single strains. However, our understanding of how members of microbial consortia interact with one another and with their hosts in nature is critical for the successful implementation of microbial synthetic communities (SynComs) with desired host outputs (Pascale et al., 2020; Tsolakidou et al., 2019). On the basis of these approaches, it will be possible to deal with challenges that agriculture shall meet in the coming years.

7 Acknowledgement

8 Where to look for further information

8.1 Special issues on plant growth promoting rhizobacteria

- https://www.mdpi.com/journal/plants/special_issues/PGPB.
- https://www.sciencedirect.com/journal/microbiological-research/special-issue/10P22CLD85N.

8.2 Key research organizations

The Asian PGPR Society for Sustainable Agriculture (http://asianpgpr.com/index.php).

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