

Minireview

Inheritance of seed and rhizosphere microbial communities through plant–soil feedback and soil memory

Hyun Gi Kong, Geun Cheol Song and
Choong-Min Ryu ^{*}

Molecular Phytobacteriology Laboratory, KRIBB,
Daejeon, 34141, South Korea.

Summary

Since the discovery of the role of microbes in the phytobiome, microbial communities (microbiota) have been identified and characterized based on host species, development, distribution, and condition. The microbiota in the plant rhizosphere is believed to have been established prior to seed germination and innate immune development. However, the microbiota in seeds has received little attention. Although our knowledge of the distribution of microbiota in plant seeds and rhizosphere is currently limited, the impact of these microbiota is likely to be greater than expected. This minireview suggests a new function of microbial inheritance from the seed to root and from the first generation of plants to the next. Surprisingly, recruitment and accumulation of microbiota by biotic and abiotic stresses affect plant immunity in the next generation through plant–soil feedback and soil memory. To illustrate this process, we propose a new term called ‘microbiota-induced soil inheritance (MISI).’ A comprehensive understanding of MISI will provide novel insights into plant–microbe interactions and plant immunity inheritance.

Plants and microbes have evolved symbiotic interactions to overcome unfavourable conditions caused by pathogen and insect attacks (Hacquard *et al.*, 2017). However, whether plant–soil–microbe interactions are important for plant survival remains largely unknown (Carvalhais *et al.*, 2015). Plants alter the biotic and abiotic characteristics of soil through both negative and positive plant–soil feedback, which influences the conditions of plant growth

(Van der Putten *et al.*, 2013). Negative soil feedback occurs when plants are unable to grow in soils previously occupied by plants with similar microbiota. An example of this phenomenon is allelopathy. Allelopathy is a common biological phenomenon in which plant-derived secondary metabolites affect growth, survival, development, and reproduction of other organisms, including microbes. The main causes of negative plant–soil feedback include the accumulation of soil-borne pathogens, allelopathy, and selective nutrient depletion in the soil. For instance, roots of a forb species with high phosphorus content may harbour more pathogenic organisms, resulting in greater negative feedback on plant growth (Rottstock *et al.*, 2014). Thus, plant species closely related to the forb species may cause negative soil feedback, as they are more likely to share pathogenic bacteria (Gilbert and Webb, 2007). On the other hand, positive plant–soil feedback occurs when plants of the same species grow better than plants of different species in the same soil; under this scenario, continuous cultivation of crop species helps inhibit soil-borne diseases. The main cause of positive plant–soil feedback is the presence of specific microbial species or microbial communities that suppress the growth and inoculum potential of soil-borne pathogens. Plants often excrete active metabolites and hormones from roots when they are exposed to biotic or abiotic stress; this also induces positive plant–soil feedback (Pineda *et al.*, 2017; Bakker *et al.*, 2018; Berendsen *et al.*, 2018). A representative example of positive soil feedback is ‘suppressive soil’ (Weller *et al.*, 2002). Continuous crop mono-cultivation may lead to the emergence of disease-suppressive soils characterized by altered microbial community composition (Mendes *et al.*, 2011; Santhanam *et al.*, 2015; Shen *et al.*, 2015), resulting in the absence of disease or a reduced disease incidence and pathogen prevalence (Mueller and Sachs, 2015).

Aboveground herbivore feeding and pathogen infection affect belowground microbial communities. Wild tobacco (*Nicotiana benthamiana*) plants infested with whitefly show a 2-fold reduction in crown gall formation induced by the tumorigenic bacterium *Agrobacterium tumefaciens* in both stems and roots (Song *et al.*, 2015). In pepper

^{*}For correspondence. E-mail cmryu@kribb.re.kr; Tel. 82-42-879-8229; Fax 82-42-860-4488.

(*Capsicum annuum* L.) plants, the abundance of insecticidal soil bacteria including *Pseudomonas* spp. and *Stenotrophomonas* spp. in the microbial community in the rhizosphere increases after whitefly feeding (Kong *et al.*, 2016). In *Arabidopsis thaliana*, the abundance of *Stenotrophomonas* spp., *Xanthomonas* spp., and *Mycobacterium* spp. is reported to increase in the rhizosphere in response to infection by the downy mildew fungal pathogen *Hyaloperonospora arabidopsidis* on leaves, leading to the induction of plant systemic resistance against *H. arabidopsidis* in the next generation (Berendsen *et al.*, 2018). Reshaping of microbial community composition is probably caused by the production of active metabolites and signalling compounds by plant roots when exposed to biotic stress.

