REVIEW ARTICLE

Plant microbiome and its functional mechanism in response to environmental stress

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Abstract

Stresses are the prime factor for limiting agricultural productivity. Protracted stress conditions are accountable for the generation of reactive oxygen species (ROS) in various cell compartments. ROS attacks biomolecules and interrupts the regular mechanism of the cell that eventually prompts to cell death. Crops requisite to acclimatize adverse external stress generated by ecological conditions with their native biological mechanisms defeated which their growths as well as productivity endure. Microbes, the supreme natural occupants of diverse environments, have developed intricate physiological and metabolic mechanism to manage with potentially toxic oxygen species that are generated by environmental stresses. Subsequently, the interaction of microbial population with plants is an essential for the ecosystem, and microbes are the natural partners that accommodate in plants to combat with antagonistic environment. Plant microbiome involves intricate mechanisms inside the plant cell. Molecular, physiological as well as biochemical studies support to understand the intricate and integrated cellular processes of plant–microbe interactions. During the incessant stress by increasing environmental variations, it is becoming more essential to characterize and decipher plant–microbe association in relation to defense against environmental challenges.

Key words: Abiotic stress, agricultural productivity, defense mechanism, phytomicrobiome

INTRODUCTION

Plants are affected by various stress conditions, and among them, abiotic stress is the prime cause of limiting the crop production in worldwide.[1,2] The effect of abiotic factor on the plant depends on its quantity or intensity. The plant requires a certain quantity of abiotic environmental factor for their optimal growth. Any alteration from such optimal environmental conditions, which is deficit in the chemical or physical environment, is considered as abiotic stress and critically impacts on plant growth, development, and productivity.[1] They are chronic features of nearly all the world's climatic regions since several critical environmental risks and these threats are mobilized by global climate change and population growth.[3-5]

Anomaly environmental conditions generate abiotic stresses that are the primary restrictive factors for limiting crop production.[6,7] Abiotic stresses comprise of heat, cold, drought, alkaline conditions and salinity, waterlogging, light intensity, and nutrient deficiency.[2,8-12] Drought has affected 64% of the worldwide land area, salinity 6%, anoxia 13%, soil alkalinity 15%, mineral starvation 9%, and cold 57%.[13] Of the world's 5.2 billion ha of dryland agriculture, 3.6 billion ha is influenced by the issues of soil erosion, degradation, and salt stress.[14]

Plants adapt with the rapid alteration and affliction of ecological conditions as a result of their natural metabolic mechanisms.[15] Deviations in the external environment conditions could put the plant metabolism out of homeostasis[16] and make the need for the plant to harbor some metabolic and genetic mechanisms in the cell.[17,18] Plants retain a variety of defense mechanism to combat abiotic stress conditions.[19] These mechanisms involve in the metabolic reprogramming

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in cellular system to enable biophysicochemical processes of the external conditions.[20-25] Several time, plants reduced the burden of abiotic stresses with the help of the inhabitant microbiome.[26,27]

Microbes are the integral part of ecological system and important for crop production. Microorganisms are important inhabitants of seeds also and proliferate as germinate in the soils to form mutual associations at the surface or endophytic associations inside the roots, stems, or leaves. Plant microbiome gives principal support to the plants in securing supplements, opposing against infections, and enduring abiotic stresses.[26] Microbial inherent metabolic and hereditary abilities make them reasonable organisms to cope up with environmental challenges.[28,29] Their communications with the plants incited a few fundamental responses that improved the metabolic mechanism of the plants for defense against abiotic stress conditions as shown in Figure 1.[30] Several studies reported the imperative characteristics of the microbial communications with plants that propose mechanisms based on plant-microorganism associations that accentuated the biochemical, molecular, and cellular mechanisms of plant defense against stresses.[31,32]

Studies on plant microbiome at molecular, physiological, and biochemical levels observed that plant–microbes associations communicate plant responses against stress conditions.[33] Technological developments also facilitated understanding of gene editing systems, RNAi-mediated gene silencing, mutant technology, proteomic analysis, and metabolite profiling to reveal voluminous molecular information that helped in improving our understanding of microbe-interactions. In this study, we summarize the impact of environmental stresses on plants and defense responses induce in plants in terms of biochemical and molecular mechanisms.

HOW ENVIRONMENTAL STRESS EFFECT PLANTS?

Diminishing of Physiological Process of Plant

Plants required abiotic environment for their physiological and developmental mechanism. Unfavorable abiotic environment is intricate set of stress conditions that limit plant growth and development. Plants can detect and respond to stresses in various ways that support their nourishment.[34-36] Plants not only recognize the previous exposure to stresses but also the mechanisms involved in defense, and again when the same stress exposes, they can adapted consequently.[37] The most obvious effect of unfavourable conditions initially appear at the cellular levels after that, physiological symptoms are observable. Water stress antagonistically influences physiological status of plants including the photosystem.[38] Prolong exposure of water stress reduces leaf size, seed number, size, and viability, declines water potential and stomatal opening, reduces root growth, delays flowering, and restrains plant growth and productivity.[39,40] Hence, plants have sagaciously evolved distinctive mechanisms to limit utilization of optimum water assets and regulate their growth till they expose with adverse conditions.[41] Exposure of adverse light intensities reduces the physiological process and unfavorably impacts on plant development. Abundance light prompts photooxidation that enhances the fabrication of reactive oxygen species (ROS) to influence enzymes and other biomolecules.[42-44]

Biochemical Changes During Environmental Stress

Several abiotic factors affect plant development and limit crop production, different levels of acidic conditions unfavorably effect on soil nutrients that cause a nutrient deficiency in plant and disrupt normal physiological ability for plant growth and development.[45-47] Prolonged exposure to salinity stress leads to toxicity within the cell along with interruption of osmotic balance. Effect of ionic followed with osmotic stresses leads to altered plant growth and development.[48] Forbearance to salinity stress needed to regulate ionic and osmotic balance in the cells. For resistance toward salinity, plants protect delicate plant tissues from high salinity area or by emanating ions from roots or keeping ions away from the cytoplasm.[49] During freezing conditions, some plants developed a mechanism to cope up with cold temperatures by elevating their defense response by the process of cold acclimation.[50] After sensing the stress, plants show a quick and compelling reaction to initiate an intricate stress-specific signaling by synthesizing plant hormone and accumulation of phenolic acids and flavonoids.[51-57]

Generation of ROS

Abiotic stresses are primary cause for the generation of ROS. The generation and elimination of ROS are at balance under normal conditions, whereas under environmental stress, it disturbs this equilibrium by increasing the production of ROS as shown in Figure 1. ROS is very toxic for the organism as they adversely impact on the structure and function of the biomolecules. The ROS produced in plants in chloroplasts, mitochondria, and peroxisomes. Oxygen radicals and hydrogen peroxide are produced in mitochondria due to the overreduction of the electron transport chain. Chloroplasts are the main source of the production of O^2 and H^2O^2,[58] due to higher oxygen pressure and reduced molecular oxygen than in other organelles in the electron transport chain within PSI.[59] These superoxides are converted to hydrogen peroxide either spontaneously or by the action of the enzyme superoxide dismutase (SOD). Hydrogen peroxide is also responsible for the production of hydroxyl radicals. It has been reported that peroxisomes are a major producer of H^2O^2 and responsible for the production of superoxides (O^{2-}). In peroxisomes, the production of O^{2-} occurs in the peroxisomal matrix and the peroxisomal membrane. In the peroxisomal matrix, the oxidation of xanthine and hypoxanthine to uric acid in the presence of the enzyme xanthine oxidase generates O^{2-} radicals.[60] They damage the biomolecules such as proteins, lipids, carbohydrates, and DNA, which leads to cell death.[16]

