Microbiological Research 263 (2022) 127148

Contents lists available at ScienceDirect

Microbiological Research

journal homepage: www.elsevier.com/locate/micres

Plant probiotics – Endophytes pivotal to plant health

Shiv Shanker Pandey[a,*,1], Rahul Jain[a,1], Priyanka Bhardwaj[a,c], Ankita Thakur[a,c], Manju Kumari[a,c], Shashi Bhushan[a,b], Sanjay Kumar[a,*]

[a] Biotechnogy Division, Council of Scientific and Industrial Research (CSIR)-Institute of Himalayan Bioresource Technology, Palampur, H.P. 176061, India
[b] Dietetics & Nutrition Technology Division, CSIR-Institute of Himalayan Bioresource Technology (IHBT), Palampur, H.P. 176061, India
[c] Academy of Scientific and Innovative Research (AcSIR), Ghaziabad 201002, India

ARTICLE INFO

Keywords:
Endophyte
Endophytic diversity
Endophytic community
Plant-endophyte interactions
Endophyte-based formulation
Plant probiotics
Endophytic-consortium

ABSTRACT

Endophytes as a ubiquitous associate of the plant are considered as a promising candidate for sustainable agriculture. These organisms play a pivotal role in the regulation of the primary and secondary metabolism of their host plant. The direct and long-lasting interaction of endophytes with the host enables them to escape from harsh environmental conditions. Especially, their endophytic nature makes them better candidates over epiphytes and rhizospheric microbes in interaction with plants. Current research findings revealed that the endophytes help plants in making nutrient acquisition from the soil, nitrogen fixation, phosphate availability, phytohormone and antimicrobial production. There is a huge potential for developing novel products like endophytes-based microbial formulations and elicitors to improve plant health, ameliorating stress tolerance in plants and source of therapeutically important secondary metabolites. The present review specifically dealt with attributes such as host-tissue specificity of endophytes, the importance of seed-associated endophytes, endophyte-parasite plant-host plant interaction as well as their applications in plant *in-vitro* systems and as microbial consortium. In addition, the conserved endophytic microbial communities in different plants are also looked upon possibly to understand the plant-endophytic microbiome on similar lines of the animal-gut microbiome. Primarily, the purpose of this review is to implicate the endophytic flora as probiotics influencing overall plant health and their survival under extreme environmental conditions.

1. Introduction

The world population is expected to reach 9.9 billion by 2050 that will require a quantum jump in food production through enhanced agricultural productivity per unit area with reduced production costs and environmental issues. Changing climatic conditions are also hurting crop productivity around the globe (Raza et al., 2019). Diverse approaches such as plant breading, transgenic generation and the use of chemicals as fertilizers and pesticides are deployed for a long time to increase crop yield. However, these practices are confined to colossal production costs, limited social acceptability and environmental concern (Qaim, 2020). Therefore, other sustainable approaches need to be explored for attaining required agricultural productivity. In addition, societies are more interested in the natural and sustainable means of food production that led to immense use of plant cell and tissue culture technology over the past decade (Espinosa-Leal, 2018). Organically produced food crops are also becoming the preferred choice for most consumers (Willer et al., 2021). Therefore, it is necessary to develop environmentally sustainable methods to improve crop productivity with no or limited demand for chemical fertilizers and pesticides.

In nature, plants harbor distinct microbial communities associated outside and inside their tissues, described as the plant microbiome (Schlaeppi and Bulgarelli, 2015). It consists of the microbes associated with the rhizosphere (i.e., plant roots-soil interface), phyllosphere (air-plant interface) and endosphere (the internal tissues of the plant) (Compant et al., 2019). Several studies have demonstrated the importance of plant-associated microbial communities in the improvement of plant growth, protection from environmental stresses (biotic and abiotic) and modulation of secondary metabolite biosynthesis, thus, confirming their significant role in plant life (Liu et al., 2020; Oleńska et al., 2020). Exploring plant microbiome has enormous potential for sustainable agriculture and to mitigate the effect of climate change on

---

[*] Corresponding authors.
E-mail addresses: shivpandey@ihbt.res.in (S.S. Pandey), sanjaykumar@ihbt.res.in (S. Kumar).

[1] **Equal contribution**

https://doi.org/10.1016/j.micres.2022.127148
Received 21 January 2022; Received in revised form 22 April 2022; Accepted 26 July 2022
Available online 27 July 2022
0944-5013/© 2022 Elsevier GmbH. This article is made available under the Elsevier license (http://www.elsevier.com/open-access/userlicense/1.0/).

plant productivity.

Plant-associated microbes, residing within the plant tissues referred to as endophytes, have specific significance as they interact directly with the plant cells (Santoyo et al., 2016). Endophytes are associated with almost all plant species and found to play a crucial role in plant growth and development (Khare et al., 2018). In this article, the main emphasis is to understand the diversity of endophytes associated with different crops, the presence of conserved endophytic community as "core microbiota", factors affecting the endophytic diversity, plant host and tissue specificity, endophyte-parasitic plant-host interaction and importance of seed-associated endophytes as plant probiotics. In addition, the aspects such as application of endophytes in plant tissue culture as probiotics, biotic elicitors, their consortium application as a substitute of transgenic (expressing multiple genes), plant endophytic vs. animal gut flora, endophytes as probiotics for animals, limitations for using endophytes and future approaches are also discussed. Primarily, this review comprehends the role of endophytes as plant probiotics similar to animals-probiotics, used to improve the gut microbiome and animal health.

2. Endophytes

Endophytes are the plant-associated microbes residing inside the plant tissue (inter- or intra-cellularly) without producing any negative impact, harm, or symptoms to the plant host (Hirsch and Braun, 1992). Research related to endophytes started in the middle of the 19th century, as Anton de Bary introduced the term "endophytes" for fungi that live inside the host plant tissue for the first time (de Bary, 1866). Afterward, this term was extended for the bacteria and actinomycetes with similar living strategies inside the host plant. The term endophyte originates from two Greek words, "endon" which means within and "phyton" means plant i.e., within the plant. Several studies have demonstrated the role of endophytes in the improvement of plant growth, protection from abiotic and biotic stress, improvement of secondary metabolite production, and as a source of important bioactive compounds (Gupta et al., 2020; Rodriguez and Redman, 2008; Schultz and Boyle, 2005; Sieber, 2002;). Occasionally endophytes start to produce the secondary metabolites similar to their host plants for e.g., camptothecin (Puri et al., 2005; Shweta et al., 2010), deoxypodophyllotoxin (Kusari et al., 2009a), podophyllotoxin (Eyberger et al., 2006), emodin and hypericin (Kusari et al., 2008, 2009b), taxol (Soliman et al., 2011), azadirachtin (Kusari et al., 2012), vincristine and vinblastine (Kumar et al., 2013), and cryptotanshinone (Naik et al., 2019; Teimoori-Boghsani et al., 2020). Therefore, endophytes are potential candidates that can be used as an in-vitro platform for the production of therapeutically important plant secondary metabolites (Venugopalan and Srivastava, 2015). Modern research on endophytes has also indicated their essential role in plant survival and health (Khare et al., 2018; Potshangbam et al., 2017; Rho et al., 2020). Recently the presence of beneficial cultivable endophytes having multiple plant growth promoting attributes has been demonstrated in *Arnebia euchroma* which is an endangered medicinal plant of cold desert in the Himalayas (Jain et al., 2021). Therefore, endophytes have huge potential for sustainable agriculture for enhancing crop yield. The mechanism associated with plant-endophyte interaction is not very clear. Very little is known about the mechanism of entry of endophytes inside the plants, the way of colonization in different parts of plants, and the components involved in modulating host plant metabolism.

Primarily, endophytes promote plant growth by enhancing nutrient acquisition through improved phosphate solubilization, nitrogen fixation, production of siderophores, and modulating phytohormones status of plants (Afzal et al., 2019; Chhabra and Dowling, 2017; Santoyo et al., 2016). Besides, endophytes also protect plants from abiotic and biotic stresses (Issa et al., 2018; Miotto-Vilanova et al., 2016; Molina-Montenegro et al., 2020; Qin et al., 2016). A plant acquires its endo-microbiota through either horizontal transmission from the soil, air, water droplets, and insects via roots, stomata, and wounds or vertical transmission from parents through seeds and pollens (Berg and Raaijmakers, 2018; Cordovez et al., 2019; Mitter et al., 2017; Shade et al., 2017). The plant-endosphere is a restricted area; therefore, only microbes with distinct characteristics can penetrate and colonize the internal plant tissues (Vandenkoornhuyse et al., 2015). These characters include the presence of enzymes for plant polymer degradation, detoxification of reactive oxygen species, protein secretion systems, quorum sensing, etc. (Sessitsch et al., 2012). Furthermore, plant immunity and secretion signals also play an essential role in successful colonization by specific microbes inside the plant endosphere (Chagas et al., 2017; Chen et al., 2020; López-Ráez et al., 2017; Rozpądek et al., 2018). Bulgarelli et al. (2013) proposed a "two-step selection model" for differentiation of root-microbiota which also applies to select the endophytic communities in roots. This model stated that, firstly, edaphic factors govern the bacterial communities in the soil. While at the second step, convergent host-genotype-dependent selection in and around the roots finely adjust the microbial community profile thriving on the rhizoplane as well as within plant roots.

Various colonization routes specific to endophytes have been described, and specific interactions have been suggested. Endophytes have the ability to actively penetrate the endodermis to reach the vegetative parts of a plant using the xylem vascular tissues as the main transport route (James et al., 2002). Moreover, some deleterious bacteria disrupt the endodermis, passively providing a passage for other endophytic bacteria into the xylem vessel. Migration through xylem vessels is a major route of internal colonization by bacterial endophytes, probably because these vessels act as open conduits for microbial movement, whereas, migration through intercellular spaces involves secretion of enzymes with cell wall degrading activity (Compant et al., 2005; Straub et al., 2013). However, such active cellular penetration by the endophytes may activate plant host defense mechanisms. Further the movement of bacterial endophytes inside the host plant is supported by the bacterial flagella and/or transpiration stream of host plant (Compant et al., 2010; James et al., 2002). However, all endophytes are not able to successfully colonize the aerial parts of a plant and remain restricted to the roots only (Hallmann, 2001), as for this they have to pass over several physiological, biochemical and molecular barriers and also they need to have specific physiological requirements to establish successful colonization in different plant niches. However, some endophytes such as leaf-nodulating nitrogen-fixing *Burkholderia* symbionts and root-nodulating bacteria can actively penetrate the plant tissues. Besides this, the highly specific chemical signals (e.g., flavonoids) are also thought to be involved in such plant-bacterial interactions (Khare et al., 2018). Fig. 1 exhibit the important aspects of plant endophytes interaction.

2.1. Diversity of endophytes

With the functional recognition of endophytes as plant probiotics, identification of plant-associated endophytic microbial diversity and its composition has become crucial. The conventional culture dependent approaches provide far less information on the microbial diversity in comparison to the high throughput next-generation sequencing approaches. However, the conventional methods have advantages, as microbial functions and their interactions with host can be investigated in more details. Culturomics to culture plant microbiota are still emerging and new advancements are required to get the most out of the plant endosphere and to study their diversity (Papik et al., 2020; Sarhan et al., 2019). Advancement in sequencing technologies has made it possible to decode the complete endophytic diversity inhabiting inside the plant tissues and to decipher the microbial composition and abundance at a deeper level. Microbiome sequencing using Illumina MiSeq is the mostly used platform for diversity analysis. The technique relies on sequencing short conserved domain in 16S rRNA (bacteria) and ITS region (fungi) to assess the microbial diversity. Recently, a reverse approach was also

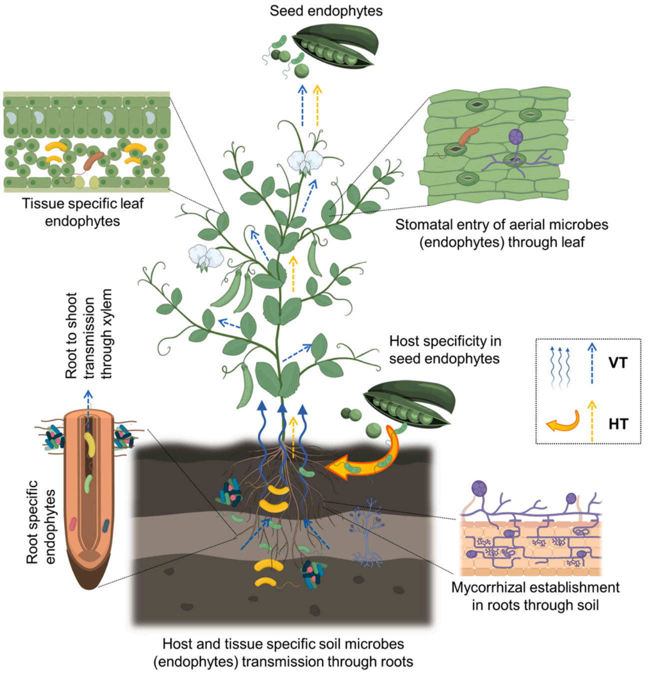

Fig. 1. Plant-endophyte interaction. Soil is the major source of specific endophytes for a specific plant (host specificity). Endophytes are present in different parts of host plant including root, stem, leaves, flower, fruit and seeds. Endophytes enters into the plant mainly from plant roots and transmit to different parts of plant through xylem [vertical transmission (VT)]. Aerial microbes (endophytes) may also enter into the host plant through stomata. Plant-tissue specificity of endophytes is an important attribute determining their plant tissue specific role. Seed endophytes have promising importance as they transmit to the next generation [horizontal transmission (HT)].

suggested for mining microbiome information from plant transcriptome data (Han et al., 2021). Metagenomics has emerged as a useful approach to study potential of uncultured endophytic microbes besides their diversity in an ecological community, evading the need for isolation and cultivation of individual isolates. In addition, comparative metagenomics can improve understanding of functional diversity of endophytes in different plant tissues and host plants. Besides, Illumina which is a short read sequencing technology, Oxford nanopore has proved to be an efficient long-read sequencing technology to generate high quality metagenome assembled genomes (Ciuffreda et al., 2021) as well as get enhanced taxonomic resolution using full length reads of informative loci domains (e.g., entire 16S rRNA) (Kerkhof, 2021).

