Annals of R.S.C.B., ISSN: 1583-6258, Vol. 26, Issue 1, 2022, Pages. 1216 - 1226
Received 08 November 2021; Accepted 15 December 2021.

Perspectives and Applications of Plant Microbe Interactions in Post Genomic Era

Asif Iqbal[1], Saif Ali[2], Muhammad Asad[3], Muhammad Saeed[4], Najeeb Ullah[5], Adnan Ihsan[5], Riaz Hussain[6], WajidMunir Qureshi[7]

1. Department of Microbiology, Hazara University Mansehra, KPK, Pakistan
2. Institute of Soil and Environmental Sciences, University of Agriculture, Faisalabad, Pakistan.
3. KhwajaFareed University of engineering and information technology, Rahim Yar Khan, Pakiatan.
4. Senior Scientist, Maize & Millets Research Institute, Yusafwala, Sahiwal, Pakistan.
5. Department of Entomology, The University of Agriculture Peshawar, Pakistan.
6. Department of Entomology, The University of Agriculture Swat, Pakistan.
7. Institute of Plant Breeding and Biotechnology, Muhammad Nawaz Sharif University of Agriculture Multan, Pakistan

Corresponding Author: - Asif Iqbal, email;- microbiologist119@gmail.com

Abstract

Addressing the plant–microbe interactions is an important step in understanding the nature of the positive and negative aspects of microbes that can help for crop improvement.The progress that has been made in sequencing technology and different omics tools has significantly accelerated the research that has been done in the field of biological sciences. The most recent developments as well as those that are still being made, provide a unique strategy to analysis these complex interactions and hypothesis. The interaction between plants and pathogens and how it affects crop improvement is the main focus of the current review paper.Research has generally focused on plant innate immunity and it leads to the significant facts of plant defense mechanism against the microbes.In addition, the current review paper gives an overview of beneficial plant–microbe interactions.This paper provides an overview of several elements of plant-pathogen interactions in order to bridge the gap between plant microbial ecology and immunological responses.

Introduction

Plants and microbes/pathogens have a wide range of relationships, which have been living with microbes/pathogens below, above, and within plants (Vorholt, 2012; Bulgarelli et al., 2013).Microbes can interact endophytically and epiphytically with plant roots, the environment, and soil. Plant-microbe interactions can be positive, neutral, or unfavourable, affecting plant growth, health, and development (Newton et al., 2010).A single plant species hosts few microbes/pathogens, and vice versa. Specialization and specificity lead to microbial diversity and evolution over millions of years (Galagan et al., 2005).

However, microbe-plant interactions can be harmful, causing plant illness (Strange and Scott, 2005).Belowground and aboveground bacteria provide mutualistic advantages to plants. The bacteria that colonise plants can be classed as epiphytes, endophytes, phyllospheric, and rhizospheric. The rhizosphere is the most active, influencing the plant's nutrition and growth (Lakshmanan et al., 2014a).Belowground and aboveground bacteria provide mutualistic advantages to plants. The

Annals of R.S.C.B., ISSN: 1583-6258, Vol. 26, Issue 1, 2022, Pages. 1216 - 1226
Received 08 November 2021; Accepted 15 December 2021.

bacteria that colonise plants can be classed as epiphytes, endophytes, phyllospheric, and rhizospheric. The rhizosphere is the most active, influencing the plant's nutrition and growth (Lakshmanan et al., 2014b).With advances in genome and proteome identification and analysis, research study the mutual interaction between plant and microorganisms to boost agricultural yield (Bakker et al., 2013; Oldroyd, 2013).

If the qualities responsible for building microbial communities in the rhizosphere and their influence on plants are uncovered, they can be used for a sustainable alternative in agroecosystems to improve stability and agricultural productivity in the long run (Quiza et al., 2015; Knapp et al., 2018)

Micro-biota of Plants Found Aboveground

Different aboveground plant tissues such as vegetative foliar tissues, leaves, and floral parts provide unique environments for endophytic and epiphytic microbial diversities, yet there are major differences in the ecology of endospheric and phyllospheric microbes (Compant et al., 2020).The research on the interactions between plants and microbes has primarily concentrated on three areas: the oldest symbiosis, which is between plants and mycorrhizae; (Smith and Smith, 2011), the process by which plants fix nitrogen (Oldroyd et al., 2011),as well as the pathogenicity (Wirthmueller et al., 2013). Depending on supply allocation, different plant compartments have different endophyte populations. The soil environment drives the mobility of phyllospheric bacteria, according to reports (Vorholt, 2012; Wallace et al., 2018).

This leads to genus and species-level microorganism distribution in endospheric and phyllospheric zones. Pseudomonas, Sphingomonas, Frigoribacterium, Curtobacterium, Bacillus, Enterobacter, Acinetobacter, Erwinia, Citrobacter, Pantoea, and Methylobacterium are prevalent in the grapevine phyllosphere or carposphere (Kecskeméti et al., 2016).Ralstonia, Burkholderia, Pseudomonas, Staphylococcus, Mesorhizobium, Propionibacterium, Dyella, and Bacillus dominated grape berry endophytes (Campisano et al., 2014).