PHYSIOLOGICAL AND MOLECULAR DEFENSE MECHANISM OF PLANTS AGAINST ENVIRONMENTAL STRESS

Plants smartly sense and defense against the changing environmental conditions. Their approaches and responses to abiotic stresses involve an interactive metabolic cross talk within various biosynthetic pathways. Root architecture is sensitive in sensing abiotic stress signals and responding accordingly in the soils.[61] It is an intricate mechanism that involves changes at genetic, cellular, metabolic, and physiological levels.[62] The prime impact of abiotic stresses is generated water-deficient conditions within cells followed by the development of biochemical, molecular, and phenotypic action against stresses.[38,63] Plants experienced many stresses in the environment so as the complexity of their responses to multiple stresses in comparison to individual stress. The complexity occurs due to activating specific gene expression along with metabolic programming in cells against to individual stresses encountered. Tolerance to stresses is a vital phenomenon including different stages of plants development. Abiotic stress responses may reduce or increase the susceptibility of plants toward biotic stresses caused due to pests or pathogens.[64] This becomes more important in account to agricultural crops because, in various agricultural systems, most crops grow in unfavorable environmental conditions that are restricted to the genetic potential of the plants for growth and development.[1]

Plant Responses Against Drought Stress

Plants are sensitive to water stress. During drought conditions, peroxidation induced that leads to disturb antioxidant metabolism.[65,66] Rehydrating further reduced the peroxidation level and rejuvenates the growth and development of newly growing plant parts and stomatal opening. In roots, both drought and waterlogging lead to high accumulation of ROS.[65] Drought responses vary from different plant species in account to the activity of SOD enzyme that performed a critical role in antioxidant metabolism.[66] In bluegrass, SOD activity was not influenced by drought stress, and gene expression of FeSOD and Cu/ZnSOD is downregulated. In Alfalfa, FeSOD and CU/ZnSOD are upregulated by drought stress, suggesting that defense responses differ from species and tissues.[16,67] An enhanced level of salts in the soil is harmful to the plant cells, and different cells in a tissue respond differently to the stresses caused due to salinity.[68] Stressed cells are detrimental to their location, whether at the root surface or within tissues, and altered their gene expression during the stress condition.[69] The osmotic potential of the soil declined due to the enhanced level of salt, which leads to ion toxicity in the plants. This situation can adversely affect on the physiology of the plants by suppressing seed germination and growth of the seedlings and early senescence of the plants and finally cause death.[70,71] Salinity stress declines the amino acids levels such as cysteine, arginine, and methionine. Proline synthesis in the cells is a prominent alleviated approach from salinity stress.[72] Similarly, production of nitric oxide, activation of antioxidant enzymes, modulation of hormones, and synthesis of glycine betaine are some other changes within plants during salinity stress.[73] This principally occurs due to water deficiency and deterioration in the nutrient availability caused due to high salinity that disturbs plant tissues and adversely affects crop productivity.

Plant Responses Against Heat Stress

Heat stress is a severe agricultural problem as it adversely impacts on functional, structural, biochemical, and genetic modifications in plants that affect crop production. A complete study on plant defense mechanisms against heat stress could help in the improvement of better approaches for crop productivity.[74] High temperature negatively impacts on plants during different growth stages, and it reduces seed germination, disturbs photosynthetic activities, and declines in membrane permeability.[66] Plants respond against heat stress by modulating the level of phytohormones, metabolites, increasing the expression of heat shock and related proteins, and accumulation of ROS.[75] Defense mechanism in plants against heat stress not only includes maintenance of membrane stability and activation of mitogen-activated protein kinase and calcium-dependent protein kinase but also involves scavenging of ROS,[76] accumulation of antioxidant metabolites, chaperone signaling, and transcriptional modulation.[74]

Plant Responses Against Multiple Stress Conditions

Plants are more effectively response against multiple stress conditions rather than specific stress alone. Multiple stresses diminish the harmful destructive impact of each other subsequently, enhancing the probability of healthier survival of plants. It has been reported that the consolidated effect of ozone and drought in plants brought about improved tolerance.[77] The cumulative effect was responsible to reduced stomatal conductance. Increased the level of ascorbic acid and glutathione adequately scavenges ROS. In addition, it is a troublesome errand for plant to fight toward particular stress, especially when it is developing in the field from the effect of various stresses. Multiple stresses arise at the same time in field conditions and thus occur simultaneously in field conditions and so mitigating plant mechanisms to combat with hastily fluctuating environmental conditions.[78]

Role of Plant Hormones in Responses to Stress Conditions

Plant hormones are not only important for the plant growth and development but also involve in defense mechanism against environmental stresses.[79] Plants approach their physiological resources for adjusting in the adverse environmental conditions that make them exceptionally susceptible to biotic stresses.[80,81] Abscisic acid-mediated abiotic stress response pathways are most important followed by other phytohormone-dependent defense pathways, namely, ethylene (ET), jasmonic acid, and salicylic acid that provoke plants for environmental stress response. It has been observed that jasmonic acid has active defense responses against necrotrophs.[82]

PLANT MICROBIOME: ROLE IN STRESS AND ITS MECHANISM

The plant–microbial interactions are imperative for the adjustment and survival of both the accomplices in any environmental conditions. The function of microbes to increase abiotic stresses in plants has enticing attention by investigators in recent decades.[83-85] Microbes with their potential intrinsic metabolic and genetic capabilities, contribute to alleviate abiotic stresses in the plants.[86] The function of various rhizomicrobes belongs to the genera of *Pseudomonas*, Azotobacter, Rhizobium, Azospirillum, Pantoea, Bacillus, Enterobacter, Bradyrhizobium, Burkholderia, Trichoderma, and Cyanobacteria in plant growth and combating different environmental challenges.[87-92] It has been reported that *Trichoderma harzianum* responses against stress in rice by upregulating the stress-related genes, namely, dehydrin, malondialdehyde, and aquaporin genes including physiological parameters. Several microbes induce plant responses which altered the level of many defense proteins, antioxidant enzymes, polysaccharides, and phytohormones, for example, Rhizobacteria-induced drought endurance and resilience.[93] These approaches make plants able to cope up with environmental stress conditions.[94] Improved oil content in *Brassica juncea* affected with NaCl was testified by the treatment of *T. harzianum* that enhanced the uptake of vital nutrients, improved aggregation of osmolytes and antioxidants as well as reduced the uptake of NaCl.[35] Followed by such reports, *Trichoderma* synthesizes 1-aminocyclopropane-1-carboxylate (ACC) deaminase to amend salinity stress.[95] Similarly, *Pseudomonas* sp. and *Acinetobacter* sp. increase the production of indole acidic acid (IAA) and ACC deaminase in oats and barley under salinity stress.[96] It has been reported that the *Streptomyces* sp. strain PGPA39 alleviated salinity stress and promoted growth in tomato plants.[97] *Burkholderia phytofirmans* strain PsJN combat drought stress in wheat,[98] maize,[99] and salinity stress in *Arabidopsis thaliana*.[100]

Physiological Mechanism of Phytomicrobiome Against Stress

Several studies have enhanced our understanding on physiological methods associated with roots, chemical molecules produced by roots, signaling between microbes and root, and possible defense mechanisms.[101-106] Researchers have given special attention to microbes associated with root in soil among other symbiotic associations between many plants and microorganisms. Mycorrhiza is eminent by fungal colonization inside or outside the cell that helps in nutrient assumption.[107] Rhizobacteria form root nodules of leguminous plants, involve in nitrogen fixation, and deliver it to the plants.[108] These affiliations have given data about mutualistic relationship since plants have created constitutive and inducible defense mechanism to keep away from destructive communications.

