Chapter 2 Microbes Associated with Crops: Functional Attributes for Crop Productivity

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Abstract Microorganisms associated with plants can affect their health positively or negatively, thus influencing hugely crop yield and productivity. Several investigations have reported that the microbes associated with different plants are much diversified. Especially, those microorganisms of agricultural interest belong mainly to bacteria and fungi. Additionally, they are various mechanisms of plant/microorganisms interaction, which are already elucidated and well documented, bringing together two principal categories; by one side, the implication of germs in biotic and abiotic stress reactions; by the other side, the all aspects related to plant responses. This work aimed to expose some aspects of the microbe's associates to plants and the functional attributes for ameliorating crop productivity and yields.

Keywords Crop productivity · Mechanisms · PGP traits · Plant microbiome

2.1 Introduction

The industrial revolution of farming in the twentieth century has drastically transformed and accelerated the market and agricultural activities; in order to raise crops and feed the planet's increasing population (Zorner et al. [2018\)](#page-23-0). In addition, modern agriculture faces several problems, including environmental issues, and an increase in supply for durable manufacturing (Compant et al. [2019;](#page-15-0) Sharma et al. [2021\)](#page-21-0). In particular, eco-friendly and durable farming techniques are vital for ensuring food safety, like the use of effective farm-benefit microorganisms (bioinoculants) that play potential roles in sustainable crop manufacturing due to their vast characteristics for plant increase, improving adaptability and viability under stressful conditions; and

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other important utilizations that can efficiently reduce the use of pesticides and fertilizers in modern farming (Singh et al. [2016;](#page-21-1) Kumar et al. [2021\)](#page-18-0). These microbes ensure a crucial function in various farm ecosystems (Deveau et al. [2018;](#page-16-0) Prasad et al. [2021\)](#page-20-0). Since ancestor plant lines colonized the land 450 million years ago, plants and their microorganisms interacting there formed an association of organisms often designed as a "holobiont." (Hassani et al. [2018\)](#page-16-1). Particularly in the last years, intensive efforts have been dedicated to elucidate the interaction between plants and bacteria, both beneficial and pathogenic (Degrassi et al. [2012\)](#page-15-1).

Colonization is arduous for microbial populations in their niches, particularly because of their huge diversity, dynamic interactions, constant genetic interchange and deficiency of adequate analytical techniques (Singh et al. [2010\)](#page-21-2). Equally, the microbes associated with plants include algae, bacteria, fungi and viruses. Depending upon their localization on the host plant, they can be endophytic and/or epiphytic. Endophytic microbial interrelationships affect the inner part (Rana et al. [2020a;](#page-20-1) Singh et al. [2020\)](#page-21-3), whereas epiphytic microbial interrelationships affect the outer surface of plants (Kumar et al. [2017\)](#page-18-1). Notably, in the last decade, diverse studies have indicated the complicated microbial accumulations related to various plants, and particular plant compartments (Reinhold-Hurek [2015\)](#page-20-2). Moreover, several researches reported the benefits of rhizobacteria and endophytic bacteria belonging to the specific phylogenetic group on the biological characteristics of different vegetable crops (Vansuyt et al. [2007\)](#page-22-0). Generally, epiphytic, endophyte or rhizophyte interrelations can be harmful or beneficial to both the microbe or the plant and may be considered competition, amensal, synergism, commensal, mutual, parasitism or neutral (Montesinos [2003;](#page-19-0) Yadav [2021\)](#page-23-1).

2.2 Microbes Linked with Crops

2.2.1 Rhizospheric Microbiomes

Rhizosphere is the region in which the roots and related microbes engage in diverse interactions and is characterized by wide microbial diversity (Patra et al. [2016\)](#page-19-1). The exudation of roots comprises of a mixture of compounds such as sugars, organic acids, amino acids and vitamins, which attracts a diverse microbial population (Bertin et al. [2003;](#page-15-2) Kour et al. [2019b\)](#page-17-0). Proteobacteria, especially those of tα and β groups, tend to dominate. Acidbacteria, Verrucomicrobia, Actinobacteria, Bacteroidetes, Firmicutes and Planctomycetes are among the other principal groups (Turner et al. [2013\)](#page-22-1). Particularly, root and rhizosphere microbial communities are named plant growthpromoting rhizobacteria (PGPR) play key functions in determining plant health and productivity (Verbon and Liberman [2016;](#page-22-2) Hesham et al. [2021\)](#page-17-1).