Sphingomonads and Methylobacteria are the major organisms in maize leaf microbiome across 300 plant cell lines (Wallace et al., 2018). Environmental conditions also influence phyllosphere microbial makeup. (Steven et al. (2018) found Pseudomonas and Enterobacteriaceae on apple blooms. Pseudomonas is common in apple, grapefruit, almond, pumpkin, and tobacco flower studies (Aleklett et al., 2014).

In recent investigations of seed microorganisms, Firmicutes, Proteobacteria, Bacteroidetes, and Actinobacteria were found to be prominent (Rodrguez et al., 2018). In addition to being tied to soil microbiota, seed microbiota are also associated to flower and fruit bacteria (Glassner et al., 2018). Aboveground bacterial diversity comes from soil, seeds, and air, then plant tissues. Soil, environmental, and agricultural methods affect their presence on tissues. The intensity of the link between a plant and its aboveground bacterial composition depends on the host and the compartment where variety exists. Endophytes and aboveground microbiota may promote plant growth, disease resistance, and stress relief (Vishwakarma et al., 2020).

The Occurrence and Interactions of Microorganisms below Ground

Microorganisms are prevalent on plant surfaces and in soil, and plants recruit them from their surroundings, which act as microbial reservoirs (Hardoim et al., 2015). The root microbiota can be transmitted horizontally or vertically. The soil bacterial communities rich in Acidobacteria,

Annals of R.S.C.B., ISSN: 1583-6258, Vol. 26, Issue 1, 2022, Pages. 1216 - 1226
Received 08 November 2021; Accepted 15 December 2021.

Bacteroidetes, Proteobacteria, Planctomycetes, and Actinobacteria enhance the dynamic microbial populations connected with plant roots (Fierer, 2017).Seeds can transport bacterial communities vertically, providing a critical source of multiplying microorganisms from the plant's roots to its development (Hardoim et al., 2012). Plant roots provide distinct and intriguing soil microbial habitats in the rhizosphere, root, and aboveground areas to a certain extent (Hartmann et al., 2009). The rhizosphere is a very active area for microbial migration, making it one of the most complex habitats (Hiltner, 1904).In an extensive wheat cropping system, a culture-based approach (terminal restriction fragment length polymorphism) showed that the rhizosphere had a more numerous microbial community than the bulk soil (Donn et al., 2015).

Root exudation is the secretion of substances into the rhizosphere by roots, such as organic acids, sugars, amino acids, polyphenols, flavonoids, hormones, and minerals (Compant et al., 2019).This is called the rhizosphere effect. Plant roots and microbiome form habitats for microbial development. Phytochemicals and root exudates help inhibit microbial growth in the rhizosphere. The population that can expand by using root-secreted substances forms a niche for itself and helps recruit other microbes by cross-feeding, creating a new niche for other microbes (Jacoby and Kopriva, 2019).The niche selection process is plant species and chemical specific. Several secondary compounds with defensive capabilities, such as benzoxazinoids, discharged from maize roots affect root microbiome structure and influence Actinobacteria and Proteobacteria most (Hu et al., 2018). Recent research examined the dynamics of bacterial community structure and processes in Avenabarbata roots (Zhalnina et al., 2018).

Root exudate composition and substrate preference affected rhizospherebacterial population assemblage.(Fitzpatrick et al. (2018) found distinct Pseudoxanthomonasrhizobacterial species in 30 angiospermic species. The spatiotemporal organisation of the rhizosphere and variations in physicochemical circumstances also affect niche specifications and microbial diversity (Vetterlein et al., 2020). Plant species, genotypes, and root exudates alter rhizosphericmicrobiome structure and alignment (Vishwakarma et al., 2017a, b).

Endophytic bacteria colonise roots internally. Their distribution in plants depends on plant assets and endophytecolonisation ability. Piriformosporaindica, an important root endophyte, is employed in agriculture. P. indica enhances phosphorus uptake and protects crops from stress (Lahrmann et al., 2013). A cyclophilin A–like protein from P. indica protects tobacco from salt stress (Trivedi et al., 2013). Azotobacterchrococcum can modulate P. indica physiology and improve nutrient intake through synergy (Bhuyan et al., 2015).

Endophytic fungus exhibit root-exuded chemical chemotaxis. When non-pathogenic Fusariumoxysporum was tested for activity against root knot nematode (Meloidogyne incognita) in tomato plants, tomato exudates facilitated F. oxysporumcolonisation and reduced nematode occurrence (Sikora and Dababat, 2007), suggesting that root exudates preferentially select the microbes in its vicinity. Root exudate-mediated chemotaxis attracts pathogens. Gu et al. (2017) used fine biochar to prevent bacterial wilt disease in tomato.

The Plant Immune System as a Defense Mechanism:-

Plants are the best source of nutrition for bacteria, fungus, protists, and insects. Even though plants lack a complete immune system, they have created structural, chemical, and protein-based defensive mechanisms to recognize pathogens and avoid harm. Understanding how plants fight diseases is

Annals of R.S.C.B., ISSN: 1583-6258, Vol. 26, Issue 1, 2022, Pages. 1216 - 1226
Received 08 November 2021; Accepted 15 December 2021.

critical to developing disease-resistant plant species. Plants rely on innate immunity and efficient signaling pathways since they lack mobile immune cells and cellular adaptive immune systems (Chisholm et al., 2006).Disease response begins when pathogens enter plant cells. Pathogens penetrate plant cells in diverse ways. Bacteria penetrate plant cells using trichomes, lenticels, stomata and other openings, fungus employ hyphae and penetration pegs, and viruses only through physical damage (Mendgen et al., 1996).