Cross Talks between Plants and Microbes during Stress Conditions

There are several cross talks between plants and microbes during their interaction using different signaling molecules. Various microbes are harmful to plants that limit growth and development. Plants have mechanism to recognize certain compounds released by microbes and enhance defense responses. The plant signaling hormones, namely, salicylic acid, jasmonic acid, and ET are used to activate defense mechanism during the interaction between plants and microbes in response to stress conditions.[109,110] Plants identify pathogens by detecting extracellular molecules that are called pathogen-associated molecular patterns (PAMPs) or microbe-associated molecular patterns, namely, Ef-TU proteins, bacterial flagellin, lipopolysaccharides, and peptidoglycans,[111] and/or intracellular effector proteins or tissue damage using pattern recognition receptor (PRR) proteins located on the cell surface or within the cell as shown in Figure 1.[111-113] The plant immune system comprises of four level. In level 1, PAMPs of microbes are recognized and bind to specific PRRs located on the cell surface that triggers the plant immune system and leads to enhanced immunity (PTI), which prevents colonization and proliferation.[31,111,114,115] In level 2, several pathogens induced effectors that enhance virulence. The effectors hinder with PTI and lead to effector-triggered susceptibility. In level 3, nucleotide-binding leucine-rich repeat receptor proteins recognize the effector, which activated the effector-triggered immunity (ETI) that leads to disease resistance. In level 4, natural selection has motivated pathogens to conquer ETI by emerging effectors promoting virulence until plants have developed new receptors.

Impact of Plant Growth Promoting Bacteria (PGPB) on Plants

PGPB are improving plant growth and tolerance against environmental stress. Plants are exposed to different abiotic stress conditions, and phytohormones play a vital role in signaling such as abscisic acid, jasmonic acid, salicylic acid, and ET that react to stress defending plants from different environmental challenges as shown in Figure 1.[116] Further, studies reported that ACC deaminase activity of PGPB could regulate the stresses in plants.[117-119] The PGPB not only help in combating to abiotic stresses but also enhance crops productivity including rice, maize, barley, and soybean.[120-123] Improved root colonizing ability of *Pseudomonas* sp. laterally with its capability to synthesize exopolysaccharides prompts improved resistance in response to salt stress in rice during germination.[121] Similarly, it has been demonstrated that inoculation of *Bacillus pumilus* enhances rice development in response to heavy metal and salinity stresses.[61]

Phytohormones

Phytohormones play a key role in plants defense mechanism, and plants react and adapt to abiotic stresses by balancing the phytohormone levels. A few reports have revealed that PGPB fortify plant development by direct or indirect systems. In the direct mechanism, microbes accumulate phytohormones, for example, IAA, gibberellins, cytokinins, and ET that invigorate plant development as well as regulate the hormone level in plants that may likewise antagonism to phytopathogens as shown in Figure 1.[124-136] In indirect mechanism, the microbes actuate plant resistance by producing chemicals that can regulate the hormone level. PGPB can likewise animate plant development by communicating the compound ACC deaminase that severs ACC to α-ketobutyrate and alkali, diminishing the ET level in plants.[137-140] Usually, plants synthesize low ET that is valuable for plant development and improvement. Further, amid stress responses in plants, the expanded ET biosynthesis is alluded to as "stress ET"[138,141] that is a response to biotic and abiotic stress conditions.[141,142]

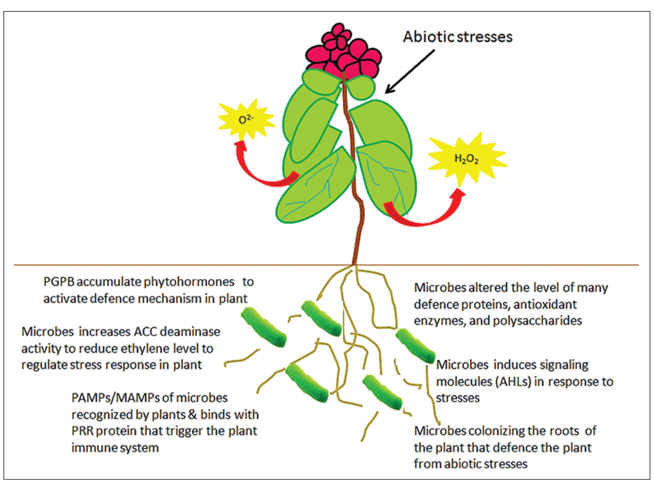

Figure 1: Role of plant microbiome in defense mechanism. Microorganism in association with plants activates different mechanism in response to abiotic stress conditions. PGPB: Plant growth promoting bacteria, ACC: 1-aminocyclopropane-1-carboxylate PAMPs/MAMPs: Pathogen-associated molecular patterns or microbe-associated molecular patterns PRR: Pattern recognition receptor AHLs: N-acyl-homoserine lactones

Root Colonization

Rhizobacteria are colonizing plant roots amid various phases of plant development and they can proliferate on roots to assemble a mutual association among plants and microorganisms, where these communications give advantages to both the partners as shown in Figure 1.[143,144] The mechanism of the microbial group to metabolize and vie for carbon sources in the rhizosphere is reliant on the synthesis of plant root exudates.[145] Once the microscopic organisms colonize the root, they can live on the surface of the roots (epiphytic) or can enter into the root and spread into the ethereal parts of the plant and vascular tissue cortex (endophytic).[146,147] Many researchers observed that Gram-negative and Gram-positive microbes enter into the root through the primary root, horizontal roots, and root hair.[148-150] Furthermore, it has been reported that *Curvularia proturberata* microorganisms colonize with the root and defense *Dichanthelium lanuginosum* and *Solanum lycopersicum* plants from drought and heat stress conditions.[83]

Quorum Sensing Mechanism

Quorum sensing is the process of communication between cells in bacteria by inducing different chemical. This encourages the microbial groups to react rapidly, hinder contending organisms, enhance supplement uptake, and adjust to changing ecological conditions. Likewise, it controls bacterial size and populace status. N-acyl-homoserine lactones (AHLs), 2-heptyl-3-hydroxy-4-quinoline, and autoinducer-2 are utilized as a part of cell-cell communication inside the bacterial group to synchronize a few activities and influence them to work more like a solitary unit as shown in Figure 1. These signaling particles are exceptional among the microbial species. AHLs in *Proteobacteria*, gamma-butyrolactones in *Streptomyces*, cis-11-methyl-2-dodecanoic acid in *Xanthomonas,* and oligopeptides in Gram-positive microorganisms are act as signaling molecules.[151]

FUNCTIONS AND ECOLOGY OF THE PLANT MICROBIOME

Several functions of the plant microbiome are essential for the host. Numerous plants cannot begin their existence without the assistance of microorganisms, for example, mosses[152] and orchids, which require the assistance of particular fungi, regularly Rhizoctonia to germinate.[153] The germination-advancing fungus Rhizoctonia involves favorable organisms and additionally pathogens. To stay away from any pathogenic collaboration after germination, the host plant processes their helping fungus totally. In these instances of germination bolster, microorganisms are basic, and this might be one reason that these cornerstone microorganisms are vertically transmitted as appeared for Sphagnum.[154] A positive effect on germination was additionally found for plant-related microbes such as *Stenotrophomonas*.[155] The mechanisms by which these microorganisms support plant growth include the production of phytohormones, the fixation of nitrogen, and the mobilization of phosphorus and minerals.[156]

Promote Stress Resistance

The plant microbiome particularly the root microbiome is engaged in the protection against biotic stresses, by going about as a defensive shield against soil-borne pathogens.[157] The components are incorporating different direct communications with plant pathogens and also backhanded associations through the plant by incitement of the immune system of plants.[158] In the recent research it has shown that the microbiome is not only involved in coping with biotic stress, it is also involved in protection against abiotic stress.[159] For instance, the plant microbiome has been appeared to be associated with defense against drought as well as high salinities stresses.[160,161] Studies reported that the plant microbiome is likewise associated with cold acclimation, an essential factor constraining the development and yield of crops.

