

<https://doi.org/10.15407/microbiolj87.05.086>

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FORMATION OF PLANT MICROBIOMES. HYPOTHESES AND CONTROVERSIES

Microorganisms play a key role in promoting plant growth, facilitating the assimilation of biogenic element compounds, increasing resistance to biogenic and abiotic stress factors. The vast majority of researchers believe that the source of rhizosphere and endophytic microorganisms is the soil (horizontal provision hypothesis). At the same time, today there is growing interest in the concept of the formation of the plant microbiome as a result of heredity (vertical provision hypothesis). A significant number of publications indicate that seed endophytic microorganisms may play a major role in this process. The presented literature review considers existing points of view on the processes of plant microbiome assembly with an emphasis on the importance of seed endophytes.

Keywords: rhizosphere, rhizoplane, endosphere, spermosphere, soil microorganisms, seed endophytes.

It is now understood that plants grow and develop in associations and symbioses — analogous to animals or humans — with a multitude of organisms that together function as a microbiome (which includes bacteria, fungi, archaea, viruses, lower and higher eukaryotes, as well as their genetic material) (Buee et al., 2009; Raaijmakers et al., 2010; Berg et al., 2020). An extremely important discovery of recent decades is that the numerous organisms of the plant microbiome are not simple background actors. Plants exhib-

it a wide range of relationships with soil organisms, encompassing different ecological scenarios such as competition, exploitation, neutrality, commensalism, and mutualism (Barea, 2015; Jacoby et al., 2017). The plant microbiome plays a key role in promoting plant growth by facilitating nutrient availability and uptake (Lugtenberg et al., 2002; Morrissey et al., 2004), increasing resistance to environmental stressors, and combating disease (Mendes et al., 2011; Zamioudis & Pieterse, 2012; Zolla et al., 2013; Santos & Ol-

Citation: Volkogon V.V., Shevchenko L.A. Formation of Plant Microbiomes. Hypotheses and Controversies. *Microbiological journal*. 2025 (5). P. 86—101. <https://doi.org/10.15407/microbiolj87.05.086>

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ivares, 2021; Darriaut et al., 2022). Plants can be considered superorganisms that rely in part on their microbiome for certain functions and traits (Berendsen et al., 2012).

Most microorganisms function in the rhizosphere soil or rhizoplane, but a relatively small subpopulation, designated as «endophytes,» is able to enter and function within plant tissues (Porrás-Alfaro & Bayman, 2011; Hardoim & van Elsas, 2013; Brader et al., 2014; Mercado-Blanco, 2015; Santoyo et al., 2016). Endophytes evade plant immune responses and colonize, without causing disease symptoms, different parts of plants (roots, shoots, leaves, fruits, and seeds), in different compartments of the plant apoplast (intercellular spaces and xylem vessels), and, in rare cases, plant cells. Some endophytes affect plant growth and the plant organism's response to pathogens, herbivores, and environmental changes or produce important secondary metabolites (Oucala et al., 2021; Chaudhary et al., 2022).

Strictly speaking, it should be recognized that representatives of other groups of microorganisms that colonize plant tissues, such as mycorrhizal fungi, rhizobia, and some pathogens, are actually also endophytes, but they are traditionally considered separately from the main group of «endophytes» because they are involved either in the transfer of nutrients from sources outside the root, i.e. soil or atmosphere, or cause disease symptoms in the host plant.

The mechanisms of plant-microorganism interactions are complex. They involve different levels of communication between organisms, gene activation and inactivation, induction and suppression of responses to different signals, and different pathways triggered by the responses (Boller & Felix, 2009; Maillet et al., 2011; Wiesel et al., 2014; Behm et al., 2014; Poncini et al., 2017; Wood & Stinchcombe, 2017; Rosier et al., 2018, etc.).