Genesis of 'microbiota-induced soil inheritance' (MISI)

The main factors responsible for the changes in microbiota studied so far include host genotype and environmental conditions (Berg *et al.*, 2016). Recent studies demonstrated that the genetic background of plants contributes to the composition of microbial communities. These studies revealed that plants of the same species but with diverse genotypes have different microbial communities. For example, the microbial communities of raspberry (*Rubus idaeus*) and kiwifruit (*Actinidia chinensis*) differ between cultivars (Purahong, 2018; Perpetuini *et al.*, 2019). However, it is unclear whether vertical transmission of microorganisms affects plant performance. Healthy seeds are typically considered aseptic (Baker and Smith, 1966; Pande *et al.*, 2007; Zheng *et al.*, 2019). However, seeds and flowers serve as the carriers of plant pathogens. Thus, over the past several decades, a variety of phytosanitary measures have been developed for seed sterilization (Miché and Balandreau,

2001; Godefroid *et al.*, 2016; Lindsey *et al.*, 2017). However, recent developments in multi-omics-based analytical techniques suggest that seeds contain plant genotype-specific microorganisms that can be transferred vertically from one generation to the next (Adam *et al.*, 2018; Johnston-Monje *et al.*, 2016; Nelson, 2017; Shade *et al.*, 2017). Microorganisms, mostly fungi and bacteria, enter the seeds through the outer seed coat or pollen granules, or naturally through infiltration of nectarthodes in flowers (Underwood *et al.*, 2007; Frank *et al.*, 2017). However, the mechanisms underlying microbial migration into seeds have only been studied with a limited number of pathogenic bacteria (Donati *et al.*, 2018). Although microorganisms within seeds are confined to seed coats, they are transferred to the soil through cotyledon defoliation and root development after seed germination, which serves as a basis for the establishment of the soil microbial community in association with the indigenous soil microbiota (Nelson *et al.*, 2018; Fig. 1). During this process, competition for food and space as well as antagonism between seed-borne and indigenous soil microbiota can occur.

Previous analysis suggested that the majority of microbiota present in seeds survive and inhabit the rhizosphere after seed germination, depending on the host genetics and indigenous soil microbiota (Adam *et al.*, 2018). Although a limited number of plant species have been studied to date, the composition of seed microbial communities appears to follow the pattern of rhizosphere microbial communities (Adam *et al.*, 2018). However, the underlying mechanism is unclear. Recent studies confirm that some endophytic bacterial genera such as *Enterobacter*, *Pantoea*, *Pseudomonas*, and *Citrobacter* present in seeds are derived from the rhizosphere microbial community of plant hosts (Johnston-Monje and Raizada, 2011; Adam *et al.*, 2018; Rybakova *et al.*, 2017). *Enterobacter asburiae* from seeds of different maize (*Zea mays*) cultivars was established in the rhizosphere after seeding (Johnston-Monje and Raizada, 2011). We therefore

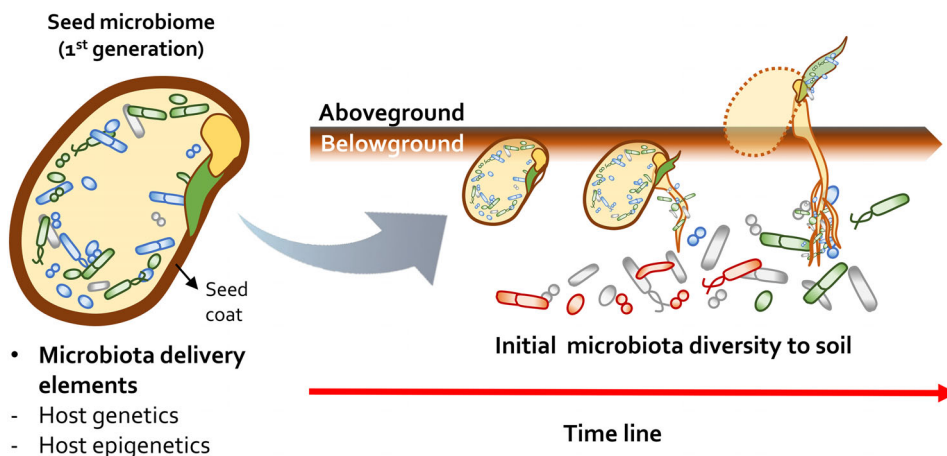


Fig. 1. Seed microbiome and introducing initial microbiota to the plant root and rhizosphere. Seed microbiome plays an important role in the formation of early rhizosphere microbial communities by exposure to rhizosphere indigenous microbiota and roots during seed germination and by establishing beneficial microbiota that promote plant health.

redefine plant seeds as a repository of rhizosphere microbial communities and propose the transfer of microbial communities among neighbouring plants or from one generation to the next (Fig. 3). On the other hand, different mechanisms may exist in perennial plants and different types of seeds (e.g., seeds that require vernalization or tegument digestion and those that are ready to germinate).

Puzzle pieces of MISI

Plants and microbiota interact in several ways both above- and belowground. The basis of microbial communication in terrestrial ecosystems is an important aspect of plant–microbe interactions. Recent discoveries of the role of microbiota–plant interactions have opened a new gateway to our understanding of the holobiome. In particular, analysis of the recognition and recruitment of microbes via plant signals initiated a new journey in the field of plant resistance and immune responses (Van Wees *et al.*, 2008). The detailed mechanisms by which plants perceive microbiota and immune signalling are activated have begun to be elucidated; however, many details remain unknown. An established microbiota that interacts with plants induces self and non-self perception and innate immunity in plants (Hacquard *et al.*, 2017). In addition, the

settling of microbial communities on plants is a powerful trigger that induces bioshield formation, which inhibits pathogen colonization on the plant surface (Berendsen *et al.*, 2018). Ultimately, the microbiota is altered because of plant immune responses, and these changes are inherited by the next generation of plants (Fig. 2).