Plant Growth and Development

The plant microbiome also affects the plant secondary metabolites that result in the development of different metabolism in plant. It has been accounted for the flavor of strawberries and the fabrication of bioactive compounds in medicinal plants.[162,163] In an examination on *A. thaliana*, the rhizosphere microbiomes are engaged in insect feeding characteristics, which was most likely an aftereffect of microbiome-driven changes in the metabolites of leaf.[164] It has been studied that the expulsion of the flower microbiome of *Sambucus nigra* leads to a decreased terpene emanation in flower, which pivotally involved in fertilization and thus in fruit and seed production.[165]

Plant Phenology

Studies on plant microbiome uncovered the immediate effect of the root microbiome on plant phenology. It has been reported that soil microbes affect the blooming time of a *Boechera stricta*.[166] Essentially, regarding fruitful transplantation of rhizosphere microbiomes from *A. thaliana* to *Brassica rapa* affected their blossoming times, bringing about comparative moves in blooming phenology.[167,168] Coadvancement of plants and related microbial groups has been estimated in the light of culture-subordinate outcomes got for the rhizosphere of wheat cultivars,[169] maize, sugar beet, and lettuce, by the use of profound sequencing techniques.[170,171]

CONCLUSION

The unfavorable environmental condition over plant systems enhances the synthesis of ROS, leading to toxicity and resulting in oxidative damage at cellular level. Plants response toward various abiotic stresses by complex of mechanism that involves changes at genetic, cellular, metabolic, and physiological levels. Plant microbiome provides fundamental support to the plants in acquiring nutrients, resisting against diseases, and tolerating abiotic stresses. The plant and their microbiome are interacted with each other through different metabolic cross talk and formed stress tolerance strategies. Microbes produced various metabolites that act as signals during stress conditions and plants have a mechanism to recognize certain compounds released by microbes and activate defense mechanism in response to stress conditions. Plant-associated microorganisms not only involved in stress tolerance but also regulated plant growth and development. The metabolism and morphology of plants and their microbiome are connected with each other, and both maintain the functioning to different crops to improve crop productivity under various environmental conditions.

REFERENCES

1. Bray EA, Bailey-Serres J, Weretilnyk E. Responses to abiotic stresses. In: Gruissem W, Buchannan B, Jones R, editors. Biochemistry and Molecular Biology of Plants. Rockville, MD: American Society of Plant Physiologists; 2000. p. 1158-203.
2. Wang W, Vinocur B, Altman A. Plant responses to drought, salinity and extreme temperatures: Towards genetic engineering for stress tolerance. Planta 2003;218:1-4.
3. Gleick PH. Water, war, and peace in the Middle East. Environment 1995;36:7-41.
4. Gleick PH. Water in crisis: Paths to sustainable water use. Ecol Appl 1998;8:571-9.
5. Gleick PH. The World's Water 2000-2001. The Biennial Report on Freshwater Recources. Washington: Island Press; 2000. p. 245.
6. Padgham J. Agricultural Development under a Changing Climate: Opportunities and Challenges for Adaptation. Washington, DC: Agriculture and Rural Development and Environmental Departments, The World Bank; 2009. p. 30-45.
7. Grayson M. Agriculture and drought. Nature 2013;501:S1.
8. Chaves MM, Oliveira MM. Mechanisms underlying plant resilience to water deficits: Prospects for water-saving agriculture. J Exp Bot 2004;55:2365-84.
9. Agarwal S, Grover A. Molecular biology, biotechnology and genomics of flooding-associated low O_2 stress response in plants. Crit Rev Plant Sci 2006;25:1-21.
10. Nakashima K, Yamaguchi-Shinozaki K. Regulons involved in osmotic stress-responsive and cold

stress-responsive gene expression in plants. Physiol Plant 2006;126:62-71.
11. Hirel B, Le Gouis J, Ney B, Gallais A. The challenge of improving nitrogenuse efficiency in crop plants: Towards a more central role for genetic variability and quantitative genetics within integrated approaches. J Exp Bot 2007;58:2369-87.
12. Bailey-Serres J, Voesenek LA. Flooding stress: Acclimations and genetic diversity. Annu Rev Plant Biol 2008;59:313-39.
13. Mittler R. Abiotic stress, the field environment and stress combination. Trends Plant Sci 2006;11:15-9.
14. Riadh K, Wided M, Hans-Werner K, Chedly A. Responses of halophytes to environmental stresses with special emphasis to salinity. Adv Bot Res 2010;53:117-45.
15. Simontacchi M, Galatro A, Ramos-Artuso F, Santa-María GE. Plant survival in a changing environment: The role of nitric oxide in plant responses to abiotic stress. Front Plant Sci 2015;6:977.
16. Foyer CH, Noctor G. Oxidant and antioxidant signalling in plants: A re-evaluation of the concept of oxidative stress in a physiological context. Plant Cell Environ 2005;28:1056-71.
17. Apel K, Hirt H. Reactive oxygen species: Metabolism, oxidative stress, and signal transduction. Annu Rev Plant Biol 2004;55:373-99.
18. Gill SS, Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiol Biochem 2010;48:909-30.
19. Yolcu S, Ozdemir F, Güler A, Bor M. Histone acetylation influences the transcriptional activation of POX in beta vulgaris L. And beta *Maritima* L. Under salt stress. Plant Physiol Biochem 2016;100:37-46.
20. Heil M, Bostock RM. Induced systemic resistance (ISR) against pathogens in the context of induced plant defences. Ann Bot 2002;89:503-12.
21. Swarbrick PJ, Schulze-Lefert P, Scholes JD. Metabolic consequences of susceptibility and resistance (race-specific and broad-spectrum) in barley leaves challenged with powdery mildew. Plant Cell Environ 2006;29:1061-76.
22. Shao HB, Chu LY, Jaleel CA, Zhao CX. Water-deficit stress-induced anatomical changes in higher plants. C R Biol 2008;331:215-25.
23. Bolton MV. Primary metabolism and plant defense-Fuel for the fire. Mol Plant Microbe Interact 2009;22:487-97.
24. Massad TJ, Dyer LA, Vega CG. Cost of defense and a test of the carbon-nutrient balanceand growth-differentation balance hypotheses for two co-occurring classes of plant defense. PLoS One 2012;7:7554.
25. Mickelbart MV, Hasegawa PM, Bailey-Serres J. Genetic mechanisms of abiotic stress tolerance that translate to crop yield stability. Nat Rev Genet 2015;16:237-51.
26. Turner TR, James EK, Poole PS. The plant microbiome. Genome Biol 2013;14:209.
27. Ngumbi E, Kloepper J. Bacterial-mediated drought tolerance: Current and future prospects. Appl Soil Ecol 2014;105:109-25.
28. Sessitsch A, Hardoim P, Döring J, Weilharter A, Krause A, Woyke T. Functional characteristics of an endophyte community colonizing roots as revealed by metagenomic analysis. Mol Plant Microbe Interact 2012;25:28-36.
29. Singh R, Singh P, Sharma R. Microorganism as a tool of bioremediation technology for cleaning environment: A review. Proc Int Acad Ecol Environ Sci 2014;4:1-6.
30. Nguyen D, Rieu I, Mariani C, van Dam NM. How plants handle multiple stresses: Hormonal interactions underlying responses to abiotic stress and insect herbivory. Plant Mol Biol 2016;91:727-40.
31. Bakker MG, Manter DK, Sheflin AM, Weir TL, Vivanco JM. Harnessing the rhizosphere microbiome through plant breeding and agricultural management. Plant Soil 2012;360:1-13.
32. Onaga G, Wydra K. Advances in plant tolerance to abiotic stresses. In: Abdurakhmonov IY, editor. Plant Genomics. Rijeka: In Tech; 2016. p. 39-49.
33. Farrar K, Bryant D, Cope-Selby N. Understanding and engineering beneficial plant–microbe interactions: Plant growth promotion in energy crops. Plant Biotechnol J 2014;12:1193-206.
34. Crane TA, Roncoli C, Hoogenboom G. Adaptation to climate change and climate variability: The importance of understanding agriculture as performance. NJAS Wag J Life Sci 2011;57:179-85.
35. Ahmad P, Hashem A, Abd-Allah EF, Alqarawi AA, John R, Egamberdieva D, *et al*. Role of *Trichoderma harzianum* in mitigating NaCl stress in Indian mustard (*Brassica juncea* L) through antioxidative defense system. Front Plant Sci 2015;6:868.
36. Jiang QY, Zhuo F, Long SH, Zhao HD, Yang DJ, Ye ZH, *et al.* Can arbuscular mycorrhizal fungi reduce cd uptake and alleviate cd toxicity of *Lonicera japonica* grown in cd-added soils? Sci Rep 2016;6:21805.
37. Hilker M, Schwachtje J, Baier M, Balazadeh S, Bäurle I, Geiselhardt S, *et al.* Priming and memory of stress responses in organisms lacking a nervous system. Biol Rev Camb Philos Soc 2016;91:1118-33.
38. Xu ZZ, Zhou GS. Combined effects of water stress and high temperature on photosynthesis, nitrogen metabolism and lipid peroxidation of a perennial grass *Leymus chinensis*. Planta 2006;224:1080-90.
39. Osakabe Y, Osakabe K, Shinozaki K. Tran LS. Response of plants to water stress. Front Plant Sci 2014;5:86-91.
40. Xu Z, Jiang Y, Jia B, Zhou G. Elevated-CO_2 response of stomata and its dependence on environmental factors. Front Plant Sci 2016;7:657.
41. Osakabe Y, Arinaga N, Umezawa T, Katsura S, Nagamachi K, Tanaka H, *et al.* Osmotic stress responses and plant growth controlled by potassium transporters in arabidopsis. Plant Cell 2013;25:609-24.
42. Li Z, Wakao S, Fischer BB, Niyogi KK. Sensing and responding to excess light. Annu Rev Plant Biol 2009;60:239-60.