As early as 1969, Rovira (1969) concluded that there were differences in the composition of rhizosphere microbial communities of different plant

species, based on information about the different compositions of their root secretions. Indeed, plant-specific microorganisms have been isolated from the roots of cereals and legumes, wheat, and rapeseed (Volkogon et al., 1991; Volkogon, 1994; Grayston et al., 1998; Germida et al., 1998). Later studies, in which rhizosphere microbiomes were characterized based on direct extraction of the total DNA community, also provide compelling evidence for the presence of plant-specific microbiomes (Miethling et al., 2000; Smalla et al., 2001; Kirk et al., 2005; Inceoglu et al., 2013). It has been shown that the roots of wheat, corn, rapeseed, and clover plants have different bacterial communities, which is due to the different compositions of root exudates (Haichar et al., 2008). In addition, it is argued that plants are evolutionarily related to microorganisms and they have evolutionary traits that regulate the formation of root sphere microbiomes (Fitzpatrick et al., 2018).

The powerful complex effect on plant nutrition and health requires explanation: how does a plant «recruit» the necessary microbiota? It should be noted that the process of obtaining a microbiome for plants is not sufficiently studied. At the same time, an analysis of existing literature indicates that in matters of plant microbiome assembly, at least two vectors can be distinguished — the origin of microorganisms from the soil and heredity.

According to a huge body of data, the source of microorganisms in the root spheres of plants is the soil. Microorganisms have the ability to quickly adapt to changing environmental conditions (Gehring et al., 2017; Lau et al., 2017). And, thus, the microbiome of the rhizosphere and endosphere can be considered a «station of plant adaptation to local conditions», primarily soil conditions (Vandenkoornhuysen et al., 2015). Accordingly, the plant microbiome originates from the local soil microbiota and is formed by the composition of the root exudate (Bais et al., 2006; Lareen et al., 2016). On the one hand, it has been reported that the composition of root-associated

microbial communities in different ecosystems strongly depends on environmental parameters (Bulgarelli et al., 2012; Lundberg et al., 2012), such as climate and weather (Brockett et al., 2012; Lladó et al., 2018), as well as soil chemical properties, especially pH and organic matter content (Zhou et al., 2002; Rousk et al., 2010; Lareen et al., 2016). On the other hand, the components of plant root exudates (sugars, vitamins, nucleotides, flavonoids, and phytohormones), which differ between plant species and even between genotypes within a species (Broeckling et al., 2008), are also different and considered important factors in structuring the soil microbiota that proliferates in the root zone (Dotaniya & Meena, 2015).

A number of researchers have particularly emphasized the origin of the root ball microbiome from the surrounding soil, noting that unlike animals, in which the gut microbiome is assembled internally and transmitted through the birth process, the plant microbiome is predominantly composed of external microorganisms in the soil (Palmer et al., 2007; Dominguez-Bello et al., 2010).

Based on studies of stable rhizosphere and endosphere microbiomes, a view has been presented that suggests that plants may shape their microbiomes in two steps, with the first step involving general rhizosphere replenishment and the second step involving root penetration due to species-specific genetic factors (Bulgarelli et al., 2013). The authors observed an initial enrichment of the rhizosphere, consistent with the attraction of diverse microorganisms to the plant's zone of influence, followed by a slowing down of the rate of accumulation of specific microbiota in the endosphere.

In support of this view, it has been reported that after initial recruitment to the rhizosphere, only a subset of microorganisms initially recruited to the rhizosphere associate with the root surface in the rhizoplane, suggesting selectivity for direct physical association with the root. This selection may be driven by the plant itself or by the ability of the microorganisms to form biofilms, as

certain members of the microbiota are known to form biofilms along the root surface (Bais et al., 2004; Walker et al., 2004). The rhizoplane may also serve a critical role as a gatekeeper of the microorganisms recruited to the rhizosphere; only a fraction may be associated in the rhizoplane, and a fraction may be able to penetrate and multiply in the endosphere. Each of these steps likely involves molecular signals from the plant, such as components of root exudates and possibly cell wall components or membrane proteins. Signals can consist of general plant metabolites as well as species- and genotype-specific molecules (Bulgarelli et al., 2013).

Edwards et al. (2015) used time-series experiments to reveal early stages of plant microbiome formation based on high spatial resolution of root habitats. The authors transplanted sterile rice seedlings into soil and sampled root habitats from time points ranging from 1 to 13 days after transplanting. Comparison of the microbiota across space and time showed that habitat-specific community structures were largely established on day 1. Although the composition of the root endosphere was organized within the first day, steady-state bacterial population sizes were reached by 13 days. This work advances the two-step model of root microbiota formation (Bulgarelli et al., 2013) to a model with at least three selective steps, where the rhizoplane is a key component that plays an important role in controlling microbial entry into host tissues.