A general view on the bacterial diversity of plants by both culture-dependent and microbiome sequencing suggests the abundance of bacteria belonging to *Proteobacteria* in the plant endosphere (Marques et al., 2015). Among *Proteobacteria*, *γ-proteobacteria* are more abundant (Hardoim et al., 2015*)* as compared to *α-* and *β-proteobacteria*. *Firmicutes*, *Actinobacteria* and *Bacteroidetes* are other abundant bacterial groups found commonly in the plant endosphere (Akinsanya et al., 2015; Furtado et al., 2019; Tian et al., 2015). Besides these, *Acidobacteria*, *Planctomycetes*, and *Verrucomicrobia* are less frequently found. In the plant's endosphere, culturable bacterial diversity has shown some of the common bacterial genera like *Pseudomonas*, *Bacillus*, *Micrococcus*, *Serratia*, *Burkholderia*, *Enterobacter*, *Rhizobium*, *Mycobacterium*, *Streptomyces*, *etc.* (Afzal et al., 2019; Liu et al., 2020; Purushotham et al., 2020). On the other side, the fungal diversity based on metagenomic sequencing of internal transcribed spacer (ITS) region suggests the dominance of Ascomycota over 95%, followed by Basidiomycota (3–4%) in the endosphere of plants (Abdelfattah et al., 2016; Furtado et al., 2019). This trend contrasts with the diversity of fungi studied in bulk forest soil, where Basidiomycota has been reported as the most abundant fungal group (Terhonen et al., 2019*)*. Culturable fungal diversity also corroborates with the culture-independent approach where the dominance of ascomycetous fungi including *Penicillium, Cladosporium, Aspergillus*, *Trichoderma*, etc. has been reported in the plant endosphere (Li et al., 2020; Silva et al., 2018; Xia et al., 2019). The dominant endophytic microbes reported in various plants have been summarized in Table 1.

2.2. *Conserved endophytic community in different crops*

Conservation of endophytic community in the specific crop has been observed representing the core microbiota of related crop. Study of microbial diversity of Kernels from populations of different teosintes (wild ancestors) and different maize varieties revealed the occurrence of core endophytic microbiota which was conserved in maize seeds across the limitations of ecology, evolution and ethnography (Johnston-Monje and Raizada, 2011). In this study, *Paenibacillus* and *Clostridium* species were found to be conserved across all *Zea* genotypes. Resilience to environmental changes and conservation of a similar group of endophytes across generations was also obtained in the rice even after recultivation in different locations (Walitang et al., 2019). In the rice seeds, few bacterial groups belonging to *Microbacterium, Enterobacter, Herbaspirillum, Xanthomonas, Curtobacterium* and *Stenotrophomonas* are reported as "core microbiota" which were conserved and dominant members of the endophytic communities (Walitang et al., 2019). Similarly, the existence of conserved endophytes belonging to *Alternaria* spp. and *Cladosporium* (Capnodiales) was found in wheat (*Triticum aestivum*) and wheat-related grasses (*Triticum dicoccoides* and *Aegilops sharonensis*) (Ofek-Lalzar et al., 2016). Vertical transmission of seed-borne bacterial endophytes from two consecutive generations in rice plants also indicated the conservation strategy of plants for associated endophytes (Hardoim et al., 2012). These studies indicate the presence of conserved endophytic communities in different crops. Common core microbiome of different crops may be explored for the improvement of multiple crops (Fig. 2).

2.3. *Factors affecting the composition of endophytic diversity in plants*

Soil is a reservoir of microorganisms and a significant source of microbial community inside the plant endosphere. The root-influenced zone of soil *i.e.*, rhizosphere, governs the diversity of root endophytes, which further can make their way as shoot endophytes. Therefore, the endophytic community inside a plant is considered as a subset of the rhizosphere communities (Marquez-Santacruz et al., 2010). Overlapping between the isolate sequences from rhizosphere and metagenomics datasets of belowground and aboveground plant parts was also observed, confirming the fact that the plants recruit bacteria from soil (Oberhofer et al., 2019). The rhizodeposits and the features associated with the host root cell wall support particular microbial population plays a critical role in initiating the soil biome community shifts. However, the root-associated bacterial microbiota is recruited from the soil, but its profile is more affected by the plant roots than by the soil or the other parts of a plant, while on the other hand, the fungal microbiota is majorly soil dependent (Tkacz et al., 2020). The type of soil used to grow a plant also governs the endophytic community composition. For instance, the same cultivar of a plant grown in different soil types can have different endophytes (Bokati et al., 2016; Rashid et al., 2012).

The origin of the host plant, its' cultivar, genotype, developmental stages, plant parts, cultivation practices, and plant health are the host-specific determinants of the endophytic community associated with a plant. Besides, the geographical location of a plant and its interaction with environmental factors, including biotic and abiotic factors, further decide the colonization of endophytes. Based on the molecular variance, it has been identified that the composition of an endophytic community is affected by the host plant species and their collection time (Ding et al., 2013; Ding and Melcher, 2016). Moreover, host-specific patterns are

Table 1

Dominant Phyla/Groups of endophytes reported in various host plants (based on 16S/ITS metagenomic sequencing).

Host Plant	Tissue	Microorganism studied	Sequencing region	Dominant Phyla/Groups (in order of decreasing abundance)	Reference
Vitis vinifera cv. Red Globe and *Vitis amurensis* cv. Shuangyou	Leaves	Fungi	ITS1	Ascomycota (62.36%), Basidiomycota (21.57%) and Zygomycota (2.10%)	(Fan et al., 2020)
Salicornia europaea L.	Root and shoot	Fungi Bacteria	ITS1 V3-V4	Ascomycota (>95%) *Proteobacteria, Bacteroidetes*	(Furtado et al., 2019)
Maple trees *(Acer campestre* and *A. platanoides*)	Leaves	Fungi Bacteria	ITS2 V6–V8	Ascomycota (95.87%), Basidiomycota (3.11%) Proteobacteria, Bacteroidetes, Deinococcus-Thermus, Actinobacteria, Firmicutes, and Patescibacteria	(Wemheuer et al., 2019)
Hybrid *Paulownia elongate* × *Paulownia fortunei*	Root and leaf	Bacteria Fungi	V3-V4 ITS-1	Proteobacteria, Bacteroidetes, Actinobacteria Ascomycota, Basidiomycota in leaves. Olpidiomycota (82.66%), Basidiomycota, and Ascomycota in roots.	(Woźniak et al., 2019)
Grapevine (*Vitis vinifera*)	Stems	Fungi	ITS1	Ascomycota (93.6%), Basidiomycota (4.2%) and Zygomycota (2.1%)	(Dissanayake et al., 2018)
Dysphania ambrosioides	Root and shoot	Fungi	ITS2	Ascomycota (62.5–79.2%) Basidiomycota (20.7–37.4%)	(Parmar et al., 2018)
Soybean	Root and Seed	Fungi	ITS1	*Fusarium* (>60%), *Rhizoctonia* (11.7%)	(Yang et al., 2018)
Cultivated Strawberry (*Fragaria x ananassa*)	Leaves, flowers, immature and mature fruits	Fungi	ITS2	Ascomycota (95.6%), Basidiomycota (3.9%)	(Abdelfattah et al., 2016)
Wheat varieties under drought stress	Leaves	Bacteria	V4	Proteobacteria, Actinobacteria, Firmicutes	(Žiarovská et al., 2020)
Sweet potato *(Ipomoea batatas)*	Tuber	Bacteria	V3–V4	Proteobacteria (85.0%), Bacteroidetes (6.6%) and Actinobacteria (6.3%)	(Puri et al., 2019)
Tomato	Root, stem, leaves, fruit parts	Bacteria	V3-V4	Proteobacteria dominant in all part except Fruit jelly. Firmicutes (73.61%) followed by Proteobacteria (22.66%) in Jelly around seeds.	(Dong et al., 2019)
	Root	Bacteria	V3-V4	Actinobacteria (48.67%), Proteobacteria (32.86%)	(Tian et al., 2015)
Distichlis spicate, Pluchea absinthioides, Gaultheria mucronata, Hieracium pilosella	Root and leaves	Bacteria	V4	Proteobacteria (14.88–68.53%), Firmicutes (26.03–41.59%), Actinobacteria (6.45–23.69%), Bacteroidetes (1.09–21.21%)	(Zhang et al., 2019)
Panax ginseng	Root	Bacteria	Shotgun metagenome	Proteobacteria, Actinobacteria	(Hong et al., 2019)
Panax notoginseng	Root, fibril, flower, leaf, and stem	Bacteria	V1	Proteobacteria, Actinobacteria, Verrucomicrobia, Bacteroidetes, Acidobacteria, Firmicutes, Gemmatimonadetes, and Chloroflexi	(Dong et al., 2018)
Dendrobium officinale	Root, stem, and leaf	Bacteria	V4	Proteobacteria (78.31%), Firmicutes (12.42%), Actinobacteria (6.48%) and Bacteroidetes (1.80%)	(Pei et al., 2017)
Aloe vera	Root, stem, and leaves	Bacteria	V3–V4	Proteobacteria, Firmicutes, Actinobacteria, Bacteriodetes	(Akinsanya et al., 2015)

observed in the selection of the most dominant bacteria groups (Ding and Melcher, 2016*)*. Interestingly, the endophytic community can also be affected by the plant growth stages, as the plant at its rich nutrient developmental stage tends to have increased microbial diversity (Shi et al., 2014). In grape, the associated fungal communities are correlated to the foliar age of plants as young leaves have higher endophytic fungal diversity and richness than mature leaves (Fan et al., 2020). A variation in microbial communities at different developmental stages of *Stevia rebaudiana* Bertoni leaves was observed by Yu et al. (2015). Authors reported the dominance of *Agrobacterium* and *Erniwia* in the seedling stage, and decline during vegetative and initial flowering stages. Whereas, *Methylobacterium* and *Sphingomonas* were found to increase in mature leaves and during harvesting time. Marques et al. (2015) suggested that the functional diversity of bacterial endophytes is influenced by the plant genotype as well as growth stages, as IAA-producing strains were dominated in one of the three genotypes of sweet potato. Similarly, a different cultivar of a plant grown in the same soil can have different endophytic inhabitants (Granér et al., 2003). According to Lundberg et al. (2012) host-genotype resulted in the enrichment of 12 OTUs as root endophytes in eight *Arabidopsis* ecotypes. Correa-Galeote et al. (2018) suggested cultivation practices as an important driver of endophytic colonization of maize. Similarly, in a study performed on four different plants including corn, tomato, pepper, and watermelon it was observed that organic and conventional farming systems can influence the fungal communities associated with plants (Xia et al., 2019). Seeds are another underestimated although an important factor that influences the endophytic communities of plants and is responsible for vertical transmission of conserved and naturally selected beneficial endophytes to the next generation of plants (Truyens et al., 2015; Walitang et al., 2019). The presence of the same endophytic microbial communities in seeds and in subsequent plant generations has been reported in several studies (Gagne-Bourgue et al., 2013; Liu et al., 2012; Ringelberg et al., 2012). Surprisingly, plant domestication has led to a shift in the microbial communities of plants from slow growing microbes such as *Bacteriodetes* on wild crop relatives or ancient cultivars (cv.) to fast growing microbes such as *Proteobacteria* in modern crop cvs. Probably, the gene pools of ancient and modern cultivars might have different potential to involve in probiotic associations with microbes in soil (Bulgarelli et al., 2013*)*. As seeds transmit domestication inspired footprints of microbial diversity, this leads to a change in the microbial composition of endophytes in subsequent modern plant generations (Berg and Raaijmakers, 2018).

Environmental and climatic factors such as light, soil temperature and pH, water and nutrient availability are also determinants of microbial communities associated with plants (Giauque and Hawkes, 2013; Murphy and Hodkinson, 2018; Penuelas et al., 2012). In case of foliar endophytic fungal diversity, which in itself considered as hyperdiverse, may be further restructured by broad scale environmental

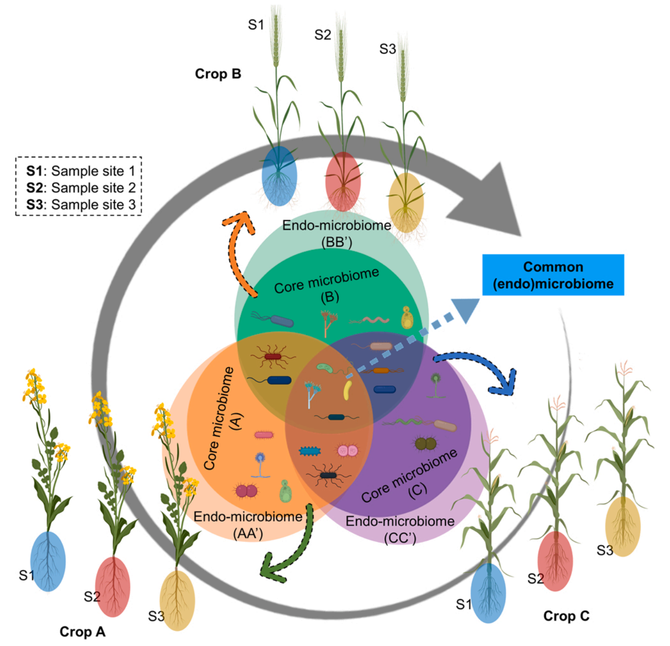

Fig. 2. Crop specificity of endophytes and core microbiome. Every crop (represented as Crop A, Crop B, Crop C) harbors crop-specific endophytic microbial community (represented as Endo-microbiome AA', BB', CC') that can be identified by analyzing the microbiome of wide samples of specific crop cultivated in different sites (sample site S1, S2, S3), represents crop specific core microbiome (A, B, C). Crop specific core microbiome can be explored for improvement of respective crop (green, orange, blue dotted arrow). Combined analysis of core microbiomes of multiple crops (A,B,C) provide the information about the common (endo)microbiome that can be used for the improvement of multiple crops.

factors such as temperature and rainfall (Whitaker et al., 2018; Zimmerman and Vitousek, 2012). However, Whitaker et al. (2018) suggested that foliar endophytes are not affected by host ecotype in *Panicum virgatum* (switchgrass). Biotic and abiotic factors can influence the endophytic communities present inside a plant. Shymanovich and Faeth (2018), concluded that differences in endophyte mediated protection against herbivores may be the major factor responsible for differences in the distribution of the two endophyte species *i.e., Epichloë alsodes* and *E. schardlii* var. *pennsylvanica* in *Poa alsodes* plant population. The presence of other plant-associated microbial communities including those with role in disease resistance and pathogens may also influence the community composition via microbe-microbe interaction (Ardanov et al., 2012; Douanla-Meli et al., 2013). A detailed review on the relationship between endophytic fungi and medicinal plants and biotic and abiotic factors affecting fungal colonization has been presented in Jia et al. (2016). Readers are further suggested to refer Terhonen et al. (2019) for a comprehensive review on forest tree species and their associated fungal endo-microbiome and the factors affecting the fungal communities.