The production of root exudates increases in response to herbivore and pathogen attack of aboveground (systemic) plant parts, suggesting that plants utilize an aggressive strategy to recruit beneficial soil microbes for the protection of distal plant parts (Tkacz *et al.*, 2015; Kong *et al.*, 2016; Berendsen *et al.*, 2018). Collectively, saprophytic microbes recruited by plant pathogens and herbivore-infected plants may promote plant innate immunity. For example, the composition of the rhizosphere microbial community of *Arabidopsis* plants, whose leaves were infected with *H. arabidopsidis*, was significantly different from that of healthy plants. Plants of the next generation grown in the same soil showed higher resistance to *H. arabidopsidis* than unexposed plants because of the changes in the soil microbiota (Berendsen *et al.*, 2018). Moreover, a survey of the inheritance of the rhizosphere microbiota in three model plants, *A. thaliana*, *Medicago truncatula* and *Brachypodium distachyon*, revealed that three bacterial genera, *Achromobacter*, *Arthrobacter* and *Massilia*, which can utilize plant-derived compounds as

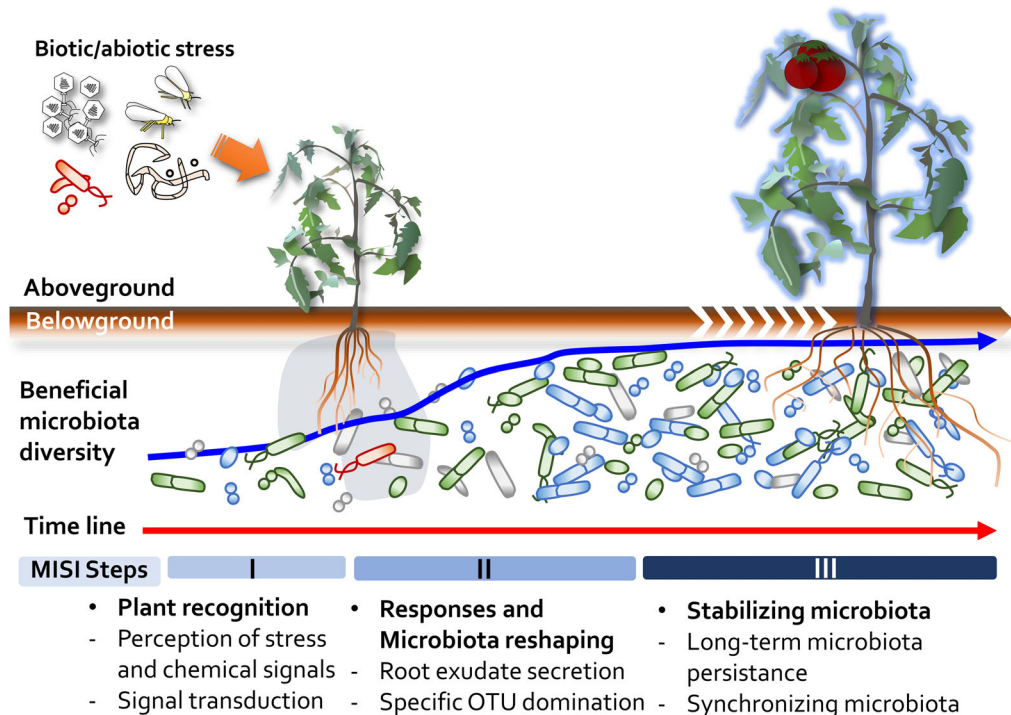


Fig. 2. Schematic representation of microbiota-induced soil inheritance (MISI) through the perception and response of aboveground plant parts to stresses and plant–soil feedback-mediated microbiota succession. MISI involves three possible steps. **Step I:** Plants recognize biotic stress stimuli, inducing downstream immune signalling cascades, such as salicylic acid and jasmonic acid signalling, through the systemic signal transduction system. **Step II:** Plant immune response alters the composition of plant root exudates, which in turn influences the microbiota to stimulate the specific microbe domination, thus boosting the plant defence system. **Step III:** The altered microbiome stabilizes and maintains long-term microbiota inheritance by accumulating keystone microbiota that promote plant health.

nutrients in the next generation, were increased in abundance, suggesting the succession of microbiota due to the root selection system and root exudates (Tkacz *et al.*, 2015). These findings indicate a closed feedback loop between plant and soil microbes after pathogen infection of above-ground plant parts. We propose a new term, MISI, to describe this process. Further multidisciplinary analysis of MISI will provide new and exciting insights into how plants and microbes interact and communicate in their natural environment (Fig. 2).

Plant recognition and microbiota reshaping

Microbiota that suppress plant disease typically accumulate in soil after a response to plant stress, such as disease occurrence, in the field. During disease development, plants secrete root exudates that recruit disease-suppressive microbiota (Yi *et al.*, 2016). Such microbiota can accumulate even after diseased plants are removed from the field.