The view of Edwards et al. (2015) is supported and developed by other authors (van der Heijden & Schlaeppi, 2015), who also believe that the enrichment process begins to act at a distance in the rhizosphere, continues in the rhizoplane, and is probably largely due to root exudation. In contrast to enrichment, the exclusion process, in their opinion, may act more closely: first in the rhizoplane and then more pronounced in the root endosphere. One explanation for the first step of exclusion is that the rhizoplane selects bacteria that are able to form biofilms and suc-

cessfully compete with others in the presence of elevated nutrient levels. Presumably, the second step of exclusion is the result of the selection of rhizoplane bacteria that possess traits that allow them to colonize the root endosphere. Such traits of microorganisms may allow bacteria, for example, to avoid recognition or manipulate host defense responses. The involvement of microbial traits that subvert host immune processes has also been suggested (van der Heijden & Schlaepi, 2015), as host plant cells are known to initiate defense responses upon detection of molecular signals that are common to the entire bacterial kingdom (Jones & Dangl, 2006). It is therefore possible that the host immune system influences the selection of the microbiota as a whole and that it has a strong influence on the second step of exclusion of root endosphere microbiota from the rhizoplane.

The view that soil is the main reservoir of microorganisms in the formation of the plant microbiome is also supported by other works (Berg & Smalla, 2009; Garbeva et al., 2008; Lundberg et al., 2012). At the same time, there is growing interest in the concept of the formation of the plant root zone microbiome due to heredity (van Opstal & Bordenstein, 2015). It is possible that the plant microbiome is an ecological unit with heritable traits, although it is a physical extension of the host, since it includes the soil habitat surrounding the roots, rather than the intact plant unit. This concept of an «extended phenotype» is not new and originates from the idea proposed by Dawkins (1989) that the phenotype of an organism should extend from its cellular components to the environment. Examples of extended phenotypes include manipulation of an organism's physical environment and changes in behavior, both of which can begin at the gene level. Other concepts in evolutionary biology offer a broader view that heredity is shaped at many levels beyond the individual, such that natural selection acts on ecological units beyond the individual. Perhaps, the most prominent of

these is the concept of multilevel selection, often called group selection.

Although it is generally believed that the source of the rhizosphere (including endophytic) microbiome is the soil, it is possible that endophytic microorganisms of the seed play a major role in this process. The seed microbiome is attracting increasing attention from scientists. Bacteria have been detected in surface-sterilized seeds of various species, including crops such as rice (Bacilio-Jiménez et al., 2001; Okunishi et al., 2005; Kaga et al., 2009; Hardoim et al., 2012; Verma et al., 2017), maize (Johnston-Monje & Raizada, 2011; Liu et al., 2013), tobacco (Mastrett et al., 2009), coffee (Vega et al., 2005), quinoa (Pitzschke, 2016), beans (López-López et al., 2010), grapevine (Compant et al., 2011), barley (Zawoznik et al., 2014), pumpkin (Fürnkranz et al., 2012), and annual ryegrass (*Lolium rigidum*) (Goggin et al., 2015). In our study of pea beans, we have found that, contrary to the rather established idea of the sterility of the seeds of this crop in green beans, a big group of microorganisms is observed inside them and in the not yet ripe green seeds, including representatives of *Rhizobium leguminosarum*. Moreover, when sowing seeds of Afghan pea (a plant that is capable of forming nitrogen-fixing symbioses only with bacteria that occur in the soils of the area of origin of this species) in the sod-podzolic soil of Ukrainian Polissia, single nodules formed on the roots of the plants. Since we did not perform any manipulations when sowing Afghan pea seeds, the only source of bacteria that formed nodules could only be the seeds (unpublished results). At the same time, when studying soybean seeds, it was concluded that they cannot be a source of *Bradyrhizobium japonicum* (Krutylo, 2007). Perhaps, this is a feature of this crop. However, it is not excluded that this may also be a consequence of the intensive selection to which soybeans had been subjected.