Once the pathogen has breached the fundamental defensive barriers, the plant immune response is divided into two branches: microbial (or pathogen) associated molecular pattern (MAMP/PAMP) triggered immunity (MTI/PTI) and effector-triggered immunity (ETI) (previously R-gene-based or vertical immunity). Plants exhibit SAR and gene silencing as immune responses (Sahu et al., 2012).Pathogens release elicitors called MAMPs, which are recognised and activated by pattern recognition receptors (PRRs), a class of plasma membrane bound extracellular receptors (Beck et al., 2012).Pathogens circumvent the MTI/PTI immune response by releasing effector molecules into plant cells, causing effector-triggered vulnerability (ETS). The effector molecule triggers ETI, an amplified form of PTI that produces HR (Muthamilarasan and Prasad, 2013).Activation of a single NB-LRR receptor (directly or indirectly) by a pathogen effector prevents pathogen transmission. R and Avr gene products interact directly and indirectly (Dodds et al., 2006). Guard Model explains how effector chemicals target the host (Dangl and Jones, 2001).

Guard Model says recent indirect effector recognition studies are conflicting. Multiple targets in hosts exist for distinct pathogen effectors, and the conventional Guard Model doesn't explain this if plants lack the R protein (van der Hoorn and Kamoun, 2008).PAMPs, which trigger innate immune responses in mammals, also stimulate plant defence. Plants have structurally comparable recognition complexes to animal PAMP receptors, suggesting a shared evolutionary basis for pathogen defence mechanisms in higher eukaryotes (Nürnberger and Brunner, 2002).

Systemic acquired resistance (SAR) is initiated at the infection site to stop the spread of infection by activating and expressing pathogenesis-related (PR) proteins (Park et al., 2007).Dual RNA-seq of plants and pathogens and the function of non-coding RNAs (ncRNAs) in controlling plant defence responses have improved simultaneous comparative data analysis of plants, pathogens, and defence responses (Meyer et al., 2016).Dual RNA-seq for the simultaneous investigation of host and pathogen transcriptomes during their interaction is probe independent and may be simply implemented for any plant-pathogen interaction research. It is an unbiased method that detects differentially expressed genes and transcriptional regulatory events (Enguita et al., 2016).MicroRNAs, phasiRNAs, and long intergenic non-coding RNAs (lincRNAs) are critical in plant responses to pathogens and boost innate immune mechanisms such PAMP- and effector-triggered defensive responses. This research revealed how epigenetic influences affect plant genes involved in pathogen defence (Meyer et al., 2016a).

Many study results show trans-generational immunological memory in plants, in addition to MAMP/PAMP-triggered immunity (MTI/PTI) and ETI. The immunological memory is passed on to the next generation. Trans-generational immunological memory in plants has been researched for environmental conditions and infections (Slaughter et al., 2012). It leads to successful responses to that stress in next-generation plants, called acquired immune power (Molinier et al., 2006).Arabidopsis challenged with an avirulent strain of Pseudomonas syringae demonstrated immediate and elevated Salicylic acid (SA) signalling pathway transcripts with higher disease resistance (laughter et al., 2012).Plant-pathogen interactions and plant immunity have always been

Annals of R.S.C.B., ISSN: 1583-6258, Vol. 26, Issue 1, 2022, Pages. 1216 - 1226
Received 08 November 2021; Accepted 15 December 2021.

important areas of research, leading to interesting information such as unique immune mechanisms of plants against pathogens, R-protein-mediated action, siRNA silencing, post-transcriptional silencing (PTGS) involving cellular RNAs, and trans-generational immune memory (Voinnet, 2008).Despite many discoveries in the field of plant immune system, many mysteries remain, including identification of many Avr genes involved in plant-pathogen interactions, plant root immune mechanisms, molecular mechanisms of pathogen colonisation in plants, regulation of cellular activity and gene expression, and signalling mechanisms involved in plant immune response. Post-genomic era advances will help us comprehend plant-pathogen interactions and plant immunity.

Beneficial Plant-Microbe Interactions

Nearly 1 billion people go hungry every day in a planet with a growing population (Reid, 2011a). Demand for food grains is driven by factors such as a lack of productivity, limited arable land and water, and disease-induced yield loss. To boost agricultural productivity, fertilizers, plant breeding, and genetic engineering are used, but they are costly, sluggish, extremely particular, and not practicable (Reid, 2011b).It's crucial to find alternatives to genetically modifying plants to resist infections. Few studies have emphasized the exploitation and harnessing of beneficial plant-associated microorganisms that have favorable impacts on plant–microbe interactions (Farrar et al., 2014).In beneficial plant–microbe interactions, plants and microbes create cooperative and beneficial relationships that improve host plant resilience to diseases, drought, salt, heavy metals, toxins, nutritional stressors, and severe temperature (Reid, 2011c). Plant–microbe collaboration will assist increase agricultural output at minimal cost. This fresh, understudied strategy has given the globe new hope and might be part of the next Green Revolution (Reid, 2011d).