2.2.2 Epiphytic Microbiomes

Plant aerial parts are the habitat of several epiphytic microorganisms, which could be noxious or useful to the plant (Sharma et al. [2019\)](#page-21-4). Epiphytic microbes live on fruit, flowers, leaves, buds and stems (Whipps et al. [2008;](#page-22-3) Mukhtar et al. [2010\)](#page-19-2). Apparently, microbial interrelations in the phyllosphere may influence soil health in native populations, crop yield production and the security of human-consuming horticultural products (Whipps et al. [2008\)](#page-22-3). This analysis points toward the soil and air as important sources of leaf and root microbial inoculums (Kumar et al. [2019a,](#page-18-2) [2019b\)](#page-18-3).

The action of insects, wind and rain could allow microorganisms to reach the surface or to leave the plant surface. This analyzes the air and soil as key root and leaf microbial inoculum provenances (Lilley et al. [1997\)](#page-18-4). The complexity, role and relation to the microbiota of the rhizosphere are also emerging research areas (Bai et al. [2015\)](#page-14-0). The content and richness of bacterial communities are specific to host, memberships of the alphaproteobacteria predominate and are widely spread in phyllosphere microbiotas, and the genera *Methylobacterium* and *Sphingomonas* are frequently observed among various hosts (Delmotte et al. [2009\)](#page-15-3).

2.2.3 Endophytic Microbiomes

Endophytes comprise all species occupying plant organs that could populate interior plant tissues at any stage of their life without doing any obvious damage to the host (Petrini [1991;](#page-19-3) Rana et al. [2020b\)](#page-20-3). Endophytes are ecologically ubiquitous and diversified in the majority of plant species and perform various fundamental functions in nature for plant productiveness, mainly by metabolism and enhancement of nutrient assimilation, synthesizing plant development hormones, controlling the host's defensive gene expression and other elementary metabolic processes (Zhou et al. [2017\)](#page-23-2).

In particular, plant-associated endophytes, including endophytic fungi, are widely distributed in nature (Jia et al. [2016\)](#page-17-2). Also, endophytic bacteria–plant relationships have been widely studied for their various roles, mainly in the improvement of plant increase, biocontrol, phytopathogenicity, resistance toward stressful factors and bioremediation (Fester et al. [2014;](#page-16-2) Yadav et al. [2021b\)](#page-23-3). Figure [2.1](#page-3-0) shows the microbes associated with crop ecology.

Fig. 2.1 Microbes associated with crops ecology. Free-living microbes are holobionts in plants: in rhizosphere as well as in phyllosphere like epiphytic and endophytic in the whole plant. In addition, they have important ecological roles evolved by living in pathogens, PGPR or saprophytes. Most such microbes–host interactions are beneficial, adversely to others which are harmful, inducing an increase or loss of crops yield and productivity

2.3 Mechanisms of Increasing Crop Productivity and Yield

Among the benefits of plant-useful microorganisms, different mechanisms can be listed like plant increase improvement, synthesizing various antibiotic/antifungal molecules inhibiting several phytopathogens, resistance to numerous environmental stress factors and microorganism-assisted elimination of organopollutants (Wu et al. [2009\)](#page-22-4). Furthermore, soil microbial populations are essential for several of the earth's biogeochemical cycles like mineralization of nutritional compounds, organic carbon decomposition and nitrogen cycle (Patra et al. [2016\)](#page-19-1). Notably, a number of soil microbial mechanisms convert unavailable nutritional elements to be easily assimilated by plants (Lalitha [2017\)](#page-18-5). Endophytes and epiphytes have no negative impacts on the plant; instead, they cause the production of certain essential chemicals like hormones (Kumar et al. [2017\)](#page-18-1). Additionally, some other microbes can synthesize auxin, which improves growth and ensures a crucial function in plant life cycle (Fernandes et al. [2011\)](#page-16-3). Globally, inside rhizosphere PGPR assist the indirect and direct increase of plants through various mechanisms. They participate in nutrient uptake, nitrogen fixation, phosphate solubility, siderophores formation, IAA and other diverse phytohormones (Pahari et al. [2016;](#page-19-4) Rai et al. [2020;](#page-20-4) Subrahmanyam

Fig. 2.2 Mechanisms developed by plant-associated microbes for protecting and increasing crop productivity and yields. (ISR: Induced Systemic Resistance; ASR: Acquired Systemic Resistance)

et al. [2020;](#page-21-5) Abdel-Azeem et al. [2021\)](#page-14-1). Figure [2.2](#page-4-0) illustrates the mechanisms developed by plant-associated microbes for protecting and increasing crop productivity and yields.