Bacteria have been found in various parts of the seed, including the seed coat, endosperm,

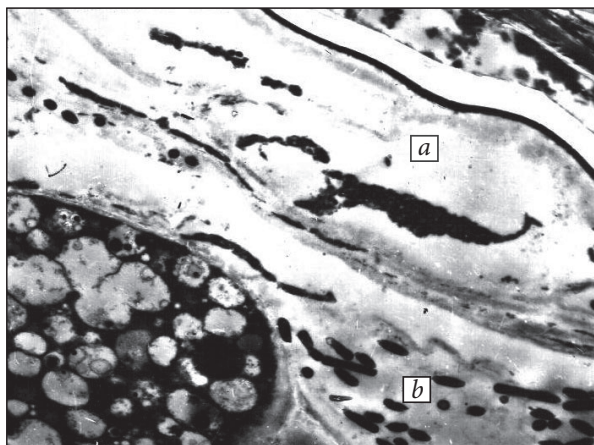


Fig.1. Electron micrograph of an ultrathin section of seed of pasture fenugreek. *a* — seed coat; *b* — bacterial cells (Volkogon et al., 1995); x 2500

and embryonic tissues (Mukhopadhyay et al., 1996; Cankar et al., 2005; Puente et al., 2009b; Mitter et al., 2017; Compant et al., 2011; Glassner et al., 2017). In electron microscopic examination of ultrathin sections of immature perennial ryegrass (*Lolium perenne*) seeds, we (Volkogon et al., 1995) found bacterial cells between the seed coat and endosperm (Fig.1).

A number of studies have demonstrated the ability of seed endophytic bacteria to actively multiply during seed germination (Barret et al., 2015; Compant et al., 2011; Cope-Selby et al., 2017; Hameed et al., 2015; Hardoim et al., 2012; Huang et al., 2016; Johnston-Monje et al., 2016; Kaga et al., 2009). For example, Barret et al. (2015) found that as seeds germinate, specific copiotrophic bacteria (representatives of the genera *Bacillus*, *Massilia*, *Pantoea*, and *Pseudomonas*), originating from the endophytic seed microbiome, increase in development within 96 hours of seed germination. Similar studies have demonstrated the development of copiotrophic bacteria from the epiphytic and endophytic seed microbiomes in the spermosphere (Huang et al., 2016).

Bacterial endophytes of seeds of some plant species could potentially constitute a major part of the species pool from which the seedling mi-

crobiome is recruited (Johnston-Monje & Raizada, 2011; Links et al., 2014). This is consistent with observations demonstrating that endophytic seed microorganisms are often distinct from the microbiota associated with the soil where the plants are grown (van Overbeek et al., 2011), suggesting the possibility that seed microorganisms may be recruited predominantly from the mother plant. In studies of cultivated populations of bacterial endophytes, estimates of abundance range from 10^1 – 10^2 CFU/g seeds (Compant et al., 2011; Ferreira et al., 2008; Rosenblueth et al., 2012) to 10^6 – 10^8 CFU/g seeds (Graner et al., 2003; Hameed et al., 2015; Truyens et al., 2015; 2016). Darrasse et al. (2007) argue that successful seedling colonization can be ensured with a minimum bacterial population size of 10^2 CFU/seed. In our studies of the abundance of the endophyte *Azospirillum lipoferum* in surface-sterilized pasture ryegrass seeds, the number of bacteria did not exceed 100 cells/seed (Volkogon et al., 1995). However, when surface-sterilized ryegrass seeds were sown in a sterile substrate (washed and sterilized river sand), significant populations of azospirilla developed during spermosphere formation. Three days after seed germination, the population of *A. lipoferum* reached 200–500 thousand/sprout (Volkogon et al., 1995). This can be explained by the active release of specific substances from the germinating seeds, which can initiate a rapid burst of microbial development and activity in the spermosphere (Nelson, 2004; Schiltz et al., 2015).