Plants and microorganisms both contribute to positive plant–microbe interactions. Examples of well-studied symbiosis include nitrogen-fixing bacteria that live in leguminous plant root nodules and develop a mutually beneficial connection (Oldroyd et al., 2011). Arbuscularmycorrhizal fungi (AMF) reside in plant roots and absorb phosphate from the soil (Smith and Smith, 2011). AMF on tropical soils reduces phosphate fertiliser usage while increasing crop output (Ramalingam et al., 2015).Biofilm development and quorum sensing allow bacterial populations to cling to surrounding surfaces, including plant tissue, cell-to-cell adhesion, and the response of plants to bacteria QSS (Farrar et al., 2014).Some microbial product, mainly bacterial enzyme, protects host plants from drought, floods, high salinity, heavy metals, and infections. Plants may avoid dryness by producing more trehalose, which stabilises membranes and enzymes. Using bacteria to give extra trehalose in conjunction with plants might be more effective than biotechnologically designing plants to create additional trehalose. Beneficial endophytes, germs that dwell within plants without causing illness, are important in inducing systemic resistance (ISR) against harmful bacteria (Kloepper and Ryu, 2006).

The introduction of NGS technology and other molecular techniques, such whole genome sequencing, metagenomics, transcriptomics, proteomics and fluorescence tagging, and localization studies are of considerable value in interpreting the biological activities and beneficial plant–microbe interaction research.

Annals of R.S.C.B., ISSN: 1583-6258, Vol. 26, Issue 1, 2022, Pages. 1216 - 1226
Received 08 November 2021; Accepted 15 December 2021.

Microbiome-analysis techniques

There are many ways to characterize sample microbial diversity. Amplicon sequencing and metagenomics are two next-generation sequencing technologies that characterize the microbiome in depth.

Metagenomics Technique

Researchers have a clearer understanding of plant-pathogen systems at the molecular level and the signalling networks that coordinate plant defensive responses. Due to the great cellular complexity and connections of cellular components to enormous numbers of internal and external variables, there is scarcely adequate study concentrated at molecular level (Collakova et al., 2012a).

Molecular research have improved, but plant metabolic modifications after pathogen infections are new. New approaches to investigate plant metabolites are emerging. Genome-scale modelling (GEMing) is a mathematical model of the metabolism obtained from genetic data. Genome-scale models make analysing host–pathogen interactions difficult (Collakova et al., 2012b).

For metabolic network modelling of plants and pathosystems, information from genomes, transcriptomics, proteomics, and metabolomics technologies is necessary. Many plant-bacterial and plant-fungus pathosystems have been explored. Recent advances in genome sequencing and annotating have made genome-wide studies of plant-pathogen interactions conceivable (Shendure et al., 2004).

The whole genome sequence aids in genome-wide annotation of proteins, enzymes, and metabolic events (Duan et al., 2013a). Merging plant and pathogen metabolic networks proved beneficial in studying negative and positive impacts of joint networks (Duan et al., 2013b). The metabolic networks of plant-pathogen pairings indicated that infections substantially influence impairment patterns. There was no kingdom-level segregation (for bacteria and fungi) (Duan et al., 2013c).

The ‘omics' network uses kinetic information. Now, non-kinetic techniques including metabolic network reconstructions, Genome-scale reconstructions, and focused metabolic reconstructions are used to research metabolic and regulatory processes (Pinzon et al., 2010). The 1995 completion of the first bacterial genome sequence, Haemophilus influenza, offered a new research path for building a computer model of an organism based only on genome sequence (Seaver et al., 2012a). The invention of a ‘virtual plant' for Arabidopsis in 2000 cleared the path for its increased usage. To build a genome-scale model of an organism, one must first understand how all genes work together to drive and maintain life (Seaver et al., 2012b). In the post-genomic age, sequencing, annotation, reconstruction, and in silico modelling of metabolic networks are key achievements (Seaver et al., 2012c).

Amplicon Sequencing

These techniques rely on the binding of universal primers to highly conserved sections of the target microbial genome. Amplicon sequencing is used to study microbial populations. It includes sequencing PCR products containing taxon-specific HVRs (D'Amore et al., 2016a). 16S rRNA gene of bacteria is most used microbiomeamplicon (Kittelmann et al., 2013). Several combinations of primers have been recommended for the bacterial 16S rRNA gene to amplify HVRs and generate PCR products of variable lengths for sequencing (D'Amore et al., 2016b).

Annals of R.S.C.B., ISSN: 1583-6258, Vol. 26, Issue 1, 2022, Pages. 1216 - 1226
Received 08 November 2021; Accepted 15 December 2021.

The sequences of 16S rRNA (for bacteria), 18S rRNA (for fungi), and internal transcribed spacer (ITS) segments (for fungus) together with metagenomic loci include information on microorganism phylogeny that may be used to infer and deduce taxonomy. Taxonomical identification utilising marker genes depends on the quality and completeness of reference databases. ITS was selected over 18S rRNA because to its large and vetted library and increased sequence diversity (Schoch et al., 2012).However, it is controversial whether unequal ITS segments improve preferred PCR amplification of shorter ITS sequences, leading to a biassed assessment of relative abundances of fungal species (De Filippis et al., 2017).