43. Koini MA, Alvey L, Allen T, Tilley CA, Harberd NP, Whitelam GC, *et al.* High temperature-mediated adaptations in plant architecture require the bHLH transcription factor PIF4. Curr Biol 2009;19:408-13.
44. Pareek A, Sopory SK, Bohnert HK, Govindjee, editors. Abiotic Stress Adaptation in Plants: Physiolgical, Molecular and Genomic Foundation. Dordrecht: Springer; 2010. p. 526.
45. Bromham L, Saslis-Lagoudakis CH, Bennett TH, Flowers TJ. Soil alkalinity and salt tolerance: Adapting to multiple stresses. Biol Lett 2013;9:20130642.
46. Emamverdian A, Ding Y, Mokhberdoran F, Xie Y. Heavy metal stress and some mechanisms of plant defense response. Sci World J 2015;2015:75-81.
47. Rorison IH. The response of plants to acid soils. Experintia 1986;42:357-62.
48. Munns R, Tester M. Mechanisms of salinity tolerance. Annu Rev Plant Biol 2008;59:651-81.
49. Silva EN, Ribeiro RV, Ferreira-Silva SL, Viégas RA, Silveira JA. Comparative effects of salinity and water stress on photosynthesis, water relations and growth of *Jatropha curcas* plants. J Arid Environ 2010;74:1130-7.
50. Thomashow MF. Molecular basis of plant cold acclimation: Insights gained from studying the CBF cold response pathway. Plant Physiol 2010;154:571-7.
51. Chinnusamy V, Schumaker K, Zhu JK. Molecular genetics perspectives on cross-talk and specifcity in abiotic stress signalling in plants. J Exp Bot 2004;55:225-36.
52. Andreasson E, Ellis B. Convergence and specificity in the arabidopsis MAPK nexus. Trends Plant Sci 2010;15:106-13.
53. Spoel SH, Dong X. Making sense of hormone crosstalk during plant immune responses. Cell Host Microbe 2008;3:348-51.
54. Qin F, Shinozaki K, Yamaguchi-Shinozaki K. Achievements and challenges in understanding plant abiotic stress responses and tolerance. Plant Cell Physiol 2011;52:1569-82.
55. Todaka D, Nakashima K, Shinozaki K, Yamaguchi-Shinozaki K. Toward understanding transcriptional regulatory networks in abiotic stress responses and tolerance in rice. Rice (N Y) 2012;5:6.
56. Singh DP, Prabha R, Yandigeri MS, Arora DK. Cyanobacteria-mediated phenylpropanoids and phytohormones in rice (*Oryza sativa*) enhance plant growth and stress tolerance. Antonie Van Leeuwenhoek 2011;100:557-68.
57. Tiwari S, Singh P, Tiwari R, Meena KK, Yandigeri M, Singh DP, *et al*. Salt-tolerant rhizobacteria-mediated induced tolerance in wheat (*Triticum aestivum*) and chemical diversity in rhizosphere enhance plant growth. Biol Fertil Soils 2011;47:907-16.
58. Davletova S, Rizhsky L, Liang H, Shengqiang Z, Oliver DJ, Coutu J, *et al.* Cytosolic ascorbate peroxidase 1 is a central component of the reactive oxygen gene network of arabidopsis. Plant Cell 2005;17:268-81.
59. Dat J, Vandenabeele S, Vranová E, Van Montagu M, Inzé D, Van Breusegem F, *et al.* Dual action of the active oxygen species during plant stress responses. Cell Mol Life Sci 2000;57:779-95.
60. Halliwell B, Gutteridge JM. Free Radicals in Biology and Medicine. 3rd ed. Oxford: Oxford University Press; 2000. p. 267.
61. Khan MA, Gemenet DC, Villordon A. Root system architecture and abiotic stress tolerance: Current knowledge in root and tuber crops. Front Plant Sci 2016;7:1584.
62. Atkinson NJ, Urwin PE. The interaction of plant biotic and abiotic stresses: From genes to the field. J Exp Bot 2012;63:3523-43.
63. Almoguera C, Coca MA, Jordano J. Differential accumulation of sunflower tetraubiquitin mRNAs during zygotic embryogenesis and developmental regulation of their heat-shock response. Plant Physiol 1995;107:765-73.
64. Rizhsky L, Liang H, Shuman J, Shulaev V, Davletova S, Mittler R, *et al.* When defense pathways collide. The response of arabidopsis to a combination of drought and heat stress. Plant Physiol 2004;134:1683-96.
65. Bian S, Jiang Y. Reactive oxygen species, antioxidant enzyme activities and gene expression patterns and recovery. Sci Hortic 2009;120:264-70.
66. Xu Z, Shimizu H, Ito S, Yagasaki Y, Zou C, Zhou G, *et al*. Effects of elevated CO_2, warming and precipitation change on plant growth, photosynthesis and peroxidation in dominant species from North China grassland. Planta 2014;239:421-35.
67. Naya L, Ladrera R, Ramos J, González EM, Arrese-Igor C, Minchin FR, *et al.* The response of carbon metabolism and antioxidant defenses of alfalfa nodules to drought stress and to the subsequent recovery of plants. Plant Physiol 2007;144:1104-14.
68. Voesenek LA, Pierik R. Plant stress profiles. Science 2008;320:880-1.
69. Dinneny JR, Long TA, Wang JY, Jung JW, Mace D, Pointer S, *et al.* Cell identity mediates the response of arabidopsis roots to abiotic stress. Science 2008;320:942-5.
70. McCue KF, Hanson AD. Salt-inducible betaine aldehyde dehydrogenase from sugar beet: CDNA cloning and expression. Plant Mol Biol 1992;18:1-1.
71. Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ. Plant cellular and molecular responses to high salinity. Annu Rev Plant Physiol Plant Mol Biol 2000;51:463-99.
72. Matysik J, Alia A, Bhalu B, Mohanty P. Molecular mechanisms of quenching of reactive oxygen species by proline under stress in plants. Curr Sci 2002;82:525-32.
73. Gupta B, Huang B. Mechanism of salinity tolerance in plants: Physiological, biochemical, and molecular characterization. Int J Genomics 2014;2014:701596.
74. Wahid A, Gelani S, Ashraf M, Foolad MR. Heat tolerance in plants: An overview. Environ Exp Bot 2007;61:199-223.
75. Iba K. Acclimative response to temperature stress