It should be noted that the number of diazotrophs in ryegrass seeds depended on the storage period of the seeds. Thus, the largest number of endophytic bacteria was found in freshly harvested seeds and in seeds of the first year of storage. By the third year of seed storage, bacteria often could not be detected; by the fourth year, endophytic bacteria were not detected. At the same time, seed germination was also lost. Preservation of viability by endophytic bacteria of seeds for two to three years is a rather long pe-

riod and can be compared only with the terms of preservation of laboratory cultures using special methods. The possibility of long-term preservation of bacteria in seeds, in our opinion, should be considered from the point of view of the conditions of seed formation. Water release at the final stages of seed formation does not occur passively, and complex physiological transformations are behind this (Ovcharov, 1976). Upon reaching the appropriate level of moisture in the seeds, the release of water into the surrounding space is suspended, and metabolic processes subside. This is largely facilitated by the seed coat. This is a complex and poorly studied component of the seed. However, even the scanty information is striking in its high degree of specialization. For example, it is known that the scar of the seed coat of legumes acts as a special valve. The slit that runs along the scar opens when the seed is in dry air and closes when the outside air becomes humid (Hude, 1954). The features of natural seed drying are quite close to the conditions of freeze-drying of biological objects. This analogy becomes even more appropriate when we consider that water molecules in the cytoplasm of cells are partially contained in the ice-like framework (Alekseev, 1969). Therefore, the viability of endophytic bacterial cells is closely related to the viability of the seed, and the seed shell can be a reliable barrier against adverse environmental conditions.

Evidence in support of vertical seed transmission of endophytes comes from studies demonstrating the similarity of seed and seedling endophyte taxa, which is consistent with vertical seed transmission of endophytes, but does not directly confirm this (Ferreira et al., 2008; Gagne-Bourgue et al., 2013; Ringelberg et al., 2012; Adam et al., 2018; Kong et al., 2019). When we studied the composition of diazotroph endophytes in seeds of certain species of cereal grasses, we found their identity with the composition of root endophytes (Volkogon, 1999). In particular, *A. lipoferum* and *Agrobacterium radiobacter* were isolated from the histosphere of perennial ryegrass (*L. perenne*)

and from surface-sterilized seeds. At the same time, the fenugreek rhizoplane was colonized by representatives of four species of diazotrophs, and a fairly significant diversity of nitrogen fixers was found in the rhizosphere soil.

Other studies have reported the continuity of certain microorganisms between generations of rice and maize (Mukhopadhyay et al., 1996), which also indirectly supports the vertical transfer hypothesis. At least for maize, there is evidence for long-term conservation of species in seed endophyte communities. Seeds of genetically related maize hybrids have been found to contain similar bacterial taxa (Ringelberg et al., 2012), and studies using 16S rDNA restriction fragment length polymorphisms have shown the presence of representatives of the same genera in several maize genotypes, including its ancestor teosinte (Johnston-Monje, Raizada, 2011). Indirect evidence for the role of vertically transmitted endophytes in plant development is also found in a study with the invasive grass *Sorghum haplense*, which showed that plants grown aseptically from surface-sterilized seeds obtained nitrogen from a source other than the nitrogen added to the substrate, suggesting vertical transmission of diazotrophs from seeds (Rout et al., 2013). The elimination of microorganisms from the plant's immune responses may be important in this regard.

Bright & Bulgheresi (2010) suggest that host-associated microorganisms can colonize the host either vertically from parent to offspring, horizontally through the environment, or by mixed means. In this context, it has been proposed to classify seed-associated microorganisms into (i) transient — found in seeds but not necessarily transmitted to seedlings, and (ii) persistent — found in seeds and transmitted to developing seedlings (Shade et al., 2017). Instead, according to Bright & Bulgheresi (2010), in many vertically transmitted symbioses, the symbiont is obligate, spending its entire life cycle inside the host, and is unable to survive in the environment.

Vertical transmission of bacterial symbionts from parents to offspring is indeed common in systems where the symbiont performs an indispensable function, such as in the well-studied trophic symbioses between bacteria and insects (Moran, 2006). In plants, vertical transmission via seeds is well documented only for certain groups of micromycete endophytes (e.g., the well-studied fungal endophytes of some grass species (Schardl, 2001)). *Epichloë* and *Neotyphodium* species (Ascomycota) are mutualistic symbionts (endophytes) of temperate grasses such as fescue (*Festuca*), ryegrass (*Lolium*), and koeleria (*Koeleria*), to which they confer numerous and significant benefits. *Epichloë festucae* is a good model for the study of endophytes, amenable to Mendelian and molecular genetic analysis.