2.3.1 Phosphate Solubilization

It is well established that plants need at least 14 mineral elements for sufficient nutrition, in addition to water, carbon dioxide and oxygen (Mengel et al. [2001\)](#page-19-5). Insufficiency of any of these mineral elements decreases plant growth and crop yields (El-Ramady et al. [2014\)](#page-16-4). In particular, microbes of various genera are capable of transforming insoluble phosphate into soluble compounds, which are then available to plants, and are generally known as phosphorus solubilizing microbes or PSMs (Shrivastava et al. [2018;](#page-21-6) Kour et al. [2020,](#page-17-3) [2021\)](#page-18-6). Phosphorus-solubilizing bacteria ensure a function in phosphate nutrition via increasing its accessibility to plants, releasing phosphate pools from organic and inorganic soil and solubilizing and mineralizing mechanisms (Khan et al. [2009\)](#page-17-4). Enhanced crop productivities arise

from PSM solubilization of fixed soil P and applied phosphates (Zaidi [1999\)](#page-23-4). They also improve soil fertility and crop productivity in organic farming (Kaur and Reddy [2014\)](#page-17-5).

2.3.2 Siderophores

Iron is a crucial plant nutritional element that operates as a cofactor in various enzymes of the respiratory system, photosynthetic activity and nitrogen fixation. Although iron is quite prevalent in soil, it is often inaccessible to microbes and plants because it arises under aerobic environment primarily as a trivalent state iron Fe(III) (Bano and Ilyas [2012\)](#page-14-2). Iron deficiency can adversely impact plant, beneficial and phytopathogenic microorganisms. For instance, the microbial surface hydrophobicity significantly reduces under iron-deficient growth conditions that also distort the surface protein constitution (Simões et al. [2007\)](#page-21-7). On the other hand, siderophores are secondary metabolites with low molecular weight and an iron-chelating capability (Kour et al. [2019c;](#page-18-7) Sharaff et al. [2020\)](#page-21-8). These are substances characterized by small peptide molecules with laterally chains and operational groups that have a ligand with great affinity that binds ferrous ions into the cellular membrane (Niehus et al. [2017\)](#page-19-6). Nearly, all microbes develop them in reaction to an iron insufficiency (Crowley [2006\)](#page-15-4). Siderophore production is controlled by well-established bacterial and fungal transcriptional factors (Troxell and Hassan [2013\)](#page-22-5); in particular, the bacteria generating siderophores are frequently isolated from the rhizospheric plant area (Calvente et al. [2001\)](#page-15-5). Plants may also produce Fe(III)-chelating molecules designed phytosiderophores forming unique and solid Fe(III) structures (Ma [2005;](#page-18-8) Kraemer et al. [2006\)](#page-18-9).

A number of investigations explain the function of siderophores as an important component in ISR protection effects (Vleesschauwer and Hofte [2009\)](#page-22-6). Mahmoud and Abd-Alla [\(2001\)](#page-18-10) mentioned that hydroxymate, a kind of siderophore produced by *Pseudomonas*sp., which stimulated the formation of nodules and fixation of nitrogen by mung bean seedlings as compared to sowing infested with *Bradyrhizobium* sp. strain solely. Furthermore, bacteria-forming siderophores play a major function in the suppression of some phytopathogenic microorganisms (Beneduzi et al. [2012\)](#page-15-6).

2.3.3 Phytohormones

Ethylene, cytokinins, abscisic acid, gibberellins and auxins are widespread among various regulating factors of growing plants and are well known for their acting processes (Kashyap et al. [2017;](#page-17-6) Suyal et al. [2021\)](#page-21-9). In this case, microorganisms interacting with plants generate main plant growth hormones such as auxins and gibberellins. Generation of gibberellins is the most usual for the development of root-associated microorganisms and auxin is widespread into whole plant-related

microbes (Yadav et al. [2017;](#page-23-5) Tiwari et al. [2020\)](#page-22-7). Especially, the great effective and typical auxin in plants is indole 3-acetic acid (IAA) (Kashyap et al. [2017\)](#page-17-6). Patten and Glick [\(1996\)](#page-19-7) mentioned the synthesis and secretion of auxin as elementary molecule of around 80% of rhizosphere microorganisms. Notably, auxins are important in phototropism and geotropism, differentiation of the vascular tissue, apical dominance, lateral and adventitious root initiation, cellular division, extension of root and stem (Grobelak et al. [2015;](#page-16-5) Rastegari et al. [2020a,](#page-20-5) [2020b\)](#page-20-6).