The initial step in recognition of a single microbe occurs at the cellular level. Plant cells detect biotic and abiotic stresses, and then this information is transmitted throughout the plant. Receptor-like kinases in plant cell membranes sense a variety of environmental stimuli and transmit these to downstream intracellular and intercellular signalling networks. Subsequently, reactive oxygen species and calcium ions (Ca⁺⁺) transmit these stimuli to downstream signalling components in the local and systemic immune system in plant cells. The transferred transducers activate kinase cascades such as mitogen-activated protein kinases and accumulate plant hormones such as abscisic acid, salicylic acid (SA), jasmonic acid (JA), and ethylene (Savatin *et al.*, 2014; Xu and Huang, 2017). Plant immune hormones including SA and JA are the important regulators of plant stress responses (Fujita *et al.*, 2006). SA is typically effective against infection by biotrophic pathogens and a major modulator of systemic acquired resistance (SAR) in major plant immunity signalling pathways, while JA and ethylene are generally effective against necrotic pathogens and chewing insects. Root metabolism and root exudates are the main physiological factors used by plants to control microbial growth (Bulgarelli *et al.*, 2012; Chaparro *et al.*, 2014; Sasse *et al.*, 2018) (Fig. 2; Step I).

Plants respond to various biotic and abiotic stresses using well-developed defence mechanisms. Under stress conditions, plants also benefit from interactions with quick-responding soil microbes (Berendsen *et al.*, 2012; Kong *et al.*, 2016; Pineda *et al.*, 2017; Santos-Medillin *et al.*, 2017). Survival of plants in the natural environment depends on their interaction with a complex and dynamic community of microbes. Root exudates include simple molecules, such as sugars, organic acids, and secondary metabolites, as well as complex, mucus-like polymers (Carvalhais *et al.*, 2011; Hu *et al.*, 2018). Root exudate composition is controlled by the

plant genotype, developmental stage, seasonal effects and stress level (Phillips *et al.*, 2008; Sasse *et al.*, 2018) (Fig. 2; Step II). The concentration of SA in root exudates of tobacco plants exposed to whitefly is 3-fold higher than that of untreated control plants. Additionally, silencing of the *isochorismate synthase 1 (ICS1)* gene, which is required for SA biosynthesis in tobacco, reduces whitefly-induced plant immunity against *Agrobacterium tumefaciens* (Song *et al.*, 2015).

Compared with that in wild-type *Arabidopsis* plants, the abundance of Firmicutes and Actinobacteria in the rhizosphere of plants with inhibited SA biosynthesis was lower, while that of 12 species of Proteobacteria was higher (Lebeis *et al.*, 2015). In addition, root exudates of *Arabidopsis* JA biosynthesis mutants contained different microbial communities and reduced levels of asparagine, ornithine and tryptophan compared with those of wild-type *Arabidopsis* plants (Carvalhais *et al.*, 2015). These findings indicate that SA and JA modulate microbial community composition directly or indirectly through root exudates (Carvalhais *et al.*, 2015; Lebeis *et al.*, 2015). Thus, changes in the levels of defence hormones and secondary metabolites of plants, due to herbivore feeding and pathogen infection, cause plants to recruit specific microbes. This suggests that changes in root exudates induced by plant defence responses play an important role in regulating microbial communities.

Synchronizing microbiota through sharing information

In addition to the vertical transmission of microbiota from one generation to the next, the plant microbiome is also transferred horizontally from neighbouring environments via synchronization (Shade *et al.*, 2017). Disease suppression in soil within an ecosystem can be uniformly generated by the synchronization of MISI. Plants survive and adapt to the environment through root–root interactions. In tobacco, SAR is transmitted to neighbouring plants via root–root connections (Song *et al.*, 2016), suggesting the possibility of synchronization of microbial communities by interactions among plants. Surrounding plants respond to an alert signal sent by the plant under attack, and microbes exhibit similar changes in response to plant exudates. In addition to direct contact between roots, a rhizosphere mycorrhizal network is also involved in this process. Synchronization through plant roots and mycorrhiza not only provides information about the composition of microbial communities but also represents positive aspects of evolved plant communities in the next generation (Fig. 3). Collectively, the transmitted microbiota is influenced by the mycorrhizal network. Indeed, this network can connect distant plants, can serve as a transport system for signals, and may reside in the soil. This is a good example of the driving force for microbiota synchronization in soil.

Microbiota inheritance as a soil memory

Ecological processes that regulate the long-term assembly of microbiomes transformed by plant immune responses are crucial for the functioning of terrestrial ecosystems. The ecological succession of plant microbiome in these terrestrial ecosystems initially represents a community structure driven by root metabolites of the stimulated plant. Root exudates containing plant immune hormones such as SA and JA, especially from plants subjected to aboveground biotic and abiotic stresses, increase the population of specific microbial communities in the rhizosphere (Carvalhais *et al.*, 2015; Lebeis *et al.*, 2015). Additionally, aromatic organic acids such as nicotine, SA, cinnamic acid, and indole-3-acetic acid emitted by grasses alter the rhizosphere microbiome (Zhalnina *et al.*, 2018). Roots provide space for the microorganisms to settle (Bulgarelli *et al.*, 2012). In addition, the release of plant cell wall polymers such as cellulose and pectin from root tissues increases soil microbiota with the ability to degrade cellulose and pectin (Haichar *et al.*, 2007; Stursova *et al.*, 2012).