Protective mutualisms between plants and fungal endophytes have also been described elsewhere (Saikkonen et al., 2010; Hodgson et al., 2014). At the same time, Frank et al. (2017) consider that obligate relationships between bacteria and plants are rare. Today, only one obligate vertically formed symbiosis of bacteria with a plant is known. The nitrogen-fixing symbionts *Burkholderia* reside in each vegetative shoot tip and colonize each new leaf in angiosperms of the genera *Ardisia*, *Pavetta*, *Psychotria*, and *Sericanthe*, forming nodules (Miller, 1990). These bacteria are transferred to the tip of the floral shoot, then to the embryo sac of the developing egg, and finally to the epicotyl of the embryo, from where they enter the shoot tip of the sprout (Miller, 1990). But even in this confirmed vertically transmitted symbiosis, it is still difficult to detect the symbiont in seeds because the amount of bacterial DNA in seeds is low (Lemaire et al., 2012). Furthermore, the possibility of directly confirming vertical transfer, according to Truyens et al. (2015), will only become possible when molecular biological studies at the bacterial strain level can be performed.

Considering possible vectors for endophyte transmission to the next generation, Frank et al.

(2017) suggests that endophytes that are continuously transmitted across generations must have a route from seeds to reproductive organs either through xylem vessels or through the shoot apical meristem, which differentiates into reproductive organs. Soil bacteria can colonize the interior of the plant and become endophytes early through the germination medium (spermosphere), or later through the rhizosphere and roots of seedlings and adults. The above-ground plant surface, or phyllosphere, colonized by a variety of microorganisms, represents an alternative but less studied route of bacterial entry, originating from rainwater, bioaerosols from the surrounding soil or from dust and other particles in the atmosphere, and potentially entering through stomata. It is likely that stomata can serve as a route of transmission for plants of all life stages, but may be particularly important for foliar endophytes of trees. In addition, sap-feeders, pollinators, and other arthropods may serve as vectors for bacteria that colonize plants. Mixed modes of transmission are likely not uncommon, as, for example, bacteria deposited on flowers can be transmitted to the next generation (Darrasse et al., 2010; Dutta et al., 2014a, 2014b; Mitter et al., 2017). These observations suggest that bacteria that colonize seeds via the flower may be incorporated into the seed microbiome and, importantly, may ultimately be transferred to the seedlings that develop from that seed. This idea has also been supported by recent studies of the plant growth-promoting bacterium *Paraburkholderia phytofirmans*, which, when introduced into flowers, colonizes developing seed embryos by penetrating the stigma and establishing itself in the mature seed (Mitter et al., 2017). This and other bacteria can then be naturally transferred to the seedlings and promote plant growth (Chimwamurombe et al., 2016; Mitter et al., 2017).

Interest in seed endophyte communities is growing, as evidenced by the emergence of new publications (Gundel et al., 2011; Bergna et al., 2018; Shahzad et al., 2018; Haridoim, 2019; Ro-

chefort et al., 2019; Wassermann et al., 2019; Rodríguez et al., 2020). Most of them focus on the composition of seed microbial communities. At the same time, studies on the dynamics of establishment and transmission of microorganisms to seeds during plant development are extremely important and necessary, given that this stage is crucial in the development and continuity of the plant microbiome and considered a potential bottleneck in the vertical transmission (Abdelfattah et al., 2021).

Of course, it is also worth noting that some bacterial endophytes may be able to be transmitted horizontally. First, the diversity of bacteria in seeds and seedlings grown under sterile conditions is generally lower than that in plants grown in soil (Hardoim et al., 2012), which may indicate that some endophytes are acquired from the environment. Second, bacterial endophytes are often universals, as beneficial properties of endophytes can usually be transmitted to distantly related plants (Ma et al., 2011; Compant et al., 2005; Khan et al., 2012). Bacterial universals that infect many different plant species must move horizontally between them, and are unlikely to be transmitted strictly vertically. However, the relative importance of different transmission routes for most situations is unknown, although recent claims have emerged that the soil microbiome colonizes plant root zones only when the endogenous seed microbiome is severely disrupted, with the seed microbiome taking precedence over the soil microbiome during the process of plant microbiome recovery (Moroenyane et al., 2021).