2.3.4 N2 Fixation

Nitrogen is an important element responded in different ecosystems. For instance, inorganic nitrogen in the marine ecosystem ranges from nitrate to ammonia in various oxidation forms (Ravikumar and Kathiresan [2007\)](#page-20-7). Moreover, nitrogen is among the most essential nutrients affecting the production of crops. Especially, leguminous in combination with rhizobia provide an invaluable function, in the natural and agricultural environments, to the global nitrogen balance (Vance [2001;](#page-22-8) Rana et al. [2019\)](#page-20-8). It has been estimated that the price of utilizing N-fixing microorganisms is 1% more than the price of utilizing chemical products (Stokstad [2016\)](#page-21-10).

2.3.5 ISR and ASR

Most plants respond to a local attack by herbivores or pathogenic microorganisms through the formation of compounds aiming to mitigate or prevent further attacks, or the effectiveness of their enemies. The reactions occur in either the initially attacked plant organ (local reaction) or remote but not damaged sections (systemic reactions). One of these reactions is the induced systemic resistance (ISR), and the other is systemic acquired resistance (SAR) forming together the plant defensive system against plant pathogens (Heil and Bostock [2002\)](#page-17-7). Furthermore, a number of PGPR induce transformations related to chemical or physical protection system in the plant (Van Loon et al. [1998\)](#page-22-9). Nevertheless, combined ISR and SAR present greater protection than any of them alone, suggesting that they might act synergistically to promote pathogen tolerance (Van Wees et al. [2000\)](#page-22-10).

2.3.6 ACC Deaminase

This enzyme metabolizes ACC (1-aminocycle-1-carboxylate) in plant tissues, which is the initial precursor to ethylene (Yang and Hoffman [1984;](#page-23-6) (Kour et al. [2019a\)](#page-17-8). Moreover, ethylene, usually, is involved in crucial plant processes like differentiation of tissues, shoot and root formation primordia, root ramification and extension,

the implementation of the lateral bud, floration, flora senescence, fruit maturation and abscission, formation of anthocyanin, the elaboration of volatile organic substances responsible for the fruits aroma production (Glick [2014\)](#page-16-6). Moreover, for the germination of seed, ethylene is necessary, as it is established by its rate of production rising considerably during germination and planting growing (Abeles et al. [1992\)](#page-14-3). Additionally, ACC deaminase is a plant hormone that is largely stimulated by stress factors and can limit considerably the activity of increasing plants (Dikilitas et al. [2021\)](#page-16-7). On the other hand, a number of microorganisms could reduce the plant's rate of ethylene by assimilating the ACC, the main plant's produced ethylene precursor (Ajar et al. 2017). ACC deaminase-producing microbes convert ACC into ammonia and α -ketobutyrate (Glick [2005\)](#page-16-8). In particular, plant growth-promoting rhizobacteria endowed with ACC deaminase properties stimulate plant development and productivity and can be effectively enclosed in bioengineering of biofertilizers (Shaharoona et al. [2006\)](#page-21-11). The root-interacting bacteria decrease the rate of ethylene by ACC cleavage ultimately plant stress tolerance (Van de Poel and Van Der Straeten [2014\)](#page-22-11). Importantly, it has been reported that the use of bacteria-producing ACC deaminase against a variety of biotic and abiotic factors improved plant resistance against different stressful factors (Glick [2014;](#page-16-6) Yadav et al. [2020a,](#page-23-7) [2020b,](#page-23-8) [2021a\)](#page-23-9).