Sometimes it's hard to distinguish spontaneous genetic changes from sequencing mistakes, which are less than 0.1% on the Illumina platform (Schirmer et al., 2015). After amplicon-based sequencing, OTU clustering is used to investigate the microbiome (for, e.g., 97 percent). OTU selecting assigns similar but slightly different sequences to the same species, implying a biological origin. Amplicon sequence variations give more specificity and sensitivity than OTU-based techniques, but they may exaggerate microbial diversity (Kopylova et al., 2016).

Conclusion and Perspectives

Our knowledge of plant–microbe interactions has advanced. We still have multiple issues and difficulties to solve this decade to produce pathogen-resistant crops for human sustainability (Misra and Chaturvedi, 2015; Thynne et al., 2015). Our understanding focuses on plant stress responses against diseases. Biotechnological advances will be needed to gather and integrate the data (Knief, 2014). In plant-pathogen interactions research, the near future poses several obstacles. Plant-pathogen battles have always been interesting, educational, and demanding (Figure 2). Understanding the molecular basis of interactions among various types of stresses and responses, identifying key factors involved in such interactions mainly during plant immune responses, understanding the progression of signals and disease to other parts of plants in nature, identification and successful ma In recent years, biomolecular research has evolved beyond genome sequencing to functional genomics and illness management (Knief, 2014). Genomic information alone, although vital, cannot explain these complex plant-pathogen interactions (Bender, 2005). Next-generation sequencing, 'omics' technologies, database building, and metabolic modelling are eliminating gaps and bringing together microbial ecology and molecular plant pathology to better understand plant immunity and pathogen virulence. Understanding plant–microbe interactions is difficult, but not impossible, so improved tactics can be applied and global food security can be addressed.

Author Contributions

All authors listed, have made substantial, direct and intellectual contribution to the work, and approved it for publication.

References

1. Vorholt, J. A. (2012). Microbial life in the phyllosphere. *Nat. Rev. Microbiol.* 10, 828–840. doi: 10.1038/nrmicro2910
2. Bulgarelli, D., Schlaeppi, K., Spaepen, S., Ver Loren Van Themaat, E., and Schulze-Lefert, P. (2013). Structure and functions of the bacterial microbiota of plants. *Annu. Rev. Plant Biol.* 64, 807–838. doi: 10.1146/annurev-arplant-050312-120106

3. Newton, A. C., Fitt, B. D. L., Atkins, S. D., Walters, D. R., and Daniell, T. J. (2010). Pathogenesis, parasitism and mutualism in the trophic space of microbe-plant interactions. *Trends Microbiol.* 18, 365–373. doi: 10.1016/j.tim.2010.06.002
4. Galagan, J. E., Henn, M. R., Ma, L. J., Cuomo, C. A., and Birren, B. (2005). Genomics of the fungal kingdom: insights into eukaryotic biology. *Genome Res.* 15, 1620–1631. doi: 10.1101/gr.3767105
5. Strange, R. N., and Scott, P. R. (2005). Plant disease: a threat to global food security. *Annu. Rev. Phytopathol.* 43, 83–116. doi: 10.1146/annurev.phyto.43.113004.133839 Lakshmanan, V., Selvaraj, G., and Bais, H. P. (2014). Update on the soil microbiome functional soil microbiome: belowground solutions to an aboveground problem. *Plant Physiol.* 166, 689–700. doi: 10.1104/pp.114.245811
6. Bakker, P. A. H. M., Berendsen, R. L., Doornbos, R. F., Wintermans, P. C. A., and Pieterse, C. M. J. (2013). The rhizosphere revisited: root microbiomics. *Front. Plant Sci.* 4:165. doi: 10.3389/fpls.2013.00165
7. Oldroyd, G. E. D. (2013). Speak, friend, and enter: signalling systems that promote beneficial symbiotic associations in plants. *Nat. Rev. Microbiol.* 11, 252–263. doi: 10.1038/nrmicro2990
8. Quiza, L., St-Arnaud, M., and Yergeau, E. (2015). Harnessing phytomicrobiome signaling for rhizospheremicrobiome engineering. *Front. Plant Sci.* 6:507. doi: 10.3389/fpls.2015.00507
9. Knapp, D. G., Németh, J. B., Barry, K., Hainaut, M., Henrissat, B., Johnson, J., et al. (2018). Comparative genomics provides insights into the lifestyle and reveals functional heterogeneity of dark septateendophytic fungi. *Sci. Rep.* 8:6321. doi: 10.1038/s41598-018-24686-4
10. Compant, S., Mitter, B., Colli-Mull, J. G., Gangl, H., and Sessitsch, A. (2011). Endophytes of grapevine flowers, berries, and seeds: identification of cultivable bacteria, comparison with other plant parts, and visualization of niches of colonization. *Microb. Ecol.* 62, 188–197. doi: 10.1007/s00248-011-9883-y
11. Smith, S. E., and Smith, F. A. (2011). Roles of arbuscularmycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystem scales. *Annu. Rev. Plant Biol.* 62, 227–250. doi: 10.1146/annurev-arplant-042110-103846
12. Oldroyd, E. D. G., Murray, J. D., Poole, P. S., and Downie, J. A. (2011). The rules of engagement in the legume-rhizobial symbiosis. *Annu. Rev. Genet.* 45, 119–144. doi: 10.1146/annurev-genet-110410-132549
13. Wirthmueller, L., Maqbool, A., and Banfield, M. J. (2013). On the front line: structural insights into plant–pathogen interactions. *Microbiol. Nat. Rev.* 11, 761–776. doi: 10.1038/nrmicro3118
14. Vorholt, J. A. (2012). Microbial life in the phyllosphere. *Nat. Rev. Microb.* 10, 828–840. doi: 10.1038/nrmicro2910
15. Wallace, J. G., Kremling, K. A., Kovar, L. L., and Buckler, E. S. (2018). Quantitative genetics of the maize leaf microbiome. *Phytobiomes J.* 2, 208–224. doi: 10.1094/pbiomes-02-18-0008-r
16. Campisano, A., Antonielli, L., Pancher, M., Yousaf, S., Pindo, M., and Pertot, I. (2014). Bacterial endophytic communities in the grapevine depend on pest management. *PLoS One* 9:e112763. doi: 10.1371/journal.pone.0112763
17. Wallace, J. G., Kremling, K. A., Kovar, L. L., and Buckler, E. S. (2018). Quantitative genetics of the maize leaf microbiome. *Phytobiomes J.* 2, 208–224. doi: 10.1094/pbiomes-02-18-0008-r
18. Steven, B., Huntley, R. B., and Zeng, Q. (2018). The influence of flower anatomy and apple cultivar on the apple flower phytobiome. *Phytobiomes J.* 2, 171–179. doi: 10.1094/pbiomes-03-18-0015-r
19. Aleklett, K., Hart, M., and Shade, A. (2014). The microbial ecology of flowers: an emerging frontier in phyllosphere research. *Botany* 92, 253–266. doi: 10.1139/cjb-2013-0166
20. Rodríguez, C. E., Mitter, B., Barret, M., Sessitsch, A., and Compant, S. (2018). Commentary: seed bacterial inhabitants and their routes of colonization. *Plant Soil* 422, 129–134. doi: 10.1007/s11104-017-3368-9
21. Glassner, H., Zchori-Fein, E., Yaron, S., Sessitsch, A., Sauer, U., and Compant, S. (2018). Bacterial niches inside seeds of *Cucumismelo* L. *Plant Soil* 422, 101–113. doi: 10.1007/s11104-017-3175-3