It has been shown that, across a wide range of plant species, seed-associated bacteria predominantly belong to the bacterial phyla Proteobacteria, Actinobacteria, Firmicutes and Bacteroidetes (Barret et al., 2015; Bulgarelli et al., 2013). This may be partly explained by the dominance of these phyla in soil, making them the most likely taxa to be found in seeds. However, selective recruitment from these environmental sources is evident, as individual bacterial species vary from

plant species to species (Links et al., 2014) and genotype to genotype (Barret et al., 2015; Johnston-Monje & Raizada, 2011).

The functional properties of seed endophytes are generally similar to those known for agronomically beneficial bacteria (PGPR). These endophyte properties may reflect the shared needs of the seed, the host, and its spermosphere (Nelson, 2004). For example, it has been reported (Johnston-Monje & Raizada, 2011) that most bacterial isolates from seeds of different maize genotypes were able to solubilize phosphorus, secrete acetoin, and fix atmospheric nitrogen. In addition, ACC deaminase activity and antibiosis were typical of endophytes from different maize genotypes (Johnston-Monje & Raizada, 2011). Cactus seed endophytes allowed cactus seedlings to grow under extreme conditions for at least a year without showing signs of stress (Puente et al., 2009a). These endophytes were able to release inorganic nutrients, such as phosphorus, from crushed rock by producing organic acids and had the ability to fix nitrogen (Puente et al., 2009b).

Several studies have shown that several endophytes isolated from seeds have antifungal properties. *Bacillus* and *Microbacterium* strains isolated from millet seeds inhibited the mycelial growth of fungal plant pathogens by producing several toxins, such as surfactins and the lipopeptides iturin and mycobacillin (Gagne-Bourgue et al., 2013). Among rice seed endophytes, the strongest antagonistic properties against *Rhizoctonia solani*, *Pythium myriotyrum*, *Guamannomyces graminis* and *Heterobasidium annosum* were found in two *Enterobacter* strains due to the production of a volatile antifungal compound, probably ammonia, and/or the chitinolytic enzyme N-acetyl- β -D-glucosaminidase (Mukhopadhyay et al. (1996). Cottyn et al. (2001) found antifungal activity among rice seed endophytes: almost half of the antagonists of *Rhizoctonia solani* and *Pyricularia grisea* were members of the genus *Bacillus*, but also some strains of *Pantoea*, *Enterobacter*, *Stenotrophomonas*, *Xanthomonas*, *Acinetobacter*, *Paeni-*

bacillus, and *Cellulomonas* showed antagonistic activity against one or both of these fungi. In addition, Ruiz et al. (2011) reported antifungal activity against *Curvularia* sp., *Fusarium oxysporum*, and *Phytium ultimum* in several strains of *Pantoea*, *Microbacterium*, *Pseudomonas*, *Paenibacillus*, and *Curtobacterium* isolated from rice seeds.

It has also been shown that endophytic bacteria of rice seeds are able to suppress early root colonization by *Azospirillum brasilense* strains when used for inoculation (Bacilio-Jiménez et al., 2001). A similar effect was confirmed in another study (Rybakova et al., 2017) using different rapeseed varieties. These results indicate the possibility of seed endophytes competing with biological agents of microbial preparations.

Thus, a brief analysis of the literature devoted to the study of seed endophytes as a source of microorganisms in the formation of the root sphere microbiome indicates a high probability of the existence of this vector. It is also possible that this aspect of the relationship between microorganisms and the plant was formed evolutionary. At the same time, nature could have created mechanisms to provide the plant with the necessary minimum of microorganisms important for its existence when the seeds fall into difficult environmental conditions. These considerations are confirmed by the conclusion of Ferreira et al. (2008), who believe that the vertical transmission of the microbiome is a strategy that allows the host to provide its offspring with mutualistic endosymbionts.