A new core bacterial consortium formed because of plant root stimulation establishes close links among the accumulated microbes and sustains the microbial community (Fig. 2; Steps II and III). With the progression of inheritance of microbiota by root stimulation, changes in mineral and nutrient concentrations in the surrounding soil gradually increase the deterministic selection of specific microbes (Eilers *et al.*, 2010). This suggests that specific microbes in the rhizosphere continue to dominate in the early and late stages of social assembly (Carvalhais *et al.*, 2015; Lebeis *et al.*, 2015).

These microbiota increase the heterogeneity of the spatial environment with the progression of inheritance, forming a new, robust, and spatially structured ecological community (Dini-Andreote *et al.*, 2015). Ecologically, most of the microbial biodiversity contains dormant populations (Fig. 2; Step II), and many of these dormant populations contribute to the persistence of microbial diversity (Jones and Lennon, 2010). Thus, MISI is driven by the increase and maintenance of microbial community selection through succession and domination, which is the driving force for long-term colonization of microbial communities, until the next generation of plants is colonized (Fig. 3).

Application and future direction of MISI

Recent technological advances have enabled the identification of keystone taxa (microbes) in the plant rhizosphere and seed microbiome. Keystone microbes from complex microbial environments can be assembled into synthetic communities in the laboratory to investigate their critical functions under field conditions (Vorholt *et al.*, 2017). Knowledge of core components of MISI and chemical trigger(s) released by plants could be applied to agriculture through the modulation and engineering of microbiota surrounding plants. However, our understanding of the formation of specific microbial communities, depending on plant diversity, remains limited to the biosynthesis and transport of various compounds in roots (Sasse *et al.*, 2018). Additionally, it is difficult to manage microbial stability, as microbiota are highly complex

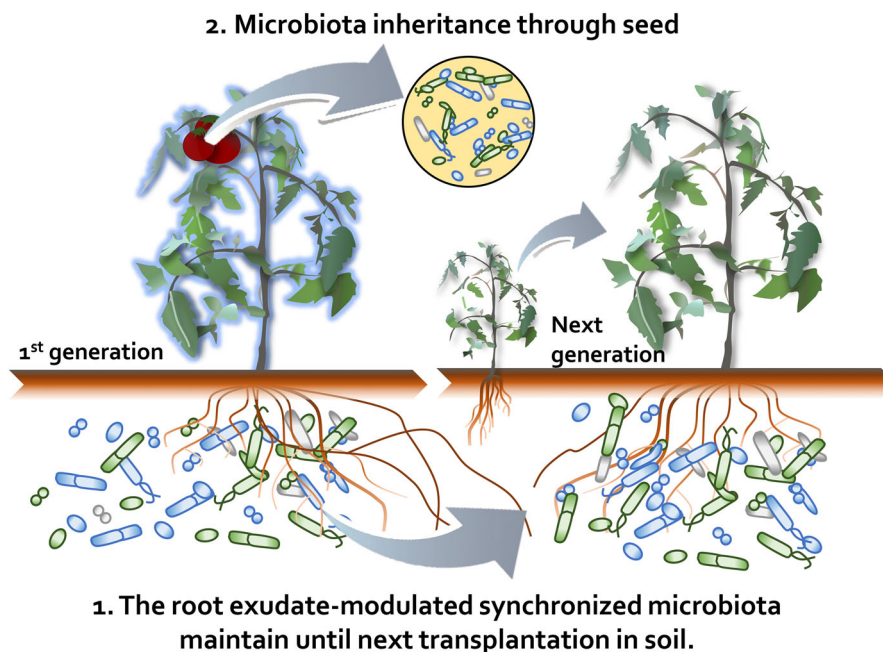


Fig. 3. Microbiota succession through seed and soil. Microbiota are synchronized and stabilized by plant-specific stimuli and root exudates. Synchronized microbiota are maintained until the next generation, thus affecting plant fitness. Additionally, certain microbiota are transferred to the next generation through the formation of seed microbiome.

systems involved in unexpected feedback processes within their ecosystems. Multifaceted approaches such as metagenomics, metatranscriptomics, and metabolomics analyses are needed to investigate the role of plants in microbial stability and the underlying genetics. Technical advances in the sensitivity and throughput of current mass spectrometry approaches will improve our understanding of the role of secondary metabolites and extracellular signalling molecules produced by plants under stress conditions in determining plant–microbe interactions. This could further lead to improvements in crop quality and productivity through uncovering structure–function relationships in microbial and plant ecosystems. Additionally, studies of new molecular signals may help to maintain the MISI activity of plant-mediated microbe recruitment. Therefore, studying the core components of root exudates and the assembly/succession of microbial communities could lead to the use of MISI for the activation of new plant immune mechanisms for crop protection. MISI will broaden our understanding of *in situ* plant–microbe interactions and help fill the gap between laboratory and field analysis of microbial inoculants, biostimulants and bioprotectants.