2.4. *Host and tissue specificity in endophytes*

Endophytes present in different parts of plants including root, stem, leaves, flower, fruits and seeds. In addition, host and plant-tissue specificity has been reported in several studies (Dastogeer et al., 2018; Li et al., 2020; Pandey et al., 2016a). In opium poppy it was observed that the leaf-associated endophytes were found to be involved in improving photosynthetic efficiency of plants and capsule (which is the site for the synthesis of benzylisoquinoline alkaloids, major alkaloids present in poppy including morphine, codeine, thebaine, papaverine and noscapine) associated endophytes were involved in improving BIA production (Pandey et al., 2016a). In *Stevia rebaudiana* the endophytic community was found to be strongly regulated by the growth stage of plant and stevioside accumulation (Yu et al., 2015). The study of fungal diversity of *Nicotiana* plants from arid regions of Northern Australia indicates host specificity of associated fungal endophytes (Dastogeer et al., 2018). It was observed that there were no differences in fungal endophyte species richness or diversity as a function of geographical locations, while differences were detected among different host genotypes and parts of plants (roots, stems and leaves tissues). In addition, a significant pattern of fungal community similarity was found with host genotypes but pattern of fungal community structuring was not consistent with geographical locations and different parts of plant. Host specificity of endophytes was also found in Sycamore maple (*Acer pseudoplatanus*) and European ash (*Fraxinus excelsior*) naturally grown in north and south of the Alps (Schlegel et al., 2018). Therefore, plant tissue specificity, physiological relations, developmental regulations, host specificity and effectivity on other crops are the important factors that should be always considered for the application of an endophyte-based microbial formulation.

2.5. *Endophyte-parasitic plant-host plant interaction*

Parasitic plants grow on other plants and take nutrition from their host by making a specialized structure called the haustorium, a structural connection of phloem and xylem in the vascular system. The endophytic community associated with these plants has specific importance. Understanding the endophyte-parasitic plant-host plant interaction is very important to reveal the possibility of horizontal transfer of endophytes from one plant to another, not like soil to plant. Mycobiome studies of host plant root-parasitic plant interactions of *Cynomorium songaricum* (rare medicinal herb plant) and its host plant *Nitraria tangutorum* suggested that endophytic fungi may be exchanged between the host and parasitic plants probably through haustorium (Cui et al., 2018). It was observed that the similarity of endophytic fungal composition was higher in parasitized plants (3.88%) than in non-parasitized plants (0.10%) (Cui et al., 2018). The study of the tripartite association of an endophytic holoparasitic plant *Cytinus hypocistis*, its Cistaceae host species and associated mycorrhizae showed that the mycorrhizal fungi are associated with both host and parasitic plants and found to be spreading in the parenchyma cells (deVega et al., 2010). The endophytic bacterial exchange was also observed during parasitization of holoparasitic plants broomrapes (*Phelipanche aegyptiaca*) on host plant *Solanum lycopersicum* and the presence of endophytic *Pseudomonas* strain PhelS10, originating from the tomato roots, suppressing seed germination of *P. aegyptiaca* and reducing parasitism was also demonstrated (Iasur Kruh et al., 2017). Holoparasitic plant *Balanophora japonica* was also found to share common endophytes (*Trichoderma-Hypocrea*) with the *Symplocos lancifolia* host plant (Ikeda et al., 2016). In contrast, endophytes associated with *Santalum album* Linn. which is hemi-parasite on roots of *Kuhnia rosmarinifolia* Vent host plant was not similar to the host plant (Sun et al., 2014). Deep understanding of endophyte-parasitic plant-host plant tripartite associations including endophytes sharing, movement, and their role may lead to discovering alternative approaches that may help to escalate the output of therapeutically important medicinal plants and new weed control methods.

2.6. *Endophytes as plant probiotics*

The term "probiotic" is a combination of two Greek words, "pro" and "bios" it means "for life". The concept of probiotics probably was first suggested by Mechnikov in 1907 as bacteria may have beneficial effects on the natural intestinal microflora (Metchnikoff, 1908). The term "probiotics" was primarily defined for animals by Fuller, 1989 as "A live microbial feed supplement which beneficially affects the host animal by improving its intestinal microbial balance" (Fuller, 1989). With time, the definition of probiotics was largely modified (very well described by

Markowiak and Śliżewska, 2018). The current definition of probiotics was formulated by experts of FAO/WHO working groups, stating that the probiotics are “live microorganisms that, when administered in adequate amounts, confer a health benefit on the host” (Hill et al., 2014). The International Scientific Association for Probiotics and Prebiotics (ISAPP) recommended the use of the term “probiotic” for the products or formulations having an appropriate count of viable cells and having beneficial effects on the host’s health including growth-stimulation and functioning of the alimentary tract (Markowiak and Śliżewska, 2018). In case of plants, the presence of beneficial microbes in root nodules of leguminous plants and identification of several potential endophytes, promoting plant growth, providing stress tolerance and modulating secondary metabolism of plants increased researcher’s interest to use them as potential plant probiotics for management of plant health.

2.7. Endophytes as probiotics for plant tissue culture

In-vitro technologies are widely used for the improvement of commercially important plants, conservation of rare, endangered and threatened (RET) plant species and production of important plant-derived substances that are used as pharmaceuticals, colors, flavors, food additives, agrochemicals and biopesticides. As these technologies are associated with specific benefits such as are independent to climatic and soil conditions, production and quality of the produce can be finely controlled, having shorter growth/production cycle compare to complete plant and there is no use of land resources, therefore, these are the preferred choice for the sustainable production of plant produce. Successful propagation of tissue culture generated plants depends upon their effective hardening and field survival. Primarily poor hardening efficiency of tissue culture generated plants in the soil and greenhouse, and their acclimatization to the field conditions is the major problem restricting their use for limited plants and acceptability at a large scale. Poor hardening efficiency and acclimatization in the greenhouse/field condition restricts successful micropropagation of most of the RET plant species localized in specific environmental conditions. Apart from this, repetitive subculturing of tissue culture planting materials (micropropagated plants and suspension/callus cultures) reduce their potential to synthesize secondary metabolites (Kusari et al., 2014). It may be due to the lack of plant-associated microbes (especially endophytes) in the plant materials generated through *in-vitro* systems due to their continuous cultivation in aseptic conditions. Earlier, the endophytes were considered as contaminants in the plant tissue culture and the researcher intended to eliminate them using various sterilizing protocols. Now, it has been well established that these endophytes are very important for plant life. Therefore, these can be used as plant probiotics for the improvement of hardening, acclimatization and to boost the performance of *in-vitro* grown plants under field conditions (Soumare et al., 2021; Kanani et al., 2020; Quambusch and Winkelmann, 2018). They may also be used to maintain the *in-planta* secondary metabolite content at the natural level or even better during repetitive subculturing using different strategies (Fig. 3). Recently, Krasova et al. (2022) demonstrated the application of lipopolysaccharide and polar-flagellum flagellin of *A. brasilense* Sp7 activate the morphogenesis of explants (from immature wheat embryos) and increased the yield of regenerated plants. Bezerra et al. (2020) demonstrated that the microbes isolated from roots of *Oncidium varicosum* could improve the growth of *in-vitro* plants and improved the acclimatization in the greenhouse. Application of endophytic synthetic microbial communities (SynComs) in banana production to develop resilience against biotic and abiotic stresses and promote plant growth and yield has been also discussed (Beltran-Garcia et al., 2021).

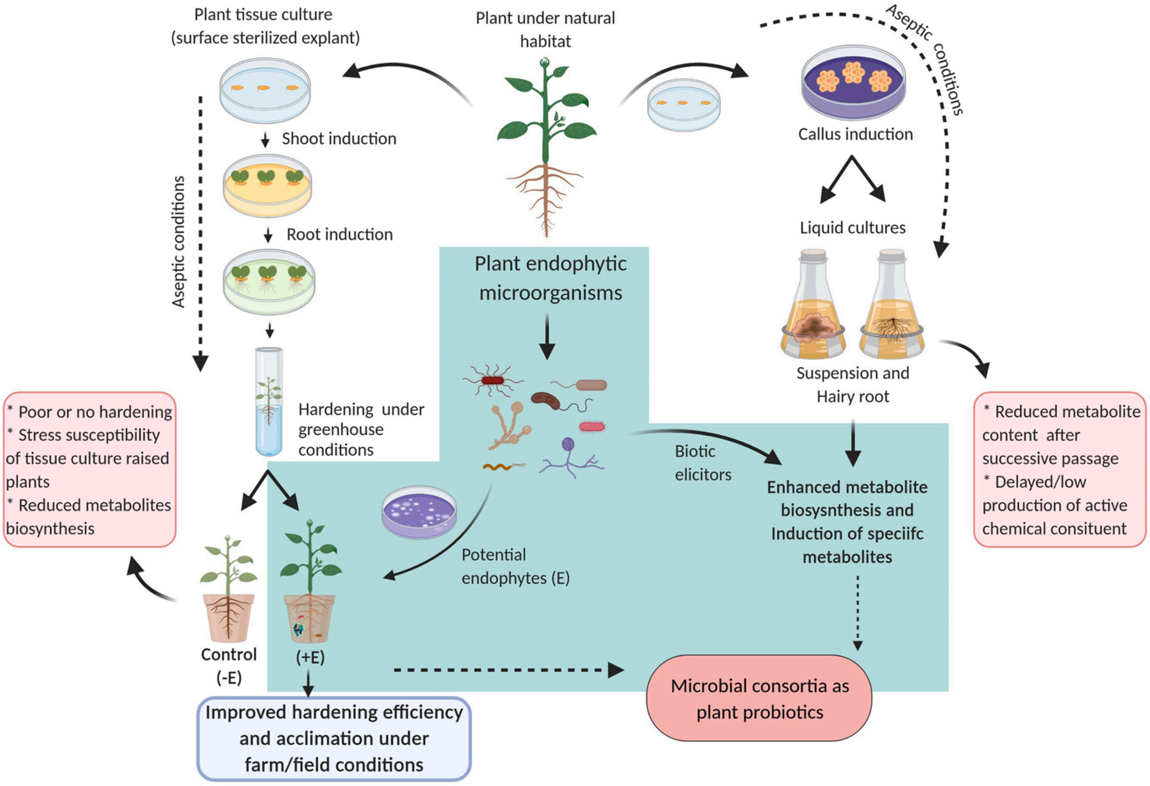

Fig. 3. Strategies for applying endophytes as probiotics in plant *in-vitro* system. Plant growing under natural habitat is the potential source of promising endophytes that can be used for *in-vitro* system of the specific host plant. As in plant *in-vitro* system, the aseptic condition is maintained, causing loss of essential microbes, which results in poor hardening efficiency, stress susceptibility, and reduced secondary metabolites content of *in-vitro* generated planting materials, therefore, supplementation with the potential endophytes at the time of hardening may improve hardening efficiency and acclimation of *in-vitro* generated plants under farm/field condition. Potential endophytes can also be used as biotic elicitor to enhance the production of specific metabolites in hairy roots/callus/suspension culture.

2.8. Endophytes as effective biotic elicitors

Elicitation using elicitors is a widely accepted and most effective strategy to induce plant defense response for providing resistance to biotic stress, tolerance to abiotic stress and enhancing the production of important secondary metabolites. (Martínez-Ballesta et al., 2008; Schreiner, 2006). Primarily various abiotic and biotic elicitors including methyl jasmonate, salicylic acid, 2,4-dichlorophenoxyacetic acid, benzyl adenine, α-naphthalene acetic acid, vanadyl sulphate, casein hydrolysate, chitosan and yeast extract are used for enhancing the production of important secondary metabolites in *in-vitro* plant cultures. Various studies demonstrated the effectiveness of endophytes-based elicitors to increase the production of secondary metabolites. Endophytes have been also used for eliciting induced systemic resistance in different plants leading to reduced disease severity (Kloepper and Ryu, 2006; Fontana et al., 2021; Sujatha et al., 2021). Almost seven-time enhancement in taxol production was obtained in *Taxus chinensis* cell suspension culture by elicitation using *Aspergillus niger*, an endophytic fungus associated with the inner bark of *Taxus chinensis* (Wang et al., 2001). Application of elicitors from *Trichoderma atroviride* D16 (an endophytic fungus associated with the root of *Salvia miltiorrhiza*) could promote the growth of hairy root and induce the tanshinones biosynthesis in the hairy root cultures of *S. miltiorrhiza* (Ming et al., 2013). Cell extracts of fungal endophytes *Chaetomium globosum* YEF20 (isolated from *Taxus baccata*) and *Paraconiothyrium brasiliense* HEF114 and *Camarosporomyces flavigenus* HEF17 (isolated from *Corylus avellana*) could enhance paclitaxel production in *C. avellana* cell suspension culture (Salehi et al., 2019, 2020a, 2020b). Application of hallotolerant endophytes (*Periconia macrospinosa* and *Neocamarosporium* sp.) isolated from desert plants could induce tolerance to drought and salinity stress in cucumber and tomato plants (Moghaddam et al., 2021). Similarly, the application of polysaccharide from an endophyte *Bionectria* sp. Fat6 as a biotic elicitor on *Fagopyrum tataricum* (Tartary buckwheat) could enhance photosynthesis, improve plant biomass and protect plants from drought stress (Xiang et al., 2021). Therefore, a combination of multiple endophytes may be used as a universal elicitor for enhancing the production of various bioactive secondary metabolites associated with different plants.