in higher plants: Approaches of gene engineering for temperature tolerance. Annu Rev Plant Biol 2002;53:225-45.
76. Wang LJ, Li SL. Salicylic acid-induced heat or cold tolerance in relation to Ca_2C homeostasis and antioxidant systems in young grape plants. Plant Sci 2006;170:685-94.
77. Iyer NJ, Tang Y, Mahalingam R. Physiological, biochemical and molecular responses to combination of drought and ozone in *Medicago truncatula*. Plant Cell Environ 2013;20:706-20.
78. Rivero RM, Mestre TC, Mittler R, Rubio F, Garcia-Sanchez F, Martinez V, *et al.* The combined effect of salinity and heat reveals a specific physiological, biochemical and molecular response in tomato plants. Plant Cell Environ 2014;37:1059-73.
79. Wani SH, Kumar V, Shriram V, Sah SK. Phytohormones and their metabolic engineering for abiotic stress tolerance in crop plants. Crop J 2016;4:162-76.
80. de Torres Zabala M, Bennett MH, Truman WH, Grant MR. Antagonism between salicylic and abscisic acid reflects early host-pathogen conflict and moulds plant defence responses. Plant J 2009;59:375-86.
81. Hey SJ, Byrne E, Halford NG. The interface between metabolic and stress signalling. Ann Bot 2010;105:197-203.
82. Matilla MA, Ramos JL, Bakker PA, Doornbos R, Badri DV, Vivanco JM, *et al. Pseudomonas putida* KT2440 causes induced systemic resistance and changes in arabidopsis root exudation. Environ Microbiol Rep 2010;2:381-8.
83. de Zelicourt A, Al-Yousif M, Hirt H. Rhizosphere microbes as essential partners for plant stress tolerance. Mol Plant 2013;6:242-5.
84. Nadeem SM, Ahmad M, Zahir ZA, Javaid A, Ashraf M. The role of mycorrhizae and plant growth promoting rhizobacteria (PGPR) in improving crop productivity under stressful environments. Biotechnol Adv 2014;32:429-48.
85. Souza RD, Ambrosini A, Passaglia LM. Plant growth-promoting bacteria as inoculants in agricultural soils. Genet Mol Biol 2015;38:401-19.
86. Gopalakrishnan S, Sathya A, Vijayabharathi R, Varshney RK, Gowda CL, Krishnamurthy L, *et al.* Plant growth promoting rhizobia: Challenges and opportunities 3 Biotech 2015;5:355-77.
87. Sahoo RK, Ansari MW, Pradhan M, Dangar TK, Mohanty S, Tuteja N, *et al.* A novel *Azotobacter vinellandii* (SRIAz3) functions in salinity stress tolerance in rice. Plant Signal Behav 2014;9:e29377.
88. Omar MN, Osman ME, Kasim WA, Abd El-Daim IA. Improvement of salt tolerance mechanisms of barley cultivated under salt stress using *Azospirillum brasiliense*. Tasks Veg Sci 2009;44:133-47.
89. Panlada T, Pongdet P, Aphakorn L, Rujirek NN, Nantakorn B, Neung T. Alleviation of the effect of environmental stresses using co-inoculation of mungbean by *Bradyrhizobium* and rhizobacteria containing stress-induced ACC deaminase enzyme. Soil Sci Plant Nut 2013;59:559-71.
90. Meena KK, Kumar M, Kalyuzhnaya MG, Yandigeri MS, Singh DP, Saxena AK, *et al*. Epiphytic pink-pigmented methylotrophic bacteria enhance germination and seedling growth of wheat (*Triticum aestivum*) by producing phytohormone. Antonie Van Leeuwenhoek 2012;101:777-86.
91. Oliveira CA, Alves VM, Marriel IE, Gomes EA, Scotti MR, Carneiro NP, *et al*. Phosphate solubilizing microorganisms isolated from rhizosphere of maize cultivated in an oxisol of the Brazilian Cerrado biome. Soil Biol Biochem 2009;41:1782-7.
92. Sorty AM, Meena KK, Choudhary K, Bitla UM, Minhas PS, Krishnani KK, *et al.* Effect of plant growth promoting bacteria associated with halophytic weed (*Psoralea corylifolia* L) on germination and seedling growth of wheat under saline conditions. Appl Biochem Biotechnol 2016;180:872-82.
93. Pandey V, Ansari MW, Tula S, Yadav S, Sahoo RK, Shukla N, *et al*. Dose-dependent response of *Trichoderma harzianum* in improving drought tolerance in rice genotypes. Planta 2016;243:1251-64.
94. Kaushal M, Wani SP. Plant-growth-promoting rhizobacteria: Drought stress alleviators to ameliorate crop production in drylands. Ann Microbiol 2016;66:35-42.
95. Brotman Y, Landau U, Cuadros-Inostroza Á, Tohge T, Fernie AR, Chet I, *et al. Trichoderma*-plant root colonization: Escaping early plant defense responses and activation of the antioxidant machinery for saline stress tolerance. PLoS Pathog 2013;9:e1003221.
96. Chang P, Gerhardt KE, Huang XD, Yu XM, Glick BR, Gerwing PD, *et al*. Plant growthpromoting bacteria facilitate the growth of barley and oats in saltimpacted soil: Implications for phytoremediation of saline soils. Int J Phytoremediation 2014;16:1133-47.
97. Palaniyandi SA, Damodharan K, Yang SH, Suh JW. *Streptomyces* sp. Strain PGPA39 alleviates salt stress and promotes growth of 'Micro Tom' tomato plants. J Appl Microbiol 2014;117:766-73.
98. Naveed M, Hussain MB, Zahir ZA, Mitter B, Sessitsch A. Drought stress amelioration in wheat through inoculation with *Burkholderia phytofirmans* strain PsJN. Plant Growth Regul 2014;73:121-31.
99. Naveed M, Mitter B, Reichenauer TG, Wieczorek K, Sessitsch A. Increased drought stress resilience of maize through endophytic colonization by *Burkholderia phytofirmans* PsJN and *Enterobacter* sp FD17. Environ Exp Bot 2014;97:30-9.
100. Pinedo I, Ledger T, Greve M, Poupin MJ. *Burkholderia phytofirmans* psJN induces long-term metabolic and transcriptional changes involved in *Arabidopsis thaliana* salt tolerance. Front Plant Sci 2015;6:466.
101. Fujishige NA, Kapadia NN, Hirsch AM. A feeling for the microorganism: Structure on a small scale. Biofilms