Concluding remarks

Plants and microbes interact in innumerable ways in terrestrial ecosystems. In this minireview, we demonstrated the role of the soil microbiota via active assembly of plant-associated microbiota around rhizospheres and inside seeds following plant stress responses. Selective enrichment of plant-protective microbiota both locally and systemically helps to protect host plants against biotic and abiotic stresses. Such MISI will provide new insights into plant–soil memory.

Acknowledgements

Financial support was obtained from the grants from the BioNano Health-Guard Research Center, funded by the Ministry of Science, ICT and Future Planning of Korea as a Global Frontier Project (Grant H-GUARD_2013M3A6B2078953), Woo Jang-Coon Project (PJ01093904) of the Rural Development Administration (RDA), Strategic Initiative for Microbiomes in Agriculture and Food, Ministry of Agriculture, Food and Rural Affairs, Republic of Korea (as part of the [multi-ministerial] Genome Technology to Business Translation Program 918017-4), and KRIBB initiative program, South Korea.

Author contributions

H.G.K., G.C.S. and C.-M.R. generated the idea. H.G.K. generated the figures. H.G.K., G.C.S., and C.-M.R. wrote the manuscript.

References

- Adam, E., Bernhart, M., Müller, H., Winkler, M., and Berg, G. (2018) The *Cucurbita pepo* seed microbiome: genotype-specific composition and implications for breeding. *Plant and Soil* **422**: 35–49. <https://doi.org/10.1007/s11104-016-3113-9>.
- Baker, K.F., and Smith, S.H. (1966) Dynamics of seed transmission of plant pathogens. *Annu Rev Phytopathol* **4**: 311–332.
- Bakker, P.A.H.M., Pieterse, C.M.J., de Jonge, R., and Berendsen, R.L. (2018) The soil-borne legacy. *Cell* **172**: 1178–1180.
- Berendsen, R.L., Pieters, C.M.J., and Bakker, P.A.H.M. (2012) The rhizosphere microbiome and plant health. *Trends Plant Sci* **17**: 478–486.
- Berendsen, R.L., Vismans, G., Yu, K., Song, Y., de Jonge, R., Burgman, W.P., *et al.* (2018) Disease-induced assemblage of a plant-beneficial bacterial consortium. *ISME J* **12**: 1496–1507.
- Berg, G., Rybakova, D., Grube, M., and Köberl, M. (2016) The plant microbiome explored: implications for experimental botany. *Exp Bot* **67**: 995–1002.
- Bulgarelli, D., Rott, M., Schlaeppi, K., Ver Loren van, T.E., Ahmadinejad, N., Assenza, F., *et al.* (2012) Revealing structure and assembly cues for *Arabidopsis* root-inhabiting bacterial microbiota. *Nature* **488**: 91–95.
- Carvalhais, L.C., Dennis, P.G., Fedoseyenko, D., Hajirezaei, M.-R., Borriss, R., and von Wieren, N. (2011) Root exudation of sugars, amino acids, and organic acids by maize as affected by nitrogen, phosphorus, potassium, and iron deficiency. *J Plant Nutr Soil Sci* **174**: 3–11.
- Carvalhais, L.C., Dennis, P.G., Badri, D.V., Kidd, B.N., Vivanco, J.M., and Schenk, P.M. (2015) Linking jasmonic acid signaling, root exudates, and rhizosphere microbiomes. *Mol Plant Microbe Interact* **28**: 1049–1058.
- Chaparro, J.M., Badri, D.V., and Vivanco, J.M. (2014) Rhizosphere microbiome assemblage is affected by plant development. *ISME J* **8**: 790–803.
- Dini-Andreote, F., Stegen, J.C., van Elsas, J.D., and Salles, J.F. (2015) Disentangling mechanisms that mediate the balance between stochastic and deterministic processes in microbial succession. *Proc Natl Acad Sci U S A* **112**: E1326–E1332.
- Donati, I., Cellini, A., Burianni, G., Mauri, S., Kay, C., Tacconi, G., and Spinelli, F. (2018) Pathways of flower infection and pollen-mediated dispersion of *Pseudomonas syringae* pv. *actinidiae*, the causal agent of kiwifruit bacterial canker. *Horticult Res* **5**: 56.
- Eilers, K.G., Lauber, C.L., Knight, R., and Fierer, N. (2010) Shifts in bacterial community structure associated with inputs of low molecular weight carbon compounds to soil. *Soil Biol Biochem* **42**: 896–903.
- Frank, A.C., Guzmán, J.P.S., and Shay, J.E. (2017) Transmission of bacterial endophytes microorganisms. **54**: 70. <https://doi.org/10.3390/microorganisms5040070>.
- Fujita, M., Fujita, Y., Noutoshi, Y., Takahashi, F., Narusaka, Y., Yamaguchi-Shinozaki, K., and Shinozaki, K. (2006) Crosstalk between abiotic and biotic stress responses: a current view from the points of convergence in the stress signaling networks. *Curr Opin Plant Biol* **9**: 436–442.