2.9. Endophytic-consortium: substitute of transgenic coexpressing multiple genes

A single endophyte does not have all the desired characteristics (like PGP attributes, antimicrobial productions, induction of plant defense response etc.) required for enhancing crop yield, protection of plants from environmental stresses and increased secondary metabolite production. Moreover, the poor performance of single strain inoculation in the field conditions and under different geographical locations also limits their use (Compant et al., 2019). Therefore, the combination of different endophytes with multiple traits, either complementing each other to combine different traits/mechanisms is essential for obtaining different/multiple effects such as plant growth improvement, enhancement of secondary metabolite production, tolerance to abiotic stress and biocontrol of pathogens. Endophyte consortia may also comprise strains showing the same mode of action but tolerating different environmental conditions or having compatibility to different plant genotypes. It has been also observed that the combinations of bacteria showing no or little plant growth promoting (PGP) effects as single inoculants showed improved PGP effects in the consortium form. Therefore, consortium application is a more promising approach compared to single strain application in the field conditions (de Vrieze et al., 2018; Parnell et al., 2016).

Endophytes have been found to affect the host metabolism at the gene expression level (Pandey et al., 2016a, 2016b; Pandey et al., 2018). It has been also observed that different endophytes target different steps of a biosynthetic pathway or have a different mode of action resulting in the desired effect (Pandey et al., 2016a; Ray et al., 2019). Therefore, different endophytes with different modes/mechanisms of action could be combined to obtain the desired effect by complimenting the inability of one endophyte by another endophyte to upregulate certain genes and finally leading to upregulation of all/most of the genes of a biosynthetic pathway resulting enhanced biosynthesis of secondary metabolites (Ray et al., 2019). These consortia of endophytes may be used as a better alternative in place of transgenic plants (overexpressing/coexpressing multiple genes) and also could be explored for the generation of designer plants. Several studies have demonstrated the effect of inoculation of different endophytes on various cellular components/targets in different plants resulting different effects (Ray et al., 2019; Pandey et al., 2018, 2016b; Ganie et al., 2021). In opium poppy application of a consortium of endophytes (upregulating different genes involved in morphine biosynthesis) is well established to maximize the production of the therapeutic compound morphine (Ray et al., 2019). Consortium of two endophytes *Acinetobacter* sp. SM1B [upregulating most of the genes of morphine biosynthesis except thebaine 6-O-demethylase (T6ODM) and codeine O-demethylase (CODM)] and *Marmoricola* sp. SM3B (upregulating T6ODM and CODM) could increase the plant yield and morphine content by upregulating pertinent benzylisoquinoline alkaloid biosynthetic genes compared to individual inoculation (Ray et al., 2019). Differential expression of genes involved in withanolide biosynthesis in leaves and roots tissues of *Withania somnifera* inoculated with different endophytes has been demonstrated and induction of the biosynthesis of withaferin A in roots (which is generally absent in roots) was observed (Pandey et al., 2018). In *Artemisia annua* application of consortium of four endophytes (*Bacillus subtilis*, *Bacillus licheniformis*, *Acinetobacter pittii* and *Burkholderia* sp.) could significantly enhanced the artemisinin yield than the monoculture inoculation (Tripathi et al., 2020). Using the consortium of different endophytes, the plant yield as well as the yield of different secondary metabolites (vindoline, vinblastine and vincristine) could be enhanced in various cultivars of *Catharanthus roseus* in two different seasons (Singh et al., 2021). Endophytes modulating the expression of transcriptional activators and repressors of terpenoid indole alkaloids biosynthesis genes have been also found in *C. roseus* (Pandey et al., 2016b). Using genome mining and gene expression studies on *Gymnosporia heterophylla* plant, it has been found that the consortium of seven endophytes is involve in the biosynthesis of maytansine which is a potential antifungal and anticancer drug used in the treatment of breast cancer (Pitakbut et al., 2022). Recently, Ganie et al., 2021, nicely reviewed the application of endophytes (including their consortium) for providing tolerance to biotic and abiotic stress to rice plants, and different endophytes targeting multiple cellular components for providing stress tolerance to rice plants is well discussed. Therefore, application of consortium of endophytes having different strategies for yield improvement and stress tolerance will be the most appropriate approach for maximizing the plant performance under field conditions. Occasionally, some microbial consortia have also been shown to diminish the plant growth promoting effects as compared to single strain inoculants indicating that a high-throughput, smart and knowledge-driven selection of effective consortia and potential strains is very essential (de Vrieze et al., 2018; Herrera Paredes et al., 2018; Rolli et al., 2015). Therefore, it is important to understand the thorough mechanism of action of potential endophytic microbes, and then a combined approach should be tested for attaining utmost yields.

3. Plant endophytic vs animal gut flora

Conspicuous similarities among animals and plants related to microbial associations distinctly point towards the importance of endophytes as probiotics for a plant similar to probiotics in animals. Plants roots have functional similarities to the animal gut. As in animals, the gut is involved in nutrient breakdown and absorption; similarly, in plants, roots are involved in nutrient absorption from the soil. Besides, spatial heterogeneity in microbial density and diversity along with organelle specific compartmentalization is also associated with both animal gut and plant roots (Hacquard et al., 2015). In the gut of animals there is a spatial heterogeneity in the microbial density in which the stomach and duodenum (proximal small intestine) have lowest microbial density that increases along the length of small intestine (the distal ileum). Large intestine harbors highest microbial density. Besides spatial heterogeneity along the digestive tract there is existence of compartmentalization in the intestinal tube as epithelial surface, mucus and lumen, and decrease in density observed from lumen to the epithelial surface (Hacquard et al., 2015). Similarly, in plants microbial heterogeneity and compartmentalization exist. In the plant root-soil-microbe tripartite interaction four types of compartment are distinct which are represented as soil, rhizosphere, rhizoplane and endosphere. Along the different compartments the microbial density changes and soil shows highest microbial density (Hacquard et al., 2015). There are commonalities among gut and plant microbiota, especially root microbiota. As in the gut, which harbors a large group of microbes that are involved in nutrient uptake, modulation of host genes expression, and protection from pathogens, similarly, in plants roots, diverse groups of microbes are associated engaged in similar type of functions (Ramírez-Puebla et al., 2013). Similar to animals gut microbiota, the plant root microbiota is involved in degradation/modifications of nutrients resulting efficient nutrient uptake and utilization, modulation of plant host gene expression of primary and secondary metabolism providing protection from pathogens and tolerance to environmental stress (Ramírez-Puebla et al., 2013). As gut microbiota varied with age, diet and species of host, similarly in plants, the microbial community is found to be dependent on developmental stage, soil health (which is the source of diet for a plant) and host type (as host specificity is found with associated-endophytes). Pathogen infection leads to a change in microbiota in both animal gut and plants. Ramakrishnan et al., 2021 described the application of pesticides in agriculture practices affect both plant rhizosphere and animal gut flora. As in animals, the use of antibiotics causes a deleterious effect on the gut microflora and affect animal health (Ribeiro et al., 2020); similarly, in plants, continuous reduction in the content of secondary metabolites in *in-vitro* (plant tissue culture) generated-plant grown on aseptic conditions also indicate the importance of endophytes for plant life and especially secondary metabolite biosynthesis.

4. Seed-associated endophytes: future potential plant probiotics

Various endophytes have been found to be associated with different parts of the plant including root, stem, leaves, flower, fruits and seeds. Several studies demonstrated that a diverse endophytic community is associated with seeds having several important features (Shahzad et al., 2018). Thus, these microbes have great potential to be used as the most effective candidates for the development of plant probiotics. It is also due to the involvement of seed in two very crucial phases of plant life including endpoint (seed maturation) and the starting point (seed germination) of life; therefore, associated microbial communities in these two phases have high potential for selecting the promising candidates for plant life (Bintarti et al., 2022). Despite this, seeds also remain in a torpid state for a long time until the optimum conditions obtain for germination and plant development (Geisen et al., 2017; Nelson, 2004). Additionally, most of the seed endophytes are able to produce endospores which protect them from changing conditions inside the seed during seed maturation and seed germination stage. Therefore, endophytes associated with seed have the potential to sustain in harsh environmental conditions. Seed endophytes are also become important due to their vertical transmission to the next generation (Cope-Selby et al., 2017; Shade et al., 2017). Vertical transmission to successive generation of these endophytes reduces their pathogenicity, support proliferation and maintain plant health and useful endosymbiont (Rudgers et al., 2009; Shade et al., 2017). Seed endophytes are also found to produce different phytohormones (modulating phytohormones status of host plant) (Shahzad et al., 2016), important enzymes, antimicrobial compounds and secondary metabolites. They are also found to improve seed germination, plant growth and protection from biotic and abiotic stress (Chee-Sanford et al., 2006; Rodríguez et al., 2018; Santoyo et al., 2016; Shahzad et al., 2017a, 2017b; Shearin et al., 2018). Seeds are the reservoirs for endophytic microbiota and act as a vehicle or carrier for their transmission to successive generations (Baker and Smith, 1966; Nelson, 2004). A rice seed endophyte *Sphingomonas melonis* was found to be responsible for disease-resistance via production of anthranilic acid which hamper the biosynthesis of virulence factor by interfering with the sigma factor RpoS of *Burkholderia plantarii* pathogen (Matsumoto et al., 2021). Treatment of endophytes associated with maize seeds could improve the plant growth and provide tolerance to drought stress (Siddique et al., 2022). Endophytes associated with seed of *Brassica oleracea* are able to improve seed germination and seedling development by producing volatile organic compounds (VOCs) (Tyc et al., 2020). Besides the conservation of seed associated endophytes through generation has been also established. A recent study by Morales Moreira et al. (2021) demonstrated that the few genera such as *Cutibacterium*, *Sphingomonas Methylobacterium*, *Tepidimonas* and *Streptococcus* are associated with seed of *Lens culinaris* which are preserved and transmitted through seeds to next generation. These microbes are independent to genotypes and soil types in which the crop is grown, offering promising way to select microbial communities to develop more resilient and yielding cultivars under future breeding programs. Therefore, endophytes associated with seeds have massive potential as promising candidates for development of plants probiotic and needs to be highly explored (Fig. 4).

5. Endophytes as probiotics for animals

Animal health depends on their diet which is obtained from animals and plant sources. Plants, which are used as vegetal diet, provides not only fibers, vitamins, minerals, essential amino acids and metabolites but also the important microbes maintaining animal gut flora. It has been observed that the gut microbiota of herbivores consists specific microbes that are common plant-associated microbes (Martínez-Romero et al., 2021). These plant microbes may have specific features like ability to degrade plant fibers, production of specific metabolites and enzymes having health-beneficial activities. *Lactobacillus plantarum* which is present in plants, intestinal tract of animals and fermented food is used as a probiotic (Martínez-Romero et al., 2021). Similarly, the *Clostridium* which is an endophyte is also present in animal gut and it has cellulose degradation capability due to having Cellulosomes. Endophytes associated with gut microbiota may have specific features like production of important enzymes such as cellulases, xylanases, pectinases, proteases, tannases, nitrogenases that may have biotechnological applications. Plant-associated microbes play an important role in maintaining human gut flora as plant-based diet feed beneficial bacteria (diet-borne bacteria) in the human digestive tract. It has been observed that the largest microbial diversity was exhibited by herbivores. This might be due to the survival of plant-associated endophytic bacteria being present inside the plant tissues from digestion in the stomach (Hong et al., 2011; Ley et al., 2008; Ramírez-Puebla et al., 2013). It has been also suggested that the ability of endophytes to produce phytohormones plays important roles in maintaining the animal-microbiota relationships and impacting animal health (Chanclud and Lacombe, 2017). Therefore, it is important to use those endophytes as probiotics that benefit both plants and animals.

6. Limitations for using endophytes as plant probiotics and future approach

Multiple aspects need to be considered for the development and application of endophyte-based formulation in agriculture. It is very important to understand the complexity and ecological behavior of endophytic microbiota. In most cases, the potential endophytic strains

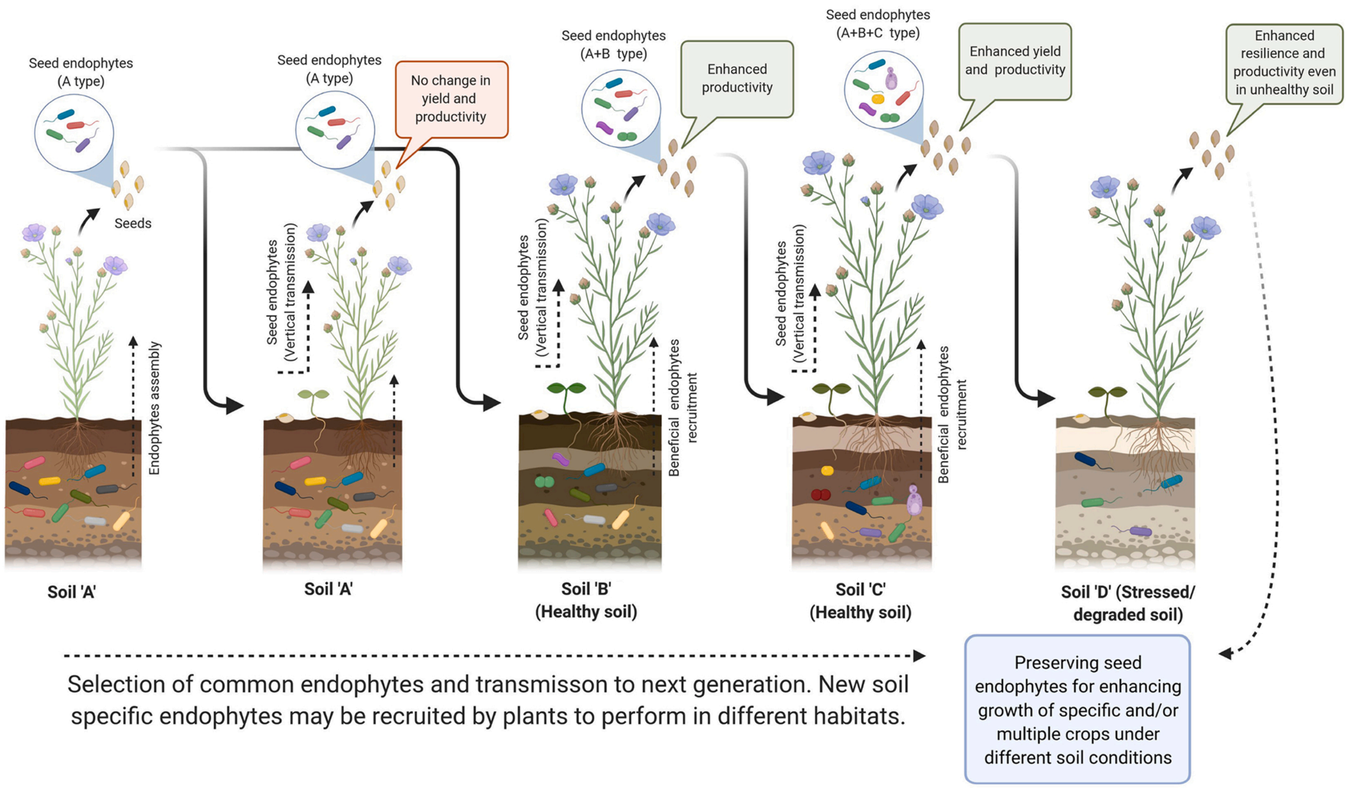

Fig. 4. Seeds as a source of potential endophytes. Seeds are the source of specific endophytes that are vertically transmitted to the next generation. The type of soil determines the seed-endophytic community. Cultivation of seeds in healthy soil (here represented as Soil 'B' and 'C') provides an opportunity for the recruitment of valuable endophytes (responsible for enhanced yield and plant productivity) into the seeds, this results establishment of a more efficient endophytic community (here represented as A+B & A+B+C type). These seeds may show enhanced resilience and productivity under stressed/degraded soil.