22. Vishwakarma, K., Kumar, N., Shandilya, C., and Varma, A. (2020). "Unravelling the role of endophytes in micronutrient uptake and enhanced crop productivity," in *Symbiotic Soil Microorganisms*, eds N. Shrivastava, S. Mahajan, and A. Varma (Cham: Springer), 63–85. doi: 10.1007/978-3-030-51916-2_4
23. Hardoim, P. R., van Overbeek, L. S., Berg, G., Pirttilä, A. M., Compant, S., Campisano, A., et al. (2015). The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. *Microbiol. Mol. Biol. Rev.* 79, 293–320. doi: 10.1128/mmbr.00050-14
24. Fierer, N. (2017). Embracing the unknown: disentangling the complexities of the soil microbiome. *Nat. Rev. Microbiol.* 15, 579–590. doi: 10.1038/nrmicro.2017.87
25. Hardoim, P. R., Hardoim, C. C., van Overbeek, L. S., and van Elsas, J. D. (2012). Dynamics of seedborne rice endophytes on early plant growth stages. *PLoS One* 7:e30438. doi: 10.1371/journal.pone.0030438
26. Hartmann, A., Schmid, M., van Tuinen, D., and Berg, G. (2009). Plant-driven selection of microbes. *Plant Soil* 321, 235–275. doi: 10.1007/s11104-008-9814-y
27. Hiltner, L. (1904). ÜberneuereErfahrungen und Probleme auf demGebiete der BodenbakteriologieunterbesondererBerücksichtigung der Gründüngung und Brache. *Soil Biol. Biochem.* 98, 59–78.
28. Donn, S., Kirkegaard, J. A., Perera, G., Richardson, A. E., and Watt, M. (2015). Evolution of bacterial communities in the wheat crop rhizosphere. *Environ. Microbiol.* 17, 610–621. doi: 10.1111/1462-2920.12452
29. Compant, S., Samad, A., Faist, H., and Sessitsch, A. (2019). A review on the plant microbiome: ecology, functions and emerging trends in microbial application. *J. Adv. Res.* 20, 29–37. doi: 10.1016/j.jare.2019.03.004
30. Jacoby, R. P., and Kopriva, S. (2019). Metabolic niches in the rhizospheremicrobiome: new tools and approaches to analyse metabolic mechanisms of plant–microbe nutrient exchange. *J. Exp. Bot.* 70, 1087–1094. doi: 10.1093/jxb/ery438
31. Hu, L., Robert, C. A. M., Cadot, S., Zhang, X., Ye, M., Li, B., et al. (2018). Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizospheremicrobiota. *Nat. Commun.* 9:2738.
32. Zhalnina, K., Louie, K., Hao, Z., Mansoori, N., da Rocha, U. N., Shi, S., et al. (2018). Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. *Nat. Microbiol.* 3, 470–480. doi: 10.1038/s41564-018-0129-3
33. Fitzpatrick, C. R., Copeland, J., Wang, P. W., Guttman, D. S., Kotanen, P. M., and Johnson, M. T. J. (2018). Assembly and ecological function of the root microbiome across angiosperm plant species. *Proc. Natl. Acad. Sci. U.S.A.* 115, E1157–E1165.
34. Vetterlein, D., Carminati, A., Kögel-Knabner, I., Bienert, G. P., Smalla, K., Oburger, E., et al. (2020). Rhizosphere spatiotemporal organization–a key to rhizosphere functions. *Front. Agron.* 2:8. doi: 10.3389/fagro.2020.00008
35. Vishwakarma, K., Mishra, M., Jain, S., Singh, J., Upadhyay, N., Verma, R. K., et al. (2017a). "Exploring the role of plant-microbe interactions in improving soil structure and function through root exudation: a key to sustainable agriculture," in *Plant-Microbe Interactions in Agro-Ecological Perspectives*, eds D. P. Singh, H. B. Singh, and R. Prabha (Singapore: Springer), 467–487. doi: 10.1007/978-981-10-5813-4_23
36. Lahrmann, U., Ding, Y., Banhara, A., Rath, M., Hajirezaei, M. R., Döhlemann, S., et al. (2013). Host-related metabolic cues affect colonization strategies of a root endophyte. *Proc. Natl. Acad. Sci. U.S.A.* 110, 13965–13970. doi: 10.1073/pnas.1301653110
37. Bhuyan, S. K., Bandyopadhyay, P., Kumar, P., Mishra, D. K., Prasad, R., Kumari, A., et al. (2015). Interaction of *Piriformosporaindica* with *Azotobacterchroococcum*. *Sci. Rep.* 5:13911.
38. Sikora, R., and Dababat, A. E. F. (2007). Influence of the mutualistic endophyte *Fusariumoxysporum* 162 on Meloidogyne incognita attraction and invasion. *Nematology* 9, 771–776. doi: 10.1163/156854107782331225
39. Gu, Y., Hou, Y., Huang, D., Hao, Z., Wang, X., Wei, Z., et al. (2017). Application of biochar reduces *Ralstoniasolanacearum* infection via effects on pathogen chemotaxis, swarming motility, and root exudate adsorption. *Plant Soil* 415, 269–281. doi: 10.1007/s11104-016-3159-8