- Gilbert, G.S., and Webb, C.O. (2007) Phylogenetic signal in plant pathogen-host range. *Proc Natl Acad Sci U S A* **104**: 4979–4983.
- Godefroid, S., Van De Vyver, A., Stoffelen, P., and Vanderborght, T. (2016) Effectiveness of dry heat as a seed sterilisation technique: implications for ex situ conservation. *Int J Dealing with all Aspects Plant Biol* **151**: 1054–1061. <https://doi.org/10.1080/11263504.2016.1231140>.
- Hacquard, S., Spaepen, S., Garrido-Oter, R., and Schulze-Lefert, P. (2017) Interplay between innate immunity and the plant microbiota. *Annu Rev Phytopathol* **4**: 565–589.
- Haichar, F.Z., Achouak, W., Christen, R., Heulin, T., Marol, C., Marais, M.F., et al. (2007) Identification of cellulolytic bacteria in soil by stable isotope probing. *Environ Microbiol* **9**: 625–634.
- Hu, et al. (2018) Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. *Nat Comm* **9**: 2738.
- Johnston-Monje, D., and Raizada, M.N. (2011) Conservation and diversity of seed associated endophytes in *Zea* across boundaries of evolution, ethnography and ecology. *PLoS One* **6**: e20396.
- Johnston-Monje, D., Lundberg, D.S., Lazarovits, G., Reis, V. M., and Raizada, M.N. (2016) Bacterial populations in juvenile maize rhizospheres originate from both seed and soil. *Plant Soil* **405**: 337–355.
- Jones, S.E., and Lennon, J.T. (2010) Dormancy contributes to the maintenance of microbial diversity. *Proc Natl Acad Sci U S A* **107**: 5881–5886.
- Kong, H.G., Kim, B.K., Song, G.C., Lee, S., and Ryu, C.-M. (2016) Aboveground whitefly infestation-mediated reshaping of the root microbiota. *Front Microbiol* **7**: 1314.
- Lebeis, S.L., Paredes, S.H., Lundberg, D.S., Breakfield, N., Gehring, J., McDonald, M., et al. (2015) Salicylic acid modulates colonization of the root microbiome by specific bacterial taxa. *Science* **349**: 860–864.
- Lindsey, B.E., Rivero, L., Calhoun, C.S., Grotewold, E., and Brkljacic, J. (2017) Standardized method for high-throughput sterilization of *Arabidopsis* seeds. *J Vis Exp* **17**: 128. <https://doi.org/10.3791/56587>.
- Mendes, R., Kruijt, M., de Bruijn, I., Dekkers, E., van der Voort, M., Schneider, J.H.M., et al. (2011) Deciphering the rhizosphere microbiome for disease-suppressive bacteria. *Science* **332**: 1097–1100.
- Miché, L., and Balandreau, J. (2001) Effects of rice seed surface sterilization with hypochlorite on inoculated *Burkholderia vietnamiensis*. *Appl Environ Microbiol* **67**: 3046–3052. <https://doi.org/10.1128/AEM.67.7.3046-3052.2001>.
- Mueller, U.G., and Sachs, J.L. (2015) Engineering microbiomes to improve plant and animal health. *Trends Microbiol* **23**: 606–617.
- Nelson, E.B. (2017) The seed microbiome: origins, interactions, and impacts. *Plant Soil* **422**: 7–34. <https://doi.org/10.1007/s11104-017-3289-7>.
- Nelson, E.B., Simoneau, P., Barret, M., Mitter, B., and Compant, S. (2018) Editorial special issue: the soil, the seed, the microbes and the plant. *Plant Soil* **422**: 1–5. <https://doi.org/10.1007/s11104-018-3576-y>.
- Pande, S., Rao, J.N., and Sharma, M. (2007) Establishment of the chickpea wilt pathogen *Fusarium oxysporum* f. sp. *ciceris* in the soil through seed transmission. *Plant pathol J* **23**: 3–6.
- Perpetuini, G., Donati, I., Cellini, A., Orrù, L., Giongo, L., Farneti, B., and Spinelli, F. (2019) Genetic and functional characterization of the bacterial community on fruit of three raspberry (*Rubus idaeus*) cultivars. *J Berry Res* : 1–21.
- Phillips, R.P., Erlitz, Y., Bier, R., and Bernhardt, E.S. (2008) New approach for capturing soluble root exudates in forest soils. *Funct Ecol* **22**: 6.
- Pineda, A., Kaplan, I., and Bezemer, T.M. (2017) Steering soil microbiomes to suppress aboveground insect pests. *Trends Plant Sci* **22**: 770–778.
- Purahong, W. (2018) Plant microbiome and its link to plant health: host species, organs and *Pseudomonas syringae* pv. *actinidiae* infection shaping bacterial phyllosphere communities of kiwifruit. *Plants Front Plant Sci* **9**: 1563. <https://doi.org/10.3389/fpls.2018.01563>.
- Rottstock, T., Joshi, J., Kummer, V., and Fischer, M. (2014) Higher plant diversity promotes higher diversity of fungal pathogens, while it decreases pathogen infection per plant. *Ecology* **95**: 1907–1917.
- Rybakova, D., Mancinelli, R., Wirkstrom, M., Birch-Jensen, F., Postma, J., et al. (2017) The seed microbiome: cultivar-dependent structure in oilseed rape affects the interaction with symbionts and pathogens. *Microbiome* **5**: 104. <https://doi.org/10.1186/s40168-017-0310-6>.
- Santhanam, R., Luu, V.T., Weinhold, A., Goldberg, J., Oh, Y., and Baldwin, I.T. (2015) Native root-associated bacteria rescue a plant from a sudden-wilt disease that emerged during continuous cropping. *Proc Natl Acad Sci U S A* **112**: E5013–E5020.
- Santos-Medellín, C., Edwards, J., Liechty, Z., Nguyen, B., and Sundaresan, V. (2017) Drought stress results in a compartment-specific restructuring of the rice root-associated microbiomes. *MBio* **8**: e00764–e00717.
- Sasse, J., Martinoia, E., and Northen, T. (2018) Feed your friends: do plant exudates shape the root microbiome? *Trends Plant Sci* **23**: 25–41.
- Savatini, D. V., Gramegna, G., Modesti, V., and Cervone, F. (2014) Wounding in the plant tissue: the defense of a dangerous passage. *Front Plant Sci* 2014; **5**: 470. doi: <https://doi.org/10.3389/fpls.2014.00470>.
- Shade, A., Jacques, M.A., and Barret, M. (2017) Ecological patterns of seed microbiome diversity, transmission, and assembly. *Curr Opin Microbiol* **37**: 15–22.
- Shen, Z., Ruan, Y., Xue, C., Zhong, S., Li, R., and Shen, Q. (2015) Soils naturally suppressive to banana *Fusarium* wilt disease harbor unique bacterial communities. *Plant Soil* **393**: 21–33.
- Song, G.C., Lee, S., Hong, J., Choi, H.K., Hong, G.H., Bae, D.W., et al. (2015) Aboveground insect infestation attenuates belowground agrobacterium-mediated genetic transformation. *New Phytol* **207**: 148–158.
- Song, G.C., Sim, H.J., Kim, S.G., and Ryu, C.M. (2016) Root-mediated signal transmission of systemic acquired resistance against above-ground and below-ground pathogens. *Ann Bot* **118**: 821–831.
- Stursová, M., Zifčáková, L., Leigh, M.B., Burgess, R., and Baldrian, P. (2012) Cellulose utilization in forest litter and