are screened for the desired characteristic (such as plant growth promoting, secondary metabolite enhancing, disease protection) in laboratory conditions followed by their efficacy check in the greenhouse condition. In these testing steps, selected microbes show significant effects, whereas under field conditions they show inconsistent effect. This indicates the significant involvement of several factors affecting the potency of tested microbes. Major challenges that need to be considered include successful colonization of applied endophytes into the targeted plants (especially to the targeted plant parts) and expression of specific characteristics/effects of endophytes mediated desired effect in the targeted plant. Presence of a large number of diverse microorganisms in the soil, where a particular plant is cultivated and the endophytes treatment has to be applied also limits the efficacy of endophyte-treatment. It may require the application of appropriate numbers of efficient endophytic microbial cells to make successful colonization into the host plant. To achieve this, a suitable carrier should be used to protect the endophytes from adverse environmental conditions including biotic and abiotic stresses. Few endophytes such as endospore-producing *Bacillus* are better candidates for the formulation development as they are resistant to adverse environmental conditions. However, gram-negative microbes are sensitive and need appropriate carrier and mode of application to achieve the best efficacy. Due to physiological adaptation in rich media and laboratory conditions of efficient endophytes (as they scale up in these conditions) reduce their competitive ability and limit their establishment. The rhizospheric environment contain root exudates and other metabolites acting as signals and nutrient source for the attraction of microbes. Attracting microbes have to cope with several unfavorable factors and conditions including competitive microbes and soil conditions (pH, oxygen availability) limiting the successful establishment of colonization of applied endophytic microbes to a particular host plant. Few endophytic microbes are host-specific and some have wide host range specificity while some may colonize in a specific niche. Synergistic or antagonistic activities of resident soil microbes with the applied endophytes also substantially affect the efficacy of the endophyte application. As several microbes are pathogenic, therefore, the application of endophytic microbes is also a concern for their pathogenicity and risk for environmental safety. The presence of a high cell number of particular endophytic strains in a formulation, its safety becomes very important. Regulatory approval of applied endophytes is also a major concern for the development and application of endophyte-based formulations. Use of microbes which are under the category of "generally considered as safe" e.g., Rhizobia do not require rigorous safety assessment before approval as these microbes have a long record of the harmless application. While in many countries, the regulatory approval of the applied microbes takes a long time due to the obligatory requirement of rigorous testing of efficacy and safety. On the other hand, regulatory approval of microbe-based products and their marketing is easier, faster and cheaper than the approval of chemical and genetically engineered products.

Our strategy for using microbial-based products is potently determined by the understanding of the application of synthetic chemicals as fertilizers and plant protecting agents. Hence the microbial products are generally developed as liquid formulations for efficient foliar applications as spraying. Other modes of application are in the form of seed coatings, pellets, powder and granules. In spite of this, the handling skills of the farmer and the availability of the facility for storage and application of microbial products to the farmer are also key determinants for the successful applicability and their efficacy depends on the viability of applied cells.

Now, a considerable amount of information is available to understand the plant-endophyte interaction and this can be used to develop the novel technology by mimicking the natural plant-endophyte interaction. The use of seed as a carrier of beneficial endophytic microbes is also a promising approach as endophytes may protect themselves in the seed and remain escaped from harsh environmental conditions, especially in the soil. This can be achieved by introducing potential endophytes into the seed at the time of flowering and seed development (by spraying at the flower) and these microbes may be vertically transmitted to the next generation of plants. Applied endophytic microbes via seed can efficiently colonize in the next generation plant at the early stage of plant development especially at seed germination, shoot and root initiation stages. Metagenome study revealed the importance of plant-microbiome association in plant phenotypic traits. Now the plant-microbiome and machine learning approach can be combined to predict crop productivity (Chang et al., 2017). It is well established that the soil is the source of endophytic microbiota, therefore, various agriculture practices also affect the endophytic microbiota. In addition, endophytic microbiota also depends on the genotype of the plant. Considering these facts, smart agricultural management and cropping practices can be applied to shape or engineer the endophytic microbiota of a particular crop for maximizing the yield.

7. Utilizing genomic approaches to explore bioactive potential of endophytes

Endophytes are considered as potential source of bioactive secondary metabolites. Their association with plant may results in the regulation of plant metabolism by harbour genetic pathways responsible for bioactive metabolite production, some of them are even similar to those in host (Ezeobiora et al., 2021; Bielecka et al., 2022). Bioactivity of many endophytic microbes remains obstructed by their un-cultivability. However, modern meta-genomics approaches can sequence uncultured endophytic communities and provide the knowledge beyond just the genomic information. Identification of endophytic genetic networks through genomics approach can also be used to establish plant-endophyte relationship in a more wholistic way (del Carmen Orozco-Mosqueda and Santoyo, 2021).

Whole genome analysis of isolated endophytes provides many ways to understand the interaction with the host plant with individual endophyte by revealing the genetic information required for endophytic colonization, and plant growth and metabolism e.g., genes for phytohormone, secondary metabolite, and antimicrobials production, mineral acquisition, and stress tolerance (Mardanov et al., 2019; Ulrich et al., 2021; Zou et al., 2021). For instance, genome sequencing of endophytic *Penicillium aurantiogriseum* revealed potential genes (phenylalanine aminomutase, geranylgeranyl diphosphate synthase, five taxane hydroxylases) involved in taxol biosynthesis by comparing with the biosynthetic genes of *Corylus avellana* (Yang et al., 2014). Similarly, endophyte *Serendipita indica* widely used in the studies on plant-microbe interactions exhibits a unique ability to biosynthesize an antifungal sesquiterpene, viridiflorol. The genome investigation of *S. indica* leads to the discovery of fungal originated terpenoid synthase gene (Ntana et al., 2021). Shotgun metagenome analysis of bacterial endophytes at different plant ages revealed that siderophore and auxin-related plant growth promoting traits are highly represented in 3-year-old plants of *Panax ginseng* (Hong et al., 2019).

Table 2

Bioactive potential of endophytic microbes identified using genomic approaches.

Endophyte	Host plant	Compounds	Activity	Genomic approach	Putative gene clusters	References
Undifilum oxytropis	*Oxytropis* spp.	Swainsonine	Immunomodulator and active chemotherapy drug	WGS (Illumina HiSeq 2000)	Saccharopine dehydrogenase, Saccharopine oxidase, Pyrroline-5-carboxylate reductase, Polyketide synthase	Lu et al., (2016)
Cyanodermella asteris	*Aster tataricus*	Skyrin	Anticancerous	WGS (Illumina MiSeq)	Atrochrysone dehydratase, 2 atrochrysone carboxylic acid dehydrogenases, ACA- synthase	Jahn et al., (2017)
Pseudofusicoccum stromaticum	*Myracrodruon urundeuva*	Rotenoids, Rotenolone, Tephrosin	Antiproliferative	WGS (Illumina MiSeq)	Chalcone isomerase-like protein	Sobreira et al., (2018)
Cyanodermella asteris	*Astaris tataricus*	Astins	Antitumorous	Illumina MiSeq	Astin synthase, Aminomutase, Astin transporter	Schafhauser et al., (2019)
Enterobacter hormaechei	*Pellaea calomelanos*	NA	Plant growth promotion	Illumina MiSeq v3	Phytohormone production, Nitrogen fixation, Transcription factor regulators	Tshishonga et al., (2019)
Serendipita indica	*Lycopersicum esculentum*	Viridifloral	Anti-mycobacterial and Anti-inflammatory	WGS; Genome mining	Terpenoid synthase	Ntana et al. (2021)
Aspergillus spp.	*Ginkgo biloba*	Terpenoids, Alkaloids, Polyphenols, Flavonoids	Hepatoprotectant, Antioxidant and Anti- inflammatory activity	PacBio Sequel system and BGISEQ-500	Phosphomevalonate kinase, hydroxymethylglutaryl-CoA synthase Tryptophan decarboxylase, Primary-amine oxidase Cinnamate 4-hydroxylase, O-hydroxycinnamoyltransferase, Cinnamyl-alcohol dehydrogenase Dihydroflavonol 4-reductase, Dnthocyanidin synthase, Anthocyanidin reductase	Zou et al. (2021)
Alternaria sp.	*Vitis vinifera*	Resveratrol, Pterostilbene and Piceatannol	Antimutagen, anti-inflammatory, anticarcinogen, antidiabetic, antiarrhythmic	de novo RNA-seq (Illumina HiSeq 2500)	Phenylalanine ammonia-lyase, 4-coumarate coenzyme A ligase 20 genes in glycolysis and 10 genes for phenylalanine biosynthesis, Chalcone synthase	Che et al. (2016)
Xylaria sp.	*Campotheca acuminata*	10-Hydroxycamptothecin	Anticancerous	RNA-seq (Illumina HiSeq 2000)	3-hydroxy-3-methylglutaryl coenzyme A reductase, Acetyl-CoA C-Acetyltransferase, Geranylgeranyl pyrophosphate synthase	Ding et al., (2017)
Cladosporium Cladosporioides	*Taxus media*	Paclitaxel	Antileukamic, antitumorous, antibacterial	de novo RNA-seq (Illumina HiSeq 2500)	Taxadiene 5-alpha-hydroxylase, Taxane 13-alpha-hydroxylase, Taxadiene synthase, 2-alpha-hydroxytaxane 2-*O*-benzoyltransferase	Miao et al. (2018)

Besides genome sequencing, transcriptome analysis, is also useful in the discovery of new genes and to understand their regulation (Che et al., 2016). The transcriptome of an endophyte *Cladosporium cladosporioides* indicated 40 unigenes which were related to paclitaxel biosynthesis (taxadiene synthase, taxadiene 5-alphahydroxylase, 2-alpha-hydroxytaxane 2-O-benzoyltransferase) and were homologous to the genes of host plant, *Taxus media* (Miao et al., 2018). Understanding metabolic potential and advantageous attributes of endophytes are very important to exploit their contribution to the host plant. Modern development in the -omics approaches are changing the way to look out the endophyte potential which was unexplored until earlier. A brief summary of genomic tools driven discovery of bioactive metabolites in endophytes are presented in Table 2.

8. Commercially available endophytes-based products

Use of *Epichloë* endophytes in grassland farming system in Australia, New Zealand, USA and some parts of South America is an excellent example of application of endophyte-based products (Johnson and Caradus, 2019; Glare and O'Callaghan 2019). A endophyte based product named as BioEnsure, developed by Adaptive Symbiotic Technologies (Seattle, Washington, US) has been approved by the US Food and Drug Administration and Department of Agriculture (Jones, 2013). Application of BioEnsure on rice and maize produced ~85% increased yield during drought season and 2–5 times increased seed germination rate during cold seasons. It was also observed that BioEnsure treatment could result in decreased (25–50%) water consumption (Jones, 2013). Now this endophyte-based product is being used on several crops and other countries also. Similarly, another endophyte based product Rootonic, (a mixture of endophyte *Piriformospora indica* biomass and magnesium sulphate) has been found to be effective for about 150 plants including Bryophytes, Pteridophytes, Gymnosperm and Angiosperm (Shrivastava and Varma, 2014). Biotelliga Ltd (Auckland, New Zealand), Grasslanz Technology Ltd (New Zealand), Intrinsyx Bio(US), Adaptive Symbiotic Technologies (US) and Agricom (New Zealand) are the leading companies which are involve in developing the endophytes-based products (Table 3). NEA2, NEA4 and NEA are the important endophytes that are being successfully used for the ryegrass cultivation in New Zealand. Similarly, various novel endophytes (such as AR1™ and AR37™ for ryegrass and MaxQ for tall fescue cultivation) producing insecticidal bioactives controlling aphids, beetles and weevils have been commercialized and are being used in huge grassland areas of New Zealand, South America, USA and Australia (Glare and O'Callaghan 2019).

9. Conclusion

Endophytes have a promising future in development of sustainable agriculture system. Microbial diversity studies revealed the presence of ubiquitous group of endophytic microbes associated with different plants with conserved endophytic community as a core microbiota in different crops. Significant involvement of endophytes in primary metabolism, secondary metabolism, plant health and protection from environmental stress is also well established. Like animals' probiotics, plant endophytes seem to have great potential as plants probiotics. However, the sessile nature of plants in the soil, endophytes have to confront with varying environmental conditions. Numerous factors like physiological activity, biotic and abiotic conditions, community composition, host range, compatibility with the target plant, interaction with native microbiota, root exudates and other metabolites, pH, oxygen availability, suitable formulations, antagonistic or synergistic effects, the appropriate number of active cells, delivery approaches, physiological adaptation are to be considered for any product development using endophytes.