2.3.7 Lytic Enzymes

Several plant growth-promoting bacteria secrete various lytic enzymes like lipase, protease, chitinase or β 1,3 glucanase, all of which contribute to cellular fungal degradation (Chet and Inbar [1994\)](#page-15-7). Thus, these enzymes affect the growth and development of phytopathogenic fungi (El-Tarabily [2006\)](#page-16-9). PGPB have been reported to have biocontrol effect toward a number of phyopathogenic fungi like *Pythium ultimum*, *Rhizoctonia solani*, *Sclerotium rolfsii*, *Fusarium oxysporum*, *Botrytis cinerea* and *Phytophta* spp. by synthesis of one or more lytic enzymes (Frankowski et al. [2001;](#page-16-10) Singh et al. [1999\)](#page-21-12). Whereas, other particular enzymes of plant-associated microbes like cutinases were identified as necessary for spore fixation on the surface of many phytopathogens such as *Blumeria graminis, Colletotrichum graminicola* and *Uromyces viciae-fabae* (Deising et al. [1992;](#page-15-8) Pascholati et al. [1993\)](#page-19-8). Generally, such activities of the diverse hydrolase enzymes are very important in rhizosphere soil, as they reflect soil capability to ensure complex biochemical processes, the fertility of the soil and plant productiveness conservation (Burns [1982;](#page-15-9) Shukla and Varma [2011;](#page-21-13) Schloter et al. [2018\)](#page-20-9). Microbial enzymes are important for soil operation and quality because of their implication in organic matter dynamics and nutrient cycles, organic compound degradation, mineralization and the release of nutritional elements including nitrogen, carbon and other important metals (Khare and Yadav [2017;](#page-17-9) Yadav et al. [2020c\)](#page-23-10).

2.3.8 Nanoparticles

Nanomaterials and nanoparticles are generally described as molecules of approximately 1–100 nm measurements that demonstrate characteristics not observed in the bulk state (Bulgari et al. [2019;](#page-15-10) Patil et al. [2021\)](#page-19-9). They are incorporated into the ground through a range of human practices, which include deliberate land releases via water and soil treatment, the extensive utilization of farming (e.g. chemical fertilization) and unconscious water, air and wastewater disposal onto the soil (Mishra and Kumar [2009\)](#page-19-10); or are produced biologically in situ in the soil by microorganisms (bacteria and fungi) in contact with contaminants such as silver. This is of particular concern for soil benefit microbes since AgNPs act as antimicrobials by inhibiting enzymatic activity, damaging DNAand generating reactive oxygen species that lead to cell death (Li et al. [2010\)](#page-18-11). Several microbial suppressive impacts of nanoparticles have been observed impacting directly microbe's survival (Lovern and Klaper [2006\)](#page-18-12). Generally, antiphytopathogenic activity, seed germination enhancement and improving crop development were reported using zinc oxide and silver nanoparticles (Gogos et al. [2012\)](#page-16-11).

2.3.9 Biofilms

Historically, microbes had been explored as planktonic cells (or free swimmings). The majority of these cells has been established in multi-cell joint to surfaces, called biofilms (Rudrappa et al. [2008\)](#page-20-10). According to Costerton et al [\(1999\)](#page-15-11), a biofilm is described as "a structural community of bacterial cells enclosed in a self-produced polymeric matrix and adherent to an inert or living surface. On plant surfaces, they are formed mostly by bacteria in pathogenic, mutualistic, or symbiotic association on leaves, roots, and in the soil (Cavalcante et al. [2017\)](#page-15-12). It is a property in plant growthpromoting bacteria that enable them to resist various abiotic stresses (Bouskill et al., [2016\)](#page-15-13). Especially, biofilm formation on plant roots appears to be associated with symbiotic interactions. For instance, these structures help to create protective niches for Rhizobia (Barriuso, [2017\)](#page-15-14). Recently, it has been shown that biofilm-mediated microcolonies formed on root hairs of finger millet by endophytic *Enterobacter* sp. conferred protection against colonization by the pathogenic organisms (Mousa et al. [2016\)](#page-19-11). Apart from the root surface, microbial biofilms are also reported on the phyllospheric region and vasculature (Torres et al. [2006\)](#page-22-12). Epiphytic microbes are often formed in biofilms, likely because these microenvironments protect bacteria from harsh environmental conditions (Monier and Lindow [2004\)](#page-19-12). Furthermore, certain bacteria in biofilm matrices have been found to stimulate plant growth and protect plants from phytopathogens while others are involved in pathogenesis (Bogino et al. [2013\)](#page-15-15).