40. Chisholm, S. T., Coaker, G., Day, B., and Staskawicz, B. J. (2006). Host–microbe interactions: shaping the evolution of the plant immune response. *Cell* 124, 803–814. doi: 10.1016/j.cell.2006.02.008
41. Mendgen, K., Hahn, M., and Deising, H. (1996). Morphogenesis and mechanisms of penetration by plant pathogenic fungi. *Annu. Rev. Phytopathol.* 34, 364–386. doi: 10.1146/annurev.phyto.34.1.367
42. Sahu, P. P., Puranik, S., Khan, M., and Prasad, M. (2012). Recent advances in tomato functional genomics: utilization of VIGS. *Protoplasma* 249, 1017–1027. doi: 10.1007/s00709-012-0421-7
43. Beck, M., Heard, W., Mbengue, M., and Robatzek, S. (2012). The Ins and OUTs of pattern recognition receptors at the cell surface. *Curr. Opin. Plant Biol.* 15, 367–374. doi: 10.1016/j.pbi.2012.05.004
44. Nürnberger, T., and Brunner, F. (2002). Innate immunity in plants and animals: emerging parallels between the recognition of general elicitors and pathogen-associated molecular patterns. *Curr. Opin. Plant Boil.* 5, 318–324. doi: 10.1016/S1369-5266(02)00265-0
45. Muthamilarasan, M., and Prasad, M. (2013). Plant innate immunity: an updated insight into defense mechanism. *J. Biosci.* 38, 433–449. doi: 10.1007/s12038-013-9302-2
46. Dangl, J. L., and Jones, J. D. G. (2001). Plant pathogens and integrated defence responses to infection. *Nature* 411, 826–833. doi: 10.1038/35081161
47. van der Hoorn, R. A. L., and Kamoun, S. (2008). From guard to decoy: a novel model for perception of plant pathogen effectors. *Plant Cell* 20, 2009–2017. doi: 10.1105/tpc.108.060194
48. Park, S. W., Kaimoyo, E., Kumar, D., Mosher, S., and Klessig, D. F. (2007). Methyl salicylate is a critical mobile signal for plant systemic acquired resistance. *Science* 318, 113–116. doi: 10.1126/science.1147113
49. Meyer, F. E., Shuey, L. S., Naidoo, S., Mamni, T., Berger, D. K., Myburg, A. A., et al. (2016). Dual RNA-sequencing of *Eucalyptus nitens* during *Phytophthoracinnamomi* challenge reveals pathogen and host factors influencing compatibility. *Front. Plant Sci.* 7:191. doi: 10.3389/fpls.2016.00191
50. Durrant, W. E., and Dong, X. (2004). Systemic acquired resistance. *Annu. Rev. Phytopathol.* 42, 185–209. doi: 10.1146/annurev.phyto.42.040803.140421
51. Molinier, J., Ries, G., Zipfel, C., and Hohn, B. (2006). Transgeneration memory of stress in plants. *Nature* 442, 1046–1049. doi: 10.1038/nature05022
52. Slaughter, A., Daniel, X., Flors, V., Luna, E., Hohn, B., and Mauch-Mani, B. (2012). Descendants of primed *Arabidopsis* plants exhibit enhanced resistance to biotic stress. *Plant Physiol.* 158, 835–843. doi: 10.1104/pp.111.191593
53. Voinnet, O. (2008). Post-transcriptional RNA silencing in plant–microbe interactions: a touch of robustness and versatility. *Curr. Opin. Plant Boil.* 11, 464–470. doi: 10.1016/j.pbi.2008.04.006
54. Reid, A. (2011). Microbes helping to improve crop productivity. *Microbe* 6, 435–439.
55. Farrar, K., Bryant, D., and Cope-Selby, N. (2014). Understanding and engineering beneficial plant–microbe interactions: plant growth promotion in energy crops. *Plant Biotechnol. J.* 12, 1193–1206. doi: 10.1111/pbi.12279
56. Kloepper, J. W., and Ryu, C. M. (2006). Bacterial endophytes as elicitors of induced systemic resistance. *Soil Biol.* 9, 33–52. doi: 10.1007/3-540-33526-9_3
57. Shendure, J., Mitra, R. D., Varma, C., and Church, G. M. (2004). Advanced sequencing technologies: methods and goals. *Nat. Rev. Genet.* 5, 335–344. doi: 10.1038/nrg1325
58. Duan, G., Christian, N., Schwachtje, J., Walther, D., and Ebenhöh, O. (2013). The metabolic interplay between plants and phytopathogens. *Metabolites* 3, 1–23. doi: 10.3390/metabo3010001
59. De Torres-Zabala, M., Truman, W., Bennett, M. H., Lafforgue, G., Mansfield, J. W., Rodriguez Egea, P., et al. (2007). *Pseudomonas syringae* pv. tomato hijacks the *Arabidopsis* abscisic acid signalling pathway to cause disease. *EMBO J.* 26, 1434–1443. doi: 10.1038/sj.emboj.7601575
60. Jones, A. M., Thomas, V., Truman, B., Lilley, K., Mansfield, J., and Grant, M. (2004). Specific changes in the *Arabidopsis* proteome in response to bacterial challenge: differentiating basal and R-gene mediated resistance. *Phyto Chem.* 65, 1805–1816.