Table 3
List of commercially available endophytes-based products.

Product Name	Manufacturing Company	Properties
BioEnsure®	Adaptive Symbiotic Technologies, WA, US	Liquid fugal inoculant, applicable directly to seed, in-furrow, or as a foliar spray, compatible with common chemicals and other biologicals, provide protection from the abiotic stresses (Drought, hot and cold temperature extremes), increase nutrient-use-efficiency, yield and yield quality, registered for sale throughout the United States, as well as being available in India, Argentina and Australia, applicable to multiple crops (Alfalfa, Canola, Corn, Cotton, Pasture grass, Legume sees, Rice, Soybean)
BioEnsure®FP	Adaptive Symbiotic Technologies, WA, US	Flowable powder based fungal inoculant based of microbes of BioEnsure®, therefore give similar effect as BioEnsure®
BioTango™	Adaptive Symbiotic Technologies, WA, US	Bacterial inoculant powder, synergize with the nutrient use efficiency provided by BioEnsure® and BioEnsureFP™. Increase plant nutrition, plant biomass, yield and yield quality, show earlier crop emergence, reduce soil compaction and better water retention. Solubilizes soil minerals such as phosphorous, potassium and other micronutrients. Having the ability to fix atmospheric nitrogen. Applicable to multiple crops (Alfalfa, Barley, Canola, Corn, Cotton, Rice, Soybean, Wheat)
BioIQ®	Adaptive Symbiotic Technologies, WA, US	Powder formulation (having microbes of BioEnsure® and BioTango™) can be applied directly to dry seed, compatible with common chemicals, fertilizers and other biologicals, provide tolerance to extreme temperatures and drought, increases nutrient use efficiency and nutrient availability. Increase crop yield & yield quality, improve seed germination, enhance seedling growth and development.
AR37	AgResearch Ltd, New Zealand	It is a novel endophyte that produces none of the alkaloids found in other commercially available endophytes that used in ryegrass. It produces a unique type of alkaloid (epoxy-janthitrems), which has never been found in any other ryegrass/endophyte combination. AR37 has resistance to more pasture insects than any other ryegrass endophyte commercially available including: Black beetle adults, Pasture mealy bug, Root aphid, Porina, Argentine stem weevil larvae
AR1	AgResearch Ltd, New Zealand	Where insect pressures are low, ryegrass with AR1 endophyte is an excellent option for animal health and production. It is non-toxic to livestock, and will give ryegrass protection against Argentine stem weevil and pasture mealybug, but only limited protection from black beetle and no protection from other pasture pests.

(*continued on next page*)

Table 3 (*continued*)

Product Name	Manufacturing Company	Properties
NEA,NEA2, NEA4	Barenbrug Agriseeds, New Zealand	Intermediate to AR1 and AR37. Provide better animal health than AR37, with very low risk of them causing ryegrass staggers, but provide broader insect control than AR1.
Avanex	Grasslanz Technology Limited, New Zealand	A natural fungus (endophyte) that lives in grass and produces chemicals that make birds feel sick when ingested, but does not harm them. This endophytic grass also reduces insect numbers, thus making the area less attractive to insect-feeding birds. The birds are deterred from flocking in those grassed areas, and it has been effective in reducing bird numbers at several New Zealand airports thus minimising the risk of bird collisions with aircraft. It has a potential for use in airports around the world, as well as orchards and golf courses, in temperate environments.
MaxQ®	Grasslanz Technology Ltd., Palmerston North, New Zealand	Also known as MaxP in Australia and New Zealand. Commercialized in the United States by Pennington Seed Co., Madison, GA in the Jesup cultivar after extensive research by the University of Georgia in collaboration with AgResearch.

Declaration of Competing Interest

The authors declare no conflicts of interest.

Acknowledgements

The Council of Scientific and Industrial Research (CSIR), India [MLP-0171 (FBR-Endophytes Network Project MLP-0048)], Department of Science and Technology, India [GAP-0269 (SRG/2020/001524)] and National Medicinal Plants Board, India [GAP-0274 (Z.18017/187/CSS/R&D/HP-02/2020-21-NMPB-IV A)] financially supported this study. Rahul Jain acknowledges CSIR, India for awarding financial support in the form of CSIR- Nehru Postdoctoral fellowship (Award no. 31/N-PDF/54(1)/2019-EMR-I). This manuscript represents CSIR-IHBT communication number 4973.

References

Abdelfattah, A., Wisniewski, M., Li Destri Nicosia, M.G., Cacciola, S.O., Schena, L., 2016. Metagenomic analysis of fungal diversity on strawberry plants and the effect of management practices on the fungal community structure of aerial organs. PLoS One 11 (8), e0160470. https://doi.org/10.1371/journal.pone.0160470.

Afzal, I., Shinwari, Z.K., Sikandar, S., Shahzad, S., 2019. Plant beneficial endophytic bacteria: mechanisms, diversity, host range and genetic determinants. Microbiol. Res. 221, 36–49. https://doi.org/10.1016/j.micres.2019.02.001.

Akinsanya, M.A., Goh, J.K., Lim, S.P., Ting, A.S.Y., 2015. Metagenomics study of endophytic bacteria in *Aloe vera* using next-generation technology. Genom. Data. 6, 159–163. https://doi.org/10.1016/j.gdata.2015.09.004.

Ardanov, P., Sessitsch, A., Häggman, H., Kozyrovska, N. and Pirttilä, A.M., 2012. Methylobacterium-induced endophyte community changes correspond with protection of plants against pathogen attack. https://doi.org/10.1371/journal.pone.0046802.

Baker, K.F., Smith, S.H., 1966. Dynamics of seed transmission of plant pathogens. Annu. Rev. Phytopathol. 4 (1), 311–332. https://doi.org/10.1146/annurev.py.04.090166.001523.

de Bary, A., 1866. Morphologie und physiologie der pilze, flechten und myxomyceten. Engelmann.

Beltran-Garcia, M.J., Martinez-Rodriguez, A., Olmos-Arriaga, I., Valdez-Salas, B., Chavez-Castrillon, Y.Y., Di Mascio, P., White, J.F., 2021. Probiotic endophytes for more sustainable banana production. Microorganisms 9 (9), 1805. https://doi.org/10.3390/microorganisms9091805.

Berg, G., Raaijmakers, J.M., 2018. Saving seed microbiomes. ISME J. 12 (5), 1167–1170. https://doi.org/10.1038/s41396-017-0028-2.

Bezerra, G.A., Gabriel, A.V.M.D., Mariano, E.D., Cardoso, J.C., 2020. In vitro culture and greenhouse acclimatization of Oncidium varicosum (Orchidaceae) with microorganisms isolated from its roots. Ornam. Hortic. 25, 407–416. https://doi.org/10.1590/2447-536X.v25i4.2046.

Bielecka, M., Pencakowski, B., Nicoletti, R., 2022. Using next-generation sequencing technology to explore genetic pathways in endophytic fungi in the syntheses of plant bioactive metabolites. Agriculture 12 (2), 187. https://doi.org/10.3390/agriculture12020187.

Bintarti, A.F., Sulesky-Grieb, A., Stopnisek, N., Shade, A., 2022. Endophytic microbiome variation among single plant seeds. Phytobiomes J. 6 (1), 45–55. https://doi.org/10.1094/PBIOMES-04-21-0030-R.

Bokati, D., Herrera, J., Poudel, R., 2016. Soil influences colonization of root-associated fungal endophyte communities of maize, wheat, and their progenitors. J. Mycol. 2016. https://doi.org/10.1155/2016/8062073.

Bulgarelli, D., Schlaeppi, K., Spaepen, S., Van Themaat, E.V.L., Schulze-Lefert, P., 2013. Structure and functions of the bacterial microbiota of plants. Annu. Rev. Plant Biol. 64, 807–838. https://doi.org/10.1146/annurev-arplant-050312-120106.

Chanclud, E., Lacombe, B., 2017. Plant hormones: key players in gut microbiota and human diseases. Trends Plant Sci. 22 (9), 754–758. https://doi.org/10.1016/j.tplants.2017.07.003.

Chang, H.X., Haudenshield, J.S., Bowen, C.R., Hartman, G.L., 2017. Metagenome-wide association study and machine learning prediction of bulk soil microbiome and crop productivity. Front. Microbiol. 8, 519. https://doi.org/10.3389/fmicb.2017.00519.

Che, J., Shi, J., Gao, Z., Zhang, Y., 2016. Transcriptome analysis reveals the genetic basis of the resveratrol biosynthesis pathway in an endophytic fungus (*Alternaria sp.* MG1) isolated from *Vitis vinifera*. Front. Microbiol. 7, 1257. https://doi.org/10.3389/fmicb.2016.01257.

Chee-Sanford, J.C., Williams, M.M., Davis, A.S., Sims, G.K., 2006. Do microorganisms influence seed-bank dynamics. Weed Sci. 54 (3), 575–587. https://doi.org/10.1614/WS-05-055R.1.

Chen, X., Marszałkowska, M., Reinhold-Hurek, B., 2020. Jasmonic acid, not salicyclic acid restricts endophytic root colonization of rice. Front. Plant Sci. 10, 1758. https://doi.org/10.3389/fpls.2019.01758.

Chhabra, S., Dowling, D.N., 2017. Endophyte-promoted nutrient acquisition: phosphorus and iron. Funct. Import. Plant Micro 21–42. https://doi.org/10.1007/978-3-319-65897-1_3.

Ciuffreda, L., Rodríguez-Pérez, H., Flores, C., 2021. Nanopore sequencing and its application to the study of microbial communities. Comput. Struct. Biotechnol. J. 19, 1497–1511. https://doi.org/10.1016/j.csbj.2021.02.020.

Compant, S., Reiter, B., Sessitsch, A., Nowak, J., Clément, C., Ait Barka, E., 2005. Endophytic colonization of *Vitis vinifera* L. by plant growth-promoting bacterium *Burkholderia sp.* strain PsJN. Appl. Environ. Microbiol. 71 (4), 1685–1693. https://doi.org/10.1128/AEM.71.4.1685-1693.2005.

Compant, S., Clément, C., Sessitsch, A., 2010. Plant growth-promoting bacteria in the rhizo-and endosphere of plants: their role, colonization, mechanisms involved and prospects for utilization. Soil Biol. Biochem. 42 (5), 669–678. https://doi.org/10.1016/j.soilbio.2009.11.024.

Compant, S., Samad, A., Faist, H., Sessitsch, A., 2019. A review on the plant microbiome: ecology, functions, and emerging trends in microbial application. J. Adv. Res 19, 29–37. https://doi.org/10.1016/j.jare.2019.03.004.

Cope-Selby, N., Cookson, A., Squance, M., Donnison, I., Flavell, R., Farrar, K., 2017. Endophytic bacteria in Miscanthus seed: implications for germination, vertical inheritance of endophytes, plant evolution and breeding. GCB Bioenergy 9 (1), 57–77. https://doi.org/10.1111/gcbb.12364.

Cordovez, V., Dini-Andreote, F., Carrión, V.J., Raaijmakers, J.M., 2019. Ecology and evolution of plant microbiomes. Annu. Rev. Microbiol. 73, 69–88. https://doi.org/10.1146/annurev-micro-090817-062524.

Correa-Galeote, D., Bedmar, E.J., Arone, G.J., 2018. Maize endophytic bacterial diversity as affected by soil cultivation history. Front. Microbiol. 9, 484. https://doi.org/10.3389/fmicb.2018.00484.

Cui, J.L., Vijayakumar, V., Zhang, G., 2018. Partitioning of fungal endophyte assemblages in root-parasitic plant *Cynomorium songaricum* and its host *Nitraria tangutorum*. Front. Microbiol. 9, 666. https://doi.org/10.3389/fmicb.2018.00666.

Dastogeer, K.M., Li, H., Sivasithamparam, K., Jones, M.G., Wylie, S.J., 2018. Host specificity of endophytic mycobiota of wild Nicotiana plants from arid regions of Northern Australia. Microb. Ecol. 75 (1), 74–87. https://doi.org/10.1007/s00248-017-1020-0.

De Vrieze, M., Germanier, F., Vuille, N., Weisskopf, L., 2018. Combining different potato-associated *Pseudomonas* strains for improved biocontrol of *Phytophthora infestans*. Front. Microbiol. 9, 2573. https://doi.org/10.3389/fmicb.2018.02573.

Ding, X., Liu, K., Zhang, Y., Liu, F, 2017. *De novo* transcriptome assembly and characterization of the 10-hydroxycamptothecin-producing *Xylaria* sp. M71 following salicylic acid treatment. J Microbiol. 55, 871–876. https://doi.org/10.1007/s12275-017-7173-1.

Ding, T., Melcher, U., 2016. Influences of plant species, season and location on leaf endophytic bacterial communities of non-cultivated plants. PLoS One 11 (3), e0150895. https://doi.org/10.1371/journal.pone.0150895.

Ding, T., Palmer, M.W., Melcher, U., 2013. Community terminal restriction fragment length polymorphisms reveal insights into the diversity and dynamics of leaf endophytic bacteria. BMC Microbiol 13 (1), 1–11. https://doi.org/10.1186/1471-2180-13-1.

Dissanayake, A.J., Purahong, W., Wubet, T., Hyde, K.D., Zhang, W., Xu, H., Zhang, G., Fu, C., Liu, M., Xing, Q., Li, X., 2018. Direct comparison of culture-dependent and culture-independent molecular approaches reveal the diversity of fungal endophytic communities in stems of grapevine (*Vitis vinifera*). Fungal Divers 90 (1), 85–107. https://doi.org/10.1007/s13225-018-0399-3.

Dong, C.J., Wang, L.L., Li, Q., Shang, Q.M., 2019. Bacterial communities in the rhizosphere, phyllosphere and endosphere of tomato plants. PLoS One 14 (11), e0223847. https://doi.org/10.1371/journal.pone.0223847.