on plant root. Bot J Linn Soc 2006;150:79-88.
102. Rudrappa T, Biedrzycki ML, Bais HP. Causes and consequences of plant-associated biofilms. FEMS Microbiol Ecol 2008;64:153-66.
103. Rinaudi LV, Giordano W. An integrated view of biofilm formation in rhizobia. FEMS Microbiol Lett 2010;304:1-1.
104. Pangesti N, Pineda A, Pieterse CM, Dicke M, van Loon JJ. Two-way plant mediated interactions between root-associated microbes and insects: From ecology to mechanisms. Front Plant Sci 2013;4:414.
105. Gutjahr C. Phytohormone signaling in arbusclar mycorrhiza development. Curr Opin Plant Biol 2014;20:26-34.
106. Kakoi K, Yamaura M, Kamiharai T, Tamari D, Abe M, Uchiumi T, *et al.* Isolation of mutants of the nitrogen-fixing actinomycete Frankia. Microbes Environ 2014;29:31-7.
107. Field KJ, Pressel S, Duckett JG, Rimington WR, Bidartondo MI. Symbiotic options for the conquest of land. Trends Ecol Evol 2015;30:477-86.
108. Gourion B, Berrabah F, Ratet P, Stacey G. Rhizobium-legume symbioses: The crucial role of plant immunity. Trends Plant Sci 2015;20:186-94.
109. Koornneef A, Pieterse CM. Cross-talk in defense signaling. Plant Physiol 2008;146:839-44.
110. Yi SY, Shirasu K, Moon JS, Lee SG, Kwon SY. The activated SA and JA signalling pathways have an influence on flg22-triggered oxidative burst and callose deposition. PLoS One 2014;9:E88951.
111. Boller T, Felix G. A renaissance of elicitors: Perception of microbe-associated molecular patterns and danger signals by pattern-recognition receptors. Annu Rev Plant Biol 2009;60:379-406.
112. Allen RL, Bittner-Eddy PD, Grenville-Briggs LJ, Meitz JC, Rehmany AP, Rose LE, *et al.* Host-parasite coevolutionary conflict between *Arabidopsis* and downy mildew. Science 2004;306:1957-60.
113. Rivas S, Thomas CM. Molecular interactions between tomato and the leaf mold pathogen *Cladosporium fulvum*. Annu Rev Phytopathol 2005;43:395-436.
114. Tör M, Lotze MT, Holton N. Receptor-mediated signalling in plants: Molecular patterns and programmes. J Exp Bot 2009;60:3645-54.
115. Newman MA, Sundelin T, Nielsen JT, Erbs G. MAMP (microbe-associated molecular pattern) triggered immunity in plants. Front Plant Sci 2013;4:139.
116. Fujita M, Fujita Y, Noutoshi Y, Takahashi F, Narusaka Y, Yamaguchi-Shinozaki K, *et al.* Crosstalk between abiotic and biotic stress responses: A current view from the points of convergence in the stress signaling networks. Curr Opin Plant Biol 2006;9:436-42.
117. Hao Y, Charles TC, Glick BR. ACC deaminase from plant growth-promoting bacteria affects crown gall development. Can J Microbiol 2007;53:1291-9.
118. Ali S, Charles TC, Glick BR. Amelioration of high salinity stress damage by plant growth-promoting bacterial endophytes that contain ACC deaminase. Plant Physiol Biochem 2014;80:160-7.
119. Glick BR. Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiol Res 2014;169:30-9.
120. Sharma A, Shankhdhar D, Shankhdhar SC. Enhancing grain iron content of rice by the application of plant growth promoting rhizobacteria. Plant Soil Environ 2013;59:89-94.
121. Sen S, Chandrasekhar CN. Effect of PGPR on growth promotion of rice (*Oryzasativ*a L.) under salt stress. Asian J Plant Sci Res 2014;4:62-7.
122. Tapias DR, Galvan AM, Diaz SP, Obando M, Rivera D, Bonilla R. Effect of inoculation with plant growth-promoting bacteria (PGPB) on amelioration of saline stress in maize (*Zea mays*). Appl Soil Ecol 2012;61:264-72.
123. Suarez C, Cardinale M, Ratering S, Steffens D, Jung S, Montoya AM, *et al*. Plant growth-promoting effects of *Hartmannibacter diazotrophicus* on summer barley (*Hordeumvulgare* L.) under salt stress. Appl Soil Ecol 2015;95:23-30.
124. Tien TM, Gaskins MH, Hubbell DH. Plant growth substances produced by *Azospirillum brasilense* and their effect on the growth of pearl millet (*Pennisetum americanum* L.). Appl Environ Microbiol 1979;37:1016-24.
125. Williams PM, de Malorca MS. Abscisic acid and gibberellin-like substances in roots and root nodules of *Glycine max*. Plant Soil 1982;65:19-26.
126. Badenoch-Jones J, Letham DS, Parker CW, Rolfe BG. Quantification of cytokinins in biological samples using antibiodies against zeatinriboside. Plant Physiol (Bethesda) 1984;75:1117-25.
127. Taller BJ, Wong TY. Cytokinins in *Azotobacter vinelandii* culture medium. Appl Environ Microbiol 1989;55:266-7.
128. Nieto KF, Frankenberger WT. Biosynthesis of cytokininsis by *Azotobacter chroococcum*. Soil Biol Biochem 1989;21:967-72.
129. Patten CL, Glick BR. Role of *Pseudomonas* putidaindoleacetic acid development of the host plant root system. Appl Environ Microbiol 2002;68:3795-801.
130. Glick BR. In: Ano T, Comi G, Shoda M, editors. Plant Growth-Promoting Bacteria: Mechanisms and Applications. Waterloo, ON: Scientifica, Hindawi Publishing Corporation; 2012. p. 1-15.
131. Rajkumar M, Ma Y, Freitas H. Improvement of Ni phytostabilization by inoculation of Ni resistance *Bacillus megaterium* SR28C. J Environ Manag 2013;128:973-80.
132. Ahmed A, Hasnain S. Auxins as one of the factors of plant growth improvement by plant growth promoting rhizobacteria. Pol J Microbiol 2014;63:261-6.
133. Fierro-Coronado RA, Quiroz-Figueroa FR, García-Pérez LM, Ramírez-Chávez E, Molina-Torres J, Maldonado-Mendoza IE, *et al.* IAA-producing rhizobacteria from chickpea (*Cicer arietinum* L.) induce

changes in root architecture and increase root biomass. Can J Microbiol 2014;60:639-48.