2.3.10 Antibiotics

Antibiotics produced by microorganisms play a major role in plant pathogens and the diseases they cause (Pal and McSpaddenGardener [2006\)](#page-19-13). The production of antibiotics is one of the important mechanisms most commonly associated with the capability of PGPB to act as antagonistic agents (Glick et al. [2007;](#page-16-12) Abdel-Azeem et al. [2021\)](#page-14-1). Furthermore, the production of antibiotics is used in the acquisition of genes coding for antibiotic resistance from transgenic plants by plant-associated bacteria (Montesinos [2003\)](#page-19-0). Amongst PGPR, species belonging to *Pseudomonas* excrete a great variety of effective antibiotics such as 2,4-diacetylphloroglucinol (2,4-DAPG), pyoluteorin, pyrrolnitrin, (Raaijmakers et al. [2002;](#page-20-11) (Singh and Yadav [2020;](#page-21-14) Yadav et al. [2020c\)](#page-23-10). In addition, some species can also produce hydrogen cyanide (HCN) that is toxic to certain pathogenic fungi (Dowling and O'Gara [1994\)](#page-16-13).

In soil, several metabolites from endophytic *Streptomyces* sp. have been characterized, which are associated with antibiotic activity (Castillo et al. [2003;](#page-15-16) Guan et al. [2005\)](#page-16-14). Furthermore, endophytic fungus, *Acremonium zeae*, has been implicated in the protection of its host against *Aspergillus flavus* and *Fusarium verticillioides* (Wicklow et al. [2005\)](#page-22-13).

2.4 Beneficial Effects on Crop Production and Yield

Plant-associated microbiomes play a pivotal role in plant biology, performing key functions in germination, growth, health and stress protection (Mendes and Raaijmakers [2015;](#page-18-13) Tiwari et al. [2021\)](#page-22-14). An increasing number of studies have shown that plant-associated microbes improve plants' nutritional conditions, resistance to abiotic stresses and inhibit pathogens and pests (Vandenkoornhuyse et al. [2015\)](#page-22-15). Importantly, rhizospheric microbes affect plant growth, development and stress resistance by diverse mechanisms (Lareen et al. [2016;](#page-18-14) Rai et al. [2020\)](#page-20-4). Beneficial effects of some plant-associated microbes on crop productivity and yields have been listed in Table [2.1.](#page-10-0)

2.4.1 Seed Germination Enhancement

Seed germination is an important stage in the life cycle of plants (Song et al. [2005\)](#page-21-15). In particular, seed-associated microorganisms can be essential for the germination process in different plant phyla (Jacquemyn et al. [2015\)](#page-17-10). Effectively, PGPB can accelerate seed germination and improve seedling emergence (Souza et al. [2015\)](#page-21-16). This is illustrated by seed treatment of legumes with Rhizobaceae that frequently leads to increase in yield (Thilakarathna and Raizada [2017\)](#page-22-16). In addition, the application of beneficial microorganisms to seeds is an efficient mechanism for the placement

Associated microbes	Crops	Effects	References
Pseudomonas spp.	Soybean and wheat	Increased straw and grain yields; increased nutrient uptake: N, P, K, Zn and Fe	(Sharma et al. 2011)
Pseudomonas fluorescens	Rice	In field experiments, the occurrence of sheath blight and leaf folder insect incidence decreased by average 62.1% and 47.7-56.1%, respectively	(Commare et al. 2002)
Serratia marcescens strain SRM	Wheat	Significantly influence wheat seedling growth at cold temperatures	(Selvakumar et al. 2008)
Bacillus thuringiensis	Maize	Increase seed germination percentage up (94%) , seedling growth to $(36.08 \text{ cm/seedling})$ and vigor index (3391.52)	(Kassogué et al. 2016)
Bacillus subtilis	Tomato	Reduce substantially seedling mortality in inoculated plants, it (6.6%) is compared to high mortality in the control seedlings (51.6%)	(Cabra Cendales et al. 2017)
Azospirillum brasilense	Wheat and oat	Yield increase up to 27% in wheat and to 6% in oat	(Swędrzyńska 2000)
Streptomyces sp. KLBMP 5084	Wheat	Increase in germination rate, concentration of N, P, Fe and Mn, shoots grown under salinity stress	(Sadeghi et al. 2012)
Trichodermaatroviridae	Indian mustard	Bioremediation by influencing uptake and translocation of Ni, Zn and Cd	(Cao et al. 2008)

Table 2.1 Beneficial effects of plant-associated microbes on some crop productivity and yields

of microbial inoculum to soil and protection against soil-borne diseases and pests (O'Callaghan [2016\)](#page-19-14).