Dong, L., Cheng, R., Xiao, L., Wei, F., Wei, G., Xu, J., Wang, Y., Guo, X., Chen, Z., Chen, S., 2018. Diversity and composition of bacterial endophytes among plant parts of *Panax notoginseng*. Chin. Med. 13 (1), 1–9. https://doi.org/10.1186/s13020-018-0198-5.

Douanla-Meli, C., Langer, E., Mouafo, F.T., 2013. Fungal endophyte diversity and community patterns in healthy and yellowing leaves of *Citrus limon*. Fungal Ecol. 6 (3), 212–222. https://doi.org/10.1016/j.funeco.2013.01.004.

Espinosa-Leal, C.A., Puente-Garza, C.A., García-Lara, S., 2018. In vitro plant tissue culture: means for production of biological active compounds. Planta 248 (1), 1–18. https://doi.org/10.1007/s00425-018-2910-1.

Eyberger, A.L., Dondapati, R., Porter, J.R., 2006. Endophyte fungal isolates from *Podophyllum peltatum* produce podophyllotoxin. J. Nat. Prod. 69 (8), 1121–1124. https://doi.org/10.1021/np060174f.

Ezeobiora, C.E., Igbokwe, N.H., Amin, D.H., Mendie, U.E., 2021. Endophytic microbes from Nigerian ethnomedicinal plants: a potential source for bioactive secondary metabolites-a review. Bull. Natl. Res Cent. 45 (1), 1–10. https://doi.org/10.1186/s42269-021-00561-7.

Fan, Y., Gao, L., Chang, P., Li, Z., 2020. Endophytic fungal community in grape is correlated to foliar age and domestication. Ann. Microbiol. 70, 1–8. https://doi.org/10.1186/s13213-020-01574-9.

Fontana, D.C., de Paula, S., Torres, A.G., de Souza, V.H.M., Pascholati, S.F., Schmidt, D., Dourado Neto, D., 2021. Endophytic fungi: Biological control and induced resistance to phytopathogens and abiotic stresses. Pathogens 10 (5), 570. https://doi.org/10.3390/pathogens10050570.

Fuller, R., 1989. A review: probiotics in man and animals. J. Appl. Microbiol. 66(5), 365–378. https://doi.org/10.1111/j.1365–2672.1989.tb05105.x.

Furtado, B.U., Gołębiewski, M., Skorupa, M., Hulisz, P., Hrynkiewicz, K., 2019. Bacterial and fungal endophytic microbiomes of *Salicornia europaea*. Appl. Environ. Microbiol. 85 (13), e00305–19. https://doi.org/10.1128/AEM.00305-19.

Gagne-Bourgue, F., Aliferis, K.A., Seguin, P., Rani, M., Samson, R., Jabaji, S., 2013. Isolation and characterization of indigenous endophytic bacteria associated with leaves of switchgrass (*Panicum virgatum* L.) cultivars. J. Appl. Microbiol 114 (3), 836–853. https://doi.org/10.1111/jam.12088.

Ganie, S.A., Bhat, J.A., Devoto, A., 2021. The influence of endophytes on rice fitness under environmental stresses. Plant Mol. Biol. 1–21. https://doi.org/10.1007/s11103-021-01219-8.

Geisen, S., Kostenko, O., Cnossen, M.C., Ten Hooven, F.C., Vreš, B., van Der Putten, W.H., 2017. Seed and root endophytic fungi in a range expanding and a related plant species. Front. Microbiol. 8, 1645. https://doi.org/10.3389/fmicb.2017.01645.

Giauque, H., Hawkes, C.V., 2013. Climate affects symbiotic fungal endophyte diversity and performance. Am. J. Bot. 100 (7), 1435–1444. https://doi.org/10.3732/ajb.1200568.

Glare, T.R., O'Callaghan, M., 2019. Microbial biopesticides for control of invertebrates: progress from New Zealand. J. Invertebr. Pathol. 165, 82–88. https://doi.org/10.1016/j.jip.2017.11.014.

Granér, G., Persson, P., Meijer, J., Alström, S., 2003. A study on microbial diversity in different cultivars of *Brassica napus* in relation to its wilt pathogen, *Verticillium longisporum*. FEMS Microbiol. Lett. 224 (2), 269–276. https://doi.org/10.1016/S0378-1097(03)00449-X.

Gupta, S., Chaturvedi, P., Kulkarni, M.G., Van Staden, J., 2020. A critical review on exploiting the pharmaceutical potential of plant endophytic fungi. Biotechnol. Adv. 39, 107462 https://doi.org/10.1016/j.biotechadv.2019.107462.

Hacquard, S., Garrido-Oter, R., González, A., Spaepen, S., Ackermann, G., Lebeis, S., McHardy, A.C., Dangl, J.L., Knight, R., Ley, R., Schulze-Lefert, P., 2015. Microbiota and host nutrition across plant and animal kingdoms. Cell Host Microbe 17 (5), 603–616. https://doi.org/10.1016/j.chom.2015.04.009.

Hallmann, J., Quadt-Hallmann, A., Miller, W.G., Sikora, R.A., Lindow, S.E., 2001. Endophytic colonization of plants by the biocontrol agent *Rhizobium etli* G12 in relation to *Meloidogyne incognita* infection. Phytopathology 91 (4), 415–422. https://doi.org/10.1094/PHYTO.2001.91.4.415.

Han, G., Wang, X., Qiu, G. 2021. Mining endophytic microbiome information from plant and animal transcriptome data. bioRxiv. 443205. https://doi.org/10.1101/2021.05.07.443205.

Hardoim, P.R., Hardoim, C.C., Van Overbeek, L.S., Van Elsas, J.D., 2012. Dynamics of seed-borne rice endophytes on early plant growth stages. PLoS One 7 (2), e30438. https://doi.org/10.1371/journal.pone.0030438.

Hardoim, P.R., Van Overbeek, L.S., Berg, G., Pirttil A.M., ä, 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. https://doi.org/10.1128/mmbr.00050-14.

Herrera Paredes, S., Gao, T., Law, T.F., Finkel, O.M., Mucyn, T., Teixeira, P.J.P.L., Salas González, I., Feltcher, M.E., Powers, M.J., Shank, E.A., Jones, C.D., 2018. Design of synthetic bacterial communities for predictable plant phenotypes. PLoS Biol. 16 (2), e2003962 https://doi.org/10.1371/journal.pbio.2003962.

Hill, C., Guarner, F., Reid, G., Gibson, G.R., Merenstein, D.J., Pot, B., Morelli, L., Canani, R.B., Flint, H.J., Salminen, S. and Calder, P.C., 2014. Expert consensus document: The International Scientific Association for Probiotics and Prebiotics consensus statement on the scope and appropriate use of the term probiotic. Nat. Rev. Gastroenterol. Hepatol. http://www.nature.com/doifinder/10.1038/nrgastro.2014.66.

Hirsch, G., Braun, U., 1992. Communities of parasitic microfungi. In Fungi in vegetation science. Springer, Dordrecht. https://doi.org/10.1007/978-94-011-2414-0_8.

Hong, C.E., Kim, J.U., Lee, J.W., Bang, K.H., Jo, I.H., 2019. Metagenomic analysis of bacterial endophyte community structure and functions in *Panax ginseng* at different ages. 3 Biotech 9 (8), 1–8. https://doi.org/10.1007/s13205-019-1838-x.

Hong, P.Y., Wheeler, E., Cann, I.K., Mackie, R.I., 2011. Phylogenetic analysis of the fecal microbial community in herbivorous land and marine iguanas of the Galápagos Islands using 16S rRNA-based pyrosequencing. ISME J. 5 (9), 1461–1470. https://doi.org/10.1038/ismej.2011.33.

Iasur Kruh, L., Lahav, T., Abu-Nassar, J., Achdari, G., Salami, R., Freilich, S., Aly, R., 2017. Host-parasite-bacteria triangle: the microbiome of the parasitic weed *Phelipanche aegyptiaca* and tomato-*Solanum lycopersicum* (Mill.) as a host. Front. Plant Sci. 8, 269. https://doi.org/10.3389/fpls.2017.00269.

Ikeda, H., Fukuda, T., Yokoyama, J., 2016. Endophytic fungi associated with a holoparasitic plant, Balanophora japonica (Balanophoraceae). Am. J. Plant Sci. 7 (1), 152–158. https://doi.org/10.4236/ajps.2016.71016.

Issa, A., Esmaeel, Q., Sanchez, L., Courteaux, B., Guise, J.F., Gibon, Y., Ballias, P., Clément, C., Jacquard, C., Vaillant-Gaveau, N., Aït Barka, E., 2018. Impacts of *Paraburkholderia phytofirmans* strain PsJN on tomato (*Lycopersicon esculentum* L.) under high temperature. Front. Plant Sci. 9, 1397. https://doi.org/10.3389/fpls.2018.01397.

Jahn, L., Schafhauser, T., Wibberg, D., Rückert, C., Winkler, A., Kulik, A., Weber, T., Flor, L., van Pee, K.H., Kalinowski, J., Ludwig-Mueller, J., et al., 2017. Linking secondary metabolites to biosynthesis genes in the fungal endophyte *Cyanodermella asteris*: The anti-cancer bisanthraquinone skyrin. J. Biotechnol. 257, 233–239. https://doi.org/10.1016/j.jbiotec.2017.06.410.

Jain, R., Bhardwaj, P., Pandey, S.S., Kumar, S., 2021. *Arnebia euchroma*, a plant species of cold desert in the himalayas, harbors beneficial cultivable endophytes in roots and leaves. Front. Microbiol. 12, 696667 https://doi.org/10.3389/fmicb.2021.696667.

James, E.K., Gyaneshwar, P., Mathan, N., Barraquio, W.L., Reddy, P.M., Iannetta, P.P., Olivares, F.L. and Ladha, J.K., 2002. Infection and colonization of rice seedlings by the plant growth-promoting bacterium Herbaspirillum seropedicae Z67. Mol. Plant-Microbe Interact. 15(9), 894–906. https://doi.org/10.1094/MPMI.2002.15.9.894.

Jia, M., Chen, L., Xin, H.L., Zheng, C.J., Rahman, K., Han, T., Qin, L.P., 2016. A friendly relationship between endophytic fungi and medicinal plants: a systematic review. Front. Microbiol. 7, 906. https://doi.org/10.3389/fmicb.2016.00906.

Johnson, L.J., Caradus, J.R., 2019. The science required to deliver Epichloë endophytes to commerce. Endophytes a Grow. World 343–370. https://doi.org/10.1017/9781108607667.017.

Johnston-Monje, D., Raizada, M.N., 2011. Conservation and diversity of seed associated endophytes in *Zea* across boundaries of evolution, ethnography and ecology. PLoS One 6 (6), e20396. https://doi.org/10.1371/journal.pone.0020396.

Jones, N., 2013. Food fuelled with fungi. Nature 504 (7479), 199. https://doi.org/10.1038/504199a.

Kanani, P., Modi, A., Kumar, A., 2020. Biotization of endophytes in micropropagation: a helpful enemy. Microb. Endophytes 357–379. https://doi.org/10.1016/B978-0-12-818734-0.00015-2.

Kerkhof, L.J., 2021. Is Oxford Nanopore sequencing ready for analyzing complex microbiomes. FEMS Microbiol. Ecol. 97(3), fiab001. https://doi.org/10.1093/femsec/fiab001.

Khare, E., Mishra, J., Arora, N.K., 2018. Multifaceted interactions between endophytes and plant: developments and prospects. Front. Microbiol. 9, 2732. https://doi.org/10.3389/fmicb.2018.02732.

Kloepper, J.W., Ryu, C.M., 2006. Bacterial endophytes as elicitors of induced systemic resistance. Microb. root endophytes 33–52. https://doi.org/10.1007/3-540-33526-9_3.

Krasova, Y.V., Tkachenko, O.V., Sigida, E.N., Lobachev, Y.V., Burygin, G.L., 2022. Lipopolysaccharide and flagellin of *Azospirillum brasilense* Sp7. Influ. callus Morphog. Plant Regen. wheat. World J. Microbiol. Biotechnol. 38 (4), 1–9. https://doi.org/10.1007/s11274-022-03247-y.

Kumar, A., Patil, D., Rajamohanan, P.R., Ahmad, A., 2013. Isolation, purification and characterization of vinblastine and vincristine from endophytic fungus *Fusarium oxysporum* isolated from *Catharanthus roseus*. PLoS One 8 (9), e71805. https://doi.org/10.1371/journal.pone.0071805.

Kusari, S., Lamshöft, M., Zühlke, S., Spiteller, M., 2008. An endophytic fungus from *Hypericum perforatum* that produces hypericin. J. Nat. Prod. 71 (2), 159–162. https://doi.org/10.1021/np070669k.

Kusari, S., Lamshöft, M., Spiteller, M., 2009a. *Aspergillus fumigatus* Fresenius, an endophytic fungus from *Juniperus communis* L. Horstmann as a novel source of the anticancer pro-drug deoxypodophyllotoxin. J. Appl. Microbiol 107 (3), 1019–1030. https://doi.org/10.1111/j.1365-2672.2009.04285.x.

Kusari, S., Zühlke, S., Spiteller, M., 2009b. An endophytic fungus from *Camptotheca acuminata* that produces camptothecin and analogues. J. Nat. Prod. 72 (1) https://doi.org/10.1021/np800455b.

Kusari, S., Verma, V.C., Lamshoeft, M., Spiteller, M., 2012. An endophytic fungus from *Azadirachta indica* A. Juss. that produces azadirachtin. World J. Microbiol. Biotechnol. 28 (3), 1287–1294. https://doi.org/10.1007/s11274-011-0876-2.

Kusari, S., Singh, S., Jayabaskaran, C., 2014. Biotechnological potential of plant-associated endophytic fungi: hope versus hype. Trends Biotechnol. 32 (6), 297–303. https://doi.org/10.1016/j.tibtech.2014.03.009.

Ley, R.E., Hamady, M., Lozupone, C., Turnbaugh, P.J., Ramey, R.R., Bircher, J.S., Schlegel, M.L., Tucker, T.A., Schrenzel, M.D., Knight, R., Gordon, J.I., 2008. Evolution of mammals and their gut microbes. Science 320 (5883), 1647–1651. https://doi.org/10.1126/science.1155725.