If the bacteria and micromycetes that proliferate and dominate the spermosphere, and later the endosphere, are recruited primarily from the endophytic microbiota of the seed, then the influence of microbial inheritance during seed development and the formation of plant-microbe interactions may be particularly important for understanding the nature of plant microbiomes (Nelson, 2018). This may also change the methodological approaches to screening for active PGPR strains.

In practical terms, other solutions are also possible. The response of seed-associated microbial communities to biological disturbances caused by seed-borne phytopathogenic agents is of considerable interest in proposing biocontrol strategies. For example, Nelson (2004) suggested that seed endophytes are highly competitive and rapidly growing colonizers of the spermosphere that help protect seedlings from pathogens by rapidly absorbing seed exudates, blocking their use by other microorganisms. This is supported by studies by Bacilio-Jiménez (2001), who showed that seed endophytes protect young rice roots from colonization by soil-borne pathogens.

In addition, studies are already underway to manipulate the microbial communities of a particular plant species by introducing organic amendments to the soil that act as prebiotics (compounds that selectively stimulate the development or activity of microorganisms) (Sheth et al., 2016; Arif et al., 2020). The use of phytohormones (auxins and cytokinins) or their synthetic analogues for seed treatment affects the formation of communities of nitrogen-fixing bacteria in the root zones of plants, which is accompanied by an increase in the activity of associative nitrogen fixation (Volkogon et al., 1995, 1996). Carvalhais et al. (2014) have demonstrated that plant hormones such as salicylic acid, methyl jasmonate, ethylene, and abscisic acid can change the composition of bacterial communities in the rhizosphere of plants, which may affect crop productivity. It was shown that changing soil properties with the ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC) can change the structure of the plant microbiome, mitigating the effects of salinity on soil and plants (Liu et al., 2019). It is believed that as this research area develops, new signaling molecules will be identified to optimize the interaction between plants and microorganisms, and new prebiotics with increased efficiency will be developed. This is very promising, since culturable microorganisms make up only a few percents of the total number

of representatives of the soil microbiota (Singh, 2010). The use of prebiotics can theoretically initiate the participation of many other seed endophytes, including non-culturable ones, in the processes of their interaction with plants. According to Batista & Singh (2021), in situ microbiome manipulation has the greatest potential for sustainable improvement of crop productivity.

Understanding the specificity and efficiency of the vertical transmission of microorganisms may open up new exciting opportunities for exploiting beneficial interactions between microbiota and plants in agriculture. For example, it may help develop new varieties that will be more able to form beneficial communities of microorganisms inside and outside the seed. Moreover, the combination of breeding and introducing beneficial microorganisms into seeds will allow

for a promising symbiotic (combination of prebiotic and probiotic treatments) approach to crop cultivation (Berg et al. 2018).

A promising research direction may also be the «back to the roots» approach proposed by Pérez-Jaramillo et al. (2016), which involves studying the microbiomes of wild relatives of crop species and their natural habitats to identify beneficial microorganisms that may have been lost during the domestication process. This fundamental knowledge could allow for the restoration of missing beneficial wild relative microbiota in the seeds of modern crop species and the identification of plant traits that can ultimately be used in specialized microbiome engineering programs.

Conflict of interest. The authors declare that there is no conflict of interest.

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Received 19.06.2025

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ФОРМУВАННЯ МІКРОБІОМІВ РОСЛИН. ГІПОТЕЗИ ТА КОНТРОВЕРСІЇ

Мікроорганізми відіграють ключову роль у сприянні росту рослин, полегшуючи асиміляцію біогенних елементів, підвищуючи стійкість до біогенних та абіогенних факторів стресу. Переважна більшість дослідників вважає, що джерелом мікроорганізмів ризосфери та ендofітів є ґрунт (гіпотеза горизонтального забезпечення). Водночас сьогодні зростає інтерес до концепції формування мікробіому рослин на основі спадковості (вертикальне забезпечення). Значна кількість публікацій вказує на те, що ендofітні мікроорганізми насіння можуть відігравати важливу роль у цьому процесі. В огляді літератури представлено існуючі точки зору на процеси формування мікробіома рослин з акцентом на важливості ендofітів насіння.

Ключові слова: ризосфера, ризоплана, ендосфера, спермосфера, ґрунтові мікроорганізми, ендofіти насіння.