The enhancement mechanism of seed germination is ensured via the production of different PGP traits. Seed treatment of cowpea with *Bacillus* sp. exhibiting multiple PGP attributes improved seed germination and yield parameters (Minaxi et al. [2012\)](#page-19-15). Paul et al. [\(2011\)](#page-19-16) reported IAA-producing bacterium *Azotobacter chroomcoccum*, particularly when co-inoculated with arbuscular mycorrhizal fungi improve seed germination.

2.4.2 Stimulation of Plant Growth

The positive response of different crops to microbial inoculation has been assessed in many experiments under greenhouse and field conditions (Calvo et al. [2014\)](#page-15-20). It has been reported that specific guilds of taxa among the soil bacterial microbiome can be selected to modify plant traits and to coordinate changes in soil resource pools (Pfeiffer et al. [2017\)](#page-20-14). Notably, plant growth-promoting rhizobacteria are beneficial microorganisms that help in promoting plant growth and significantly increase soil fertility (Kashyap et al. [2017\)](#page-17-6). Some microorganisms when given the opportunity to inhabit plant roots become root symbionts. Such root colonization by symbiotic microbes can enhance crop yields by promoting the growth, nutrient uptake, fixation, resistance to pests, diseases and abiotic environmental stress conditions stresses (Harman and Uphoff [2019;](#page-16-15) Yadav et al. [2018\)](#page-22-18).

2.5 Resistance to Abiotic Stress

Abiotic stress in soils includes extreme temperatures, pH, drought, water-logging and toxic metals (Wu [2017\)](#page-22-19), salinity (Shrivastava and Kumar [2015\)](#page-21-18) and some gases and nutrient deficiency or excess (Hayat et al. [2017\)](#page-17-12). They are greatly affecting plant growth and agricultural productivity and cause more than 50% of worldwide yield loss of major crops every year (Jarvis et al. [2006;](#page-17-13) Kumari et al. [2019\)](#page-18-15). These conditions often favor pathogens and negatively affect plant productivity and soil fertility (Dresselhaus and Hückelhoven [2018\)](#page-16-16). Particularly, drought has affected 64% of the worldwide land area, salinity 6%, anoxia 13%, soil alkalinity 15%, mineral starvation 9% and cold 57% (Mittler [2006\)](#page-19-17). For example, drought stress limits the growth and productivity of crops particularly in arid and semi-arid areas (Kramer and Boyer [1995\)](#page-18-16).

Plant-associated microbiomes have a much greater evolutionary potential for dealing with abiotic stresses than the plant itself (Jones et al. [2019\)](#page-17-14). Therefore, it is potentially more sustainable to manage abiotic stresses in a holistic and multifaceted manner. The microorganisms use indirect and direct mechanisms to promote plant growth and development during stress conditions (Kumar and Verma [2018\)](#page-18-17). Some bacteria have sigma factors to change gene expression under adverse conditions to overcome negative effects (Gupta et al. [2013\)](#page-16-17). Notably, microorganism communications with the plants incite a few fundamental responses that improve their metabolic mechanism for defense against abiotic stress conditions (Nguyen et al. [2016\)](#page-19-18).

2.5.1 Bioremediation

Environmental pollution resulting from human activities has a great impact on the biodiversity and functioning of terrestrial and aquatic ecosystems and is a major threat to human health across the globe (Alava et al. [2017\)](#page-14-4). Extensive pollution of terrestrial ecosystems with petroleum hydrocarbons (PHCs) has generated a need for hazardous and expensive physico-chemical remediation techniques. Alternatively, plant-associated bacteria and cooperation between these bacteria and their host plants allow for greater plant survivability and treatment outcomes in contaminated sites (Gkorezis et al. [2016\)](#page-16-18). Such ecological microorganisms are expected to have multiple implications for maintaining pollutant decomposition and ecological services in terrestrial environments (Shi et al. [2018\)](#page-21-19). Filamentous fungi including *Aspergillus* sp., *Mucor* sp., *Penicillium* sp. and *Trichoderma* sp. have been reported to possess capability to tolerate heavy metal stress (Ezzouhri et al. [2009;](#page-16-19) Oladipo et al. [2017\)](#page-19-19). Mycorrhizal fungi, free-living or endophytic fungi are also known for their strong degradative capacities and are often applied during phytoremediation of organic pollutants (Deng and Cao [2017\)](#page-16-20).