- soil: identification of bacterial and fungal decomposers. *FEMS Microbiol Ecol* **80**: 735–746.
- Tkacz, A., Cheema, J., Chandra, G., Grant, A., and Poole, P.S. (2015) Stability and succession of the rhizosphere microbiota depends upon plant type and soil composition. *ISME J* **9**: 2349–2359.
- Underwood, W., Melotto, M., and He, S.Y. (2007) Role of plant stomata in bacterial invasion. *Cell Microbiol* **9**: 1621–1162.
- Van der Putten, W.H., *et al.* (2013) Plant-soil feedbacks: the past, the present and future challenges. *J Ecol* **101**: 265–276.
- Van Wees, S.C., Van der Ent, S., and Pieterse, C.M. (2008) Plant immune responses triggered by beneficial microbes. *Curr Opin Plant Biol* **11**: 443–448.
- Vorholt, J.A., Vogel, C., Carlström, C.I., and Müller, D.B. (2017) Establishing causality: opportunities of synthetic communities for plant microbiome research. *Cell Host Microbe* **22**: 142–155.
- Weller, D.M., Raaijmakers, J.M., Gardener, B.B., and Thomashow, L.S. (2002) Microbial populations responsible for specific soil suppressiveness to plant pathogens. *Annu Rev Phytopathol* **40**: 309–348.
- Xu, W., and Huang, W. (2017) Calcium-dependent protein kinases in phytohormone signalling pathways. *Int J Mol Sci* **18**: 2436. <https://doi.org/10.3390/ijms18112436>.
- Yi, H.-S., Ahn, Y.-R., Song, G.C., Ghim, S.-Y., Lee, S., Lee, G., and Ryu, C.-M. (2016) Impact of a bacterial volatile 2,3-Butanediol on *Bacillus subtilis* Rhizosphere robustness. *Front Microbiol* **7**: 993. <https://doi.org/10.3389/fmicb.2016.00993>.
- Zhalnina, K., Louie, K.B., Hao, Z., Mansoori, N., Nunes da Rocha, U., 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.
- Zheng, X., Lopisso, D.T., Eseola, A.B., Koopmann, B., and Tiedemann, A.V. (2019) Potential for seed transmission of *Verticillium longisporum* in oilseed rape (*Brassica napus* L.). *Plant Disease*. <https://doi.org/10.1094/PDIS-11-18-2024-RE>.