134. Etesami H, Mirseyed Hosseini H, Alikhani HA. Bacterial biosynthesis of 1-aminocyclopropane-1-caboxylate (ACC) deaminase, a useful trait to elongation and endophytic colonization of the roots of rice under constant flooded conditions. Physiol Mol Biol Plants 2014;20:425-34.
135. Khan AL, Waqas M, Kang SM, Al-Harrasi A, Hussain J, Al-Rawahi A, *et al.* Bacterial endophyte sphingomonas sp. LK11 produces gibberellins and IAA and promotes tomato plant growth. J Microbiol 2014;52:689-95.
136. Kudoyarova GR, Melentiev AI, Martynenko EV, Timergalina LN, Arkhipova TN, Shendel GV, *et al.* Cytokinin producing bacteria stimulate amino acid deposition by wheat roots. Plant Physiol Biochem 2014;83:285-91.
137. Penrose DM, Glick BR. Methods for isolating and characterizing ACC deaminase-containing plant growth-promoting rhizobacteria. Physiol Plant 2003;118:10-5.
138. Glick BR, Todorovic B, Czarny J, Cheng Z, Duan J, McConkey B. Promotion of plant growth by bacterial ACC deaminase. Crit Rev Plant Sci 2007;26:227-47.
139. Sessitsch A, Coenye T, Sturz AV, Vandamne P, Barka EA, Salles JF, *et al*. *Burkholderia phytofirmans* sp. Nov., a novel plant-associated bacterium with plant-beneficial properties. Int J Syst Evol Microbiol 2005;55:1187-92.
140. Sun Y, Cheng Z, Glick BR. The presence of a 1-aminocyclopropane-1-carboxylate (ACC) deaminase deletion mutation alters the physiology of the endophytic plant growth-promoting bacterium *Burkholderia phytofirmans* psJN. FEMS Microbiol Lett 2009;296:131-6.
141. Stearns J, Glick BR. Transgenic plants with altered ethylene biosynthesis or perception. Biotechnol Adv 2003;21:193-210.
142. Lim JH, Kim SD. Induction of drought stress resistance by multi-functional PGPR *Bacillus licheniformis* K11 in pepper. Plant Pathol J 2013;29:201-8.
143. Hallmann J, Quadt-Hallmann A, Mahaffee WF, Kloepper JW. Bacterial endophytes in agricultural crops. Can J Microbiol 1997;43:895-914.
144. Reiter B, Sessitsch A. Bacterial endophytes of the wildflower *Crocus albifloru* sanalysed by characterization of isolates and by a cultivation-independent approach. Can J Microbiol 2006;52:140-9.
145. Farrell M, Prendergast-Miller M, Jones DJ, Hill PW, Condron LM. Soil microbial organic nitrogen uptake is regulated by carbon availability. Soil Biol Biochem 2014;77:261-7.
146. Reinhold-Hurek B, Hurek T. Life in grasses: Diazotrophic endophytes. Trends Microbiol 1998;6:139-44.
147. James EK. Nitrogen fixation in endophytic and associative symbiosis. Field Crops Res 2000;65:197-209.
148. Baldotto LE, Olivares FL, Bressan-Smith R. Structural interaction between GFP-labelled diazotrophicendophytic bacterium *Herbaspirillum seropedicae* RAM10 and Pineapple plantlets 'VitóRia'. Braz J Microbiol 2011;42:114-25.
149. Huang B, Lv C, Zhuang P, Zhang H, Fan L. Endophytic colonisation of bacillus subtilis in the roots of *Robinia pseudoacacia* L. Plant Biol (Stuttg) 2011;13:925-31.
150. Prieto P, Schilirò E, Maldonado-González MM, Valderrama R, Barroso-Albarracín JB, Mercado-Blanco J, *et al.* Root hairs play a key role in the endophytic colonization of olive roots by *Pseudomonas* spp. With biocontrol activity. Microb Ecol 2011;62:435-45.
151. Danhorn T, Fuqua C. Biofilm formation by plant-associated bacteria. Annu Rev Microbiol 2007;61:401-22.
152. Hornschuh M, Grotha R, Kutschera U. Moss-associated methylobacteria as phytosymbionts: An experimental study. Naturwissenschaften 2006;93:480-6.
153. Jacquemyn H, Waud M, Merckx VS, Lievens B, Brys R. Mycorrhizal diversity, seed germination and long-term changes in population size across nine populations of the terrestrial orchid *Neottia ovata*. Mol Ecol 2015;24:3269-80.
154. Bragina A, Berg C, Cardinale M, Shcherbakov A, Chebotar V, Berg G, *et al.* Sphagnum mosses harbour highly specific bacterial diversity during their whole lifecycle. ISME J 2012;6:802-13.
155. Alavi P, Starcher MR, Zachow C, Müller H, Berg G. Root-microbe systems: The effect and mode of interaction of stress protecting agent (SPA) *Stenotrophomonas rhizophila* DSM14405(T.). Front Plant Sci 2013;4:141.
156. Tkacz A, Poole P. Role of root microbiota in plant productivity. J Exp Bot 2015;66:2167-75.
157. Weller DM, Raaijmakers JM, Gardener BB, Thomashow LS. Microbial populations responsible for specific soil suppressiveness to plant pathogens. Annu Rev Phytopathol 2002;40:309-48.
158. Lugtenberg B, Kamilova F. Plant-growth promoting rhizobacteria. Annu Rev Microbiol 2009;63:541-56.
159. Bragina A, Cardinale M, Berg C, Berg G. Vertical transmission explains the specific burkholderia pattern in sphagnum mosses at multi-geographic scale. Front Microbiol 2013;4:394.
160. Yang J, Kloepper JW, Ryu CM. Rhizosphere bacteria help plants tolerate abiotic stress. Trends Plant Sci 2009;14:1-4.
161. Rolli E, Marasco R, Vigani G, Ettoumi B, Mapelli F, Deangelis ML, *et al.* Improved plant resistance to drought is promoted by the root-associated microbiome as a water stress-dependent trait. Environ Microbiol 2015;17:316-31.
162. Zabetakis I, Moutevelis-Minakakis P, Gramshaw JW. The role of 2-hydroxypropanal in the biosynthesis of 2, 5-dimethyl-4-hydroxy-2H-furan-3-one in strawberry (Fragaria x ananassa, cv. Elsanta) callus cultures. Food Chem 1999;64:311-4.
163. Verginer M, Siegmund B, Cardinale M, Müller H, Choi Y, Míguez CB, *et al*. Monitoring the plant epiphyte *Methylobacterium extorquens* DSM 21961 by real-time PCR and its influence on the strawberry flavor. FEMS

Microbiol Ecol 2010;74:136-45.
164. Badri DV, Zolla G, Bakker MG, Manter DK, Vivanco JM. Potential impact of soil microbiomes on the leaf metabolome and on herbivore feeding behavior. New Phytol 2013;198:264-73.
165. Peñuelas J, Farré-Armengol G, Llusia J, Gargallo-Garriga A, Rico L, Sardans J, *et al*. Removal of floral microbiota reduces floral terpene emissions. Sci Rep 2014;4:6727.
166. Wagner MR, Lundberg DS, Coleman-Derr D, Tringe SG, Dangl JL, Mitchell-Olds T, *et al*. Natural soil microbes alter flowering phenology and the intensity of selection on flowering time in a wild *Arabidopsis* relative. Ecol Lett 2014;17:717-26.
167. Panke-Buisse K, Poole AC, Goodrich JK, Ley RE, Kao-Kniffin J. Selection on soil microbiomes reveals reproducible impacts on plant function. ISME J 2015;9:980-9.
168. Partida-Martínez LP, Heil M. The microbe-free plant: Fact or artifact? Fron Plant Sci 2011;2:100-12.
169. Germida J, Siciliano S. Taxonomic diversity of bacteria associated with the roots of modern, recent and ancient wheat cultivars. Biol Fert Soils 2001;33:410-5.
170. Berg G, Grube M, Schloter M, Smalla K. The plant microbiome and its importance for plant and human health. Front Microbiol 2014;5:491.
171. Cardinale M, Grube M, Erlacher A, Quehenberger J, Berg G. Bacterial networks and co-occurrence relationships in the lettuce root microbiota. Environ Microbiol 2015;17:239-52.

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