The basic principle of bioremediation involves reducing the solubility of environmental contaminants by changing pH, the redox reactions and adsorption of contaminants from the polluted environment (Jain and Arnepalli [2019\)](#page-17-15). Especially, the in situ bioremediation processes have become an attractive way to rehabilitate various contaminated sites (Ayoub et al. [2010\)](#page-14-5). More particular, phytoremediation is using plants and associated bacteria for the treatment of soil contaminated by toxic pollutants (Salt et al. [1998\)](#page-20-15). Concerning plant-associated microbes, such as rhizospheric bacteria, implicated in "Rhizomediation", it has been demonstrated that they lead to the decomposition of polluted soil by harmful organic elements and may enhance phytoremediation (Babalola [2010\)](#page-14-5). These microbes' capacity to cleave contaminants depends on the effectiveness of their development and various metabolic surrounding conditions, including appropriate pH, temperature and humidity (Verma and Jaiswal [2016\)](#page-22-20).

2.5.2 Plant Disease and Pest Control

Plant infections typically happen in regions, forests or fields when different plant components (like leaves, fruits or flowers) are attacked (Sastry and Zitter [2014\)](#page-20-16). They are principally treated mainly by chemical pesticides. Plant-related microorganisms may also serve as biological control agents due to their protective effect based likely on the synthesis of effective inhibiting enzymes and substances like hydrolases and antibiotics destruct the phytopathogenic cell wall (Kumar et al. [2017\)](#page-18-1). Genera, including Gram-positive and Gram-negative bacteria such as *Burkholderia*, *Pantoes*, *Bacillus*, *Enterobacter*, *Paenibacillus*, *Streptomyces* and *Pseudomonas* were, in particular, mentioned for their involvement in pathogen suppression (Schlatter

et al. [2017\)](#page-20-12). Additionally, certain native plant epiphytic microorganisms could be employed in the suppression of agri-foodstuff phytopathogens (Lopez-Velasco et al. [2012\)](#page-18-18), and at a less degree of endophytic bacteria.

2.6 Factors Affecting Crop Productivity and Yield

Crop productivity and yield can be influenced by many organisms as a community contributes efficient genome and chemical exchange to create a competitive metagenome, contributing to improved plants' production and to strengthen relationships with each other (Zorner et al. [2018\)](#page-23-0). The nature and the quality of plant and microorganism interaction and soil microbial diversity can affect largely crop productivity and yields. Several experiments have also shown the direct effect of various plant species on the selection of rhizosphere populations (Marschner et al. [2004;](#page-18-19) Coleman-Derr et al. [2015\)](#page-15-21). Nevertheless, other considerations are included like developmental stage or variety (Qiao et al. [2017\)](#page-20-17) that may additionally affect their microbiome contents. In addition, microbiome balance and abiotic indicators can contribute to crop productivity and yield determination including soil structure, stability in wet aggregate, water supply potential, rigidity of the soil, pH, capability for nutritional element and cation exchange (Jeanne et al. [2019\)](#page-17-16). Furthermore, crop productivity and yield are affected by environmental impacts of unhealthy soil via microbial activities that could not sequester carbon but cause emissions of methane, $CO₂$ and other greenhouse gases that harm ecosystems in turn. For example, the increased global temperature has led adversely to high greenhouse gasses (Saha and Mandal [2009\)](#page-20-18). Similarly, soil microbial communities are impacted by meteorology (Terrat et al. [2017\)](#page-22-21). Figure [2.3](#page-14-6) illustrates the factors affecting crop productivity and yield including: Environmental factors, biotic and abiotic stresses and plants (species, genotype and stage development).

2.7 Conclusion and Future Prospects

The microbes associated with plants are much diversified and can eventually occupy all the plant parts during their all-development cycle; from seeds to maturation. These microbes can be both beneficial and harmful, leading to a loss of crop yields or countless beneficial effects for development and protection against various biotic and abiotic stresses, undoubtedly leading to an effective increase in crop productivity and yields. Furthermore, the variability and complexity of the interaction mechanisms between microbes, plants and soil always require more investigations; especially with regard to the overlap and simultaneous effects of interaction mechanisms such as the association of abiotic and biotic stress impacts on both plants and microorganisms, as well as the different strategies developed by each partnership in these specific and complex interactions.

Soil abiotic stress

Fig. 2.3 Factors affecting crop productivity and yields

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