Annals of R.S.C.B., ISSN: 1583-6258, Vol. 26, Issue 1, 2022, Pages. 1216 - 1226
Received 08 November 2021; Accepted 15 December 2021.

61. Huitema, E., Bos, J. I., Tian, M., Win, J., Waugh, M. E., and Kamoun, S. (2004). Linking sequence to phenotype in *Phytophthora*-plant interactions. *Trends Microbiol.* 12, 193–200. doi: 10.1016/j.tim.2004.02.008
62. Pinzon, A., Rodriguez, L. M., Gonzalez, A., Bernal, A., and Restrepo, S. (2010). Trageted metabolic reconstruction: a novel approach for the characterization of plant-pathogen interactions. *Brief. Bioinform.* 12, 151–162. doi: 10.1093/bib/bbq009
63. Seaver, S. M. D., Henry, C. S., and Hanson, A. D. (2012). Frontiers in metabolic reconstruction and modeling of plant genomes. *J. Exp. Bot.* 63, 2247–2258. doi: 10.1093/jxb/err371
64. D'Amore, R., Ijaz, U. Z., Schirmer, M., Kenny, J. G., Gregory, R., Darby, A. C., et al. (2016). A comprehensive benchmarking study of protocols and sequencing platforms for 16S rRNA community profiling. *BMC Genomics* 17:55. doi: 10.1186/s12864-015-2194-9
65. Kittelmann, S., Seedorf, H., Walters, W., Clemente, J. C., Knight, R., Gordon, J. I., et al. (2013). Simultaneous amplicon sequencing to explore co-occurrence patterns of bacterial, archaeal and eukaryotic microorganisms in rumen microbial communities. *PLoS One* 8:e47879. doi: 10.1371/journal.pone.0047879
66. Schoch, C. L., Seifert, K. A., Huhndorf, S., Robert, V., Spouge, J. L., Levesque, C. A., et al. (2012). Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for fungi. *Proc. Natl. Acad. Sci. U.S.A.* 109, 6241–6246.
67. De Filippis, F., Laiola, M., Blaiotta, G., and Ercolini, D. (2017). Different amplicon targets for sequencing-based studies of fungal diversity. *Appl. Environ. Microbiol.* 83:e00905-17.
68. Schirmer, M., Ijaz, U., D'Amore, R., Hall, N., Sloan, W. T., and Quince, C. (2015). Insight into biases and sequencing errors for amplicon sequencing with the IlluminaMiSeq platform. *Nucleic Acids Res.* 43:e37. doi: 10.1093/nar/gku1341
69. Kopylova, E., Navas-Molina, J. A., Mercier, C., Xu, Z. Z., Mahé, F., He, Y., et al. (2016). Open-source sequence clustering methods improve the state of the art. *mSystems* 1:e00003-15.