Li, J.L., Sun, X., Zheng, Y., Lü, P.P., Wang, Y.L., Guo, L.D., 2020. Diversity and community of culturable endophytic fungi from stems and roots of desert halophytes in northwest China. MycoKeys 62, 75 https://dx.doi.org/10.3897%2Fmycokeys.62.38923.

Liu, H., Brettell, L.E., Qiu, Z., Singh, B.K., 2020. Microbiome-mediated stress resistance in plants. Trends Plant Sci. 25 (8), 733–743. https://doi.org/10.1016/j.tplants.2020.03.014.

Liu, Y., Zuo, S., Xu, L., Zou, Y., Song, W., 2012. Study on diversity of endophytic bacterial communities in seeds of hybrid maize and their parental lines. Arch. Microbiol. 194 (12), 1001–1012. https://doi.org/10.1007/s00203-012-0836-8.

López-Ráez, J.A., Shirasu, K., Foo, E., 2017. Strigolactones in plant interactions with beneficial and detrimental organisms: the Yin and Yang. Trends Plant Sci. 22 (6), 527–537. https://doi.org/10.1016/j.tplants.2017.03.011.

Lu, H., Quan, H., Ren, Z., Wang, S., Xue, R., Zhao, B., 2016. The genome of *Undifilum oxytropis* provides insights into swainsonine biosynthesis and locoism. Sci. Rep. 6 (30760) https://doi.org/10.1038/srep30760.

Lundberg, D.S., Lebeis, S.L., Paredes, S.H., Yourstone, S., Gehring, J., Malfatti, S., Tremblay, J., Engelbrektson, A., Kunin, V., Del Rio, T.G., Edgar, R.C., 2012. Defining the core *Arabidopsis thaliana* root microbiome. Nature 488 (7409), 86–90. https://doi.org/10.1038/nature11237.

Mardanov, A.V., Chizhevskaya, E.P., Lazarev, A.M., Rakitin, A.L., Beletsky, A.V., Chebotar, V.K., Ravin, N.V., 2019. Complete genome sequences of endophytic *Bacilli* isolated from Grapevine plants. Microbiol. Resour. Announc. 8 (48), e01265–19. https://doi.org/10.1128/MRA.01265-19.

Markowiak, P., Śliżewska, K., 2018. The role of probiotics, prebiotics and synbiotics in animal nutrition. Gut Pathog. 10 (1), 1–20. https://doi.org/10.1186/s13099-018-0250-0.

Marques, J.M., da Silva, T.F., Vollu, R.E., de Lacerda, J.R.M., Blank, A.F., Smalla, K., Seldin, L., 2015. Bacterial endophytes of sweet potato tuberous roots affected by the plant genotype and growth stage. Appl. Soil Ecol. 96, 273–281. https://doi.org/10.1016/j.apsoil.2015.08.020.

Marquez-Santacruz, H.A., Hernandez-Leon, R., Orozco-Mosqueda, M.D.C., Velazquez-Sepulveda, I., Santoyo, G., 2010. Diversity of bacterial endophytes in roots of Mexican husk tomato plants (*Physalis ixocarpa*) and their detection in the rhizosphere. Genet. Mol. Res. 9 (4), 2372–2380. https://doi.org/10.4238/vol9-4gmr921.

Martínez-Ballesta, M.C., López-Pérez, L., Hernández, M., López-Berenguer, C., Fernández-García, N., Carvajal, M., 2008. Agricultural practices for enhanced human health. Phytochem Rev. 7 (2), 251–260. https://doi.org/10.1007/s11101-007-9071-3.

Martínez-Romero, E., Aguirre-Noyola, J.L., Bustamante-Brito, R., González-Román, P., Hernández-Oaxaca, D., Higareda-Alvear, V., Montes-Carreto, L.M., Martínez-Romero, J.C., Rosenblueth, M., Servín-Garcidueñas, L.E., 2021. We and herbivores eat endophytes. Microb. Biotechnol. 14 (4), 1282–1299. https://doi.org/10.1111/1751-7915.13688.

Matsumoto, H., Fan, X., Wang, Y., Kusstatscher, P., Duan, J., Wu, S., Chen, S., Qiao, K., Wang, Y., Ma, B., Zhu, G., 2021. Bacterial seed endophyte shapes disease resistance in rice. Nat. Plants 7 (1), 60–72. https://doi.org/10.1038/s41477-020-00826-5.

Metchnikoff, E., 1908. The prolongation of life. Nature 77, 289–290. https://doi.org/10.1038/077289b0.

Miao, L.Y., Mo, X.C., Xi, X.Y., Zhou, L., De, G., Ke, Y.S., Liu, P., Song, F.J., Jin, W.W. and Zhang, P., 2018. Transcriptome analysis of a taxol-producing endophytic fungus Cladosporium cladosporioides MD2. AMB Express. 8(1), 1–10. https://doi.org/10.1186/s13568–018-0567–6.

Ming, Q., Su, C., Zheng, C., Jia, M., Zhang, Q., Zhang, H., Rahman, K., Han, T., Qin, L., 2013. Elicitors from the endophytic fungus *Trichoderma atroviride* promote *Salvia miltiorrhiza* hairy root growth and tanshinone biosynthesis. J. Exp. Bot. 64 (18), 5687–5694. https://doi.org/10.1093/jxb/ert342.

Miotto-Vilanova, L., Jacquard, C., Courteaux, B., Wortham, L., Michel, J., Clément, C., Barka, E.A., Sanchez, L., 2016. *Burkholderia phytofirmans* PsJN confers grapevine resistance against *Botrytis cinerea* via a direct antimicrobial effect combined with a better resource mobilization. Front. Plant Sci. 7, 1236. https://doi.org/10.3389/fpls.2016.01236.

Mitter, B., Pfaffenbichler, N., Flavell, R., Compant, S., Antonielli, L., Petric, A., Berninger, T., Naveed, M., Sheibani-Tezerji, R., von Maltzahn, G., Sessitsch, A., 2017. A new approach to modify plant microbiomes and traits by introducing beneficial bacteria at flowering into progeny seeds. Front. Plant Sci. 8, 11. https://doi.org/10.3389/fmicb.2017.00011.

Moghaddam, M.S.H., Safaie, N., Soltani, J., Hagh-Doust, N., 2021. Desert-adapted fungal endophytes induce salinity and drought stress resistance in model crops. Plant Physiol. Biochem. 160, 225–238. https://doi.org/10.1016/j.plaphy.2021.01.022.

Molina-Montenegro, M.A., Acuña-Rodríguez, I.S., Torres-Díaz, C., Gundel, P.E., Dreyer, I., 2020. Antarctic root endophytes improve physiological performance and yield in crops under salt stress by enhanced energy production and Na+ sequestration. Sci. Rep. 10 (1), 1–10. https://doi.org/10.1038/s41598-020-62544-4.

Morales Moreira, Z.P., Helgason, B.L., Germida, J.J., 2021. Assembly and potential transmission of the Lens culinaris seed microbiome. FEMS Microbiol. Ecol. 97 (12), 166. https://doi.org/10.1093/femsec/fiab166.

Murphy, B.R., Hodkinson, T.R., 2018. Endophyte ecology, diversity and utilisation. Plant Ecol. Divers 11 (5–6), 551–554. https://doi.org/10.1080/17550874.2019.1616001.

Naik, S., Shaanker, R.U., Ravikanth, G., Dayanandan, S., 2019. How and why do endophytes produce plant secondary metabolites. Symbiosis 78 (3), 193–201. https://doi.org/10.1007/s13199-019-00614-6.

Nelson, E.B., 2004. Microbial dynamics and interactions in the spermosphere. Annu. Rev. Phytopathol. 42, 271–309. https://doi.org/10.1146/annurev.phyto.42.121603.131041.

Ntana, F., Bhat, W.W., Johnson, S.R., Jørgensen, H.J., Collinge, D.B., Jensen, B., Hamberger, B., 2021. A sesquiterpene synthase from the endophytic fungus *Serendipita indica* catalyzes formation of viridiflorol. Biomolecules 11 (6), 898. https://doi.org/10.3390/biom11060898.

Oberhofer, M., Hess, J., Leutgeb, M., Gössnitzer, F., Rattei, T., Wawrosch, C., Zotchev, S.B., 2019. Exploring actinobacteria associated with rhizosphere and endosphere of the native alpine medicinal plant *Leontopodium nivale* subspecies alpinum. Front. Microbiol. 10, 2531. https://doi.org/10.3389/fmicb.2019.02531.

Ofek-Lalzar, M., Gur, Y., Ben-Moshe, S., Sharon, O., Kosman, E., Mochli, E., Sharon, A., 2016. Diversity of fungal endophytes in recent and ancient wheat ancestors *Triticum dicoccoides* and *Aegilops sharonensis*. FEMS Microbiol. Ecol. 92 (10), fiw152. https://doi.org/10.1093/femsec/fiw152.

Oleńska, E., Małek, W., Wójcik, M., Swiecicka, I., Thijs, S., Vangronsveld, J., 2020. Beneficial features of plant growth-promoting rhizobacteria for improving plant growth and health in challenging conditions: a methodical review. Sci. Total Environ. 743, 140682 https://doi.org/10.1016/j.scitotenv.2020.140682.

de Oliveira Chagas, M.B., Dos Santos, I.P., da Silva, L.C.N., dos Santos Correia, M.T., de Araújo, J.M., da Silva Cavalcanti, M., de Menezes Lima, V.L., 2017. Antimicrobial activity of cultivable endophytic fungi associated with Hancornia speciosa gomes bark. Open Microbiol. J. 11, 179. https://doi.org/10.2174/1874285801711010179.

del Carmen Orozco-Mosqueda, M. and Santoyo, G., 2021. Plant-microbial endophytes interactions: scrutinizing their beneficial mechanisms from genomic explorations. Curr. Plant Biol. 25, 100189. https://doi.org/10.1016/j.cpb.2020.100189.

Pandey, S.S., Singh, S., Babu, C.V., Shanker, K., Srivastava, N.K., Kalra, A., 2016a. Endophytes of opium poppy differentially modulate host plant productivity and genes for the biosynthetic pathway of benzylisoquinoline alkaloids. Planta 243 (5), 1097–1114. https://doi.org/10.1007/s00425-016-2467-9.

Pandey, S.S., Singh, S., Babu, C.V., Shanker, K., Srivastava, N.K., Shukla, A.K., Kalra, A., 2016b. Fungal endophytes of *Catharanthus roseus* enhance vindoline content by modulating structural and regulatory genes related to terpenoid indole alkaloid biosynthesis. Sci. Rep. 6 (1), 1–14. https://doi.org/10.1038/srep26583.

Pandey, S.S., Singh, S., Pandey, H., Srivastava, M., Ray, T., Soni, S., Pandey, A., Shanker, K., Babu, C.V., Banerjee, S., Gupta, M.M., 2018. Endophytes of *Withania somnifera* modulate in planta content and the site of withanolide biosynthesis. Sci. Rep. 8 (1), 1–19. https://doi.org/10.1038/s41598-018-23716-5.

Papik, J., Folkmanova, M., Polivkova-Majorova, M., Suman, J., Uhlik, O., 2020. The invisible life inside plants: deciphering the riddles of endophytic bacterial diversity. Biotechnol. Adv. 44, 107614 https://doi.org/10.1016/j.biotechadv.2020.107614.

Parmar, S., Li, Q., Wu, Y., Li, X., Yan, J., Sharma, V.K., Wei, Y., Li, H., 2018. Endophytic fungal community of *Dysphania ambrosioides* from two heavy metal-contaminated sites: evaluated by culture-dependent and culture-independent approaches. Microb. Biotechnol. 11 (6), 1170–1183. https://doi.org/10.1111/1751-7915.13308.

Parnell, J.J., Berka, R., Young, H.A., Sturino, J.M., Kang, Y., Barnhart, D.M., DiLeo, M.V., 2016. From the lab to the farm: an industrial perspective of plant beneficial microorganisms. Front. Plant Sci. 7, 1110. https://doi.org/10.3389/fpls.2016.01110.

Pei, C., Mi, C., Sun, L., Liu, W., Li, O. and Hu, X., 2017. Diversity of endophytic bacteria of Dendrobium officinale based on culture-dependent and culture-independent methods. Biotechnol. Biotechnolo. Equip. 31(1), 112–119. https://doi.org/10.1080/13102818.2016.1254067.

Penuelas, J., Rico, L., Ogaya, R., Jump, A.S., Terradas, J., 2012. Summer season and long-term drought increase the richness of bacteria and fungi in the foliar phyllosphere of *Quercus ilex* in a mixed Mediterranean forest. Plant Biol. 14 (4), 565–575. https://doi.org/10.1111/j.1438-8677.2011.00532.x.

Pitakbut, T., Spiteller, M., Kayser, O., 2022. Genome mining and gene expression reveal maytansine biosynthetic genes from endophytic communities living inside *Gymnosporia heterophylla* (Eckl. and Zeyh.) Loes. and the relationship with the plant biosynthetic gene, Friedelin synthase. Plants 11 (3), 321. https://doi.org/10.3390/plants11030321.

Potshangbam, M., Devi, S.I., Sahoo, D., Strobel, G.A., 2017. Functional characterization of endophytic fungal community associated with *Oryza sativa* L. and *Zea mays* L. Front. Microbiol. 8, 325. https://doi.org/10.3389/fmicb.2017.00325.

Puri, R.R., Adachi, F., Omichi, M., Saeki, Y., Yamamoto, A., Hayashi, S., Ali, M.A., Itoh, K., 2019. Metagenomic study of endophytic bacterial community of sweet potato (*Ipomoea batatas*) cultivated in different soil and climatic conditions. World J. Microbiol. Biotechnol. 35 (11), 1–8. https://doi.org/10.1007/s11274-019-2754-2.

Puri, S.C., Verma, V., Amna, T., Qazi, G.N., Spiteller, M., 2005. An endophytic fungus from *Nothapodytes foetida* that produces Camptothecin. J. Nat. Prod. 68 (12), 1717–1719. https://doi.org/10.1021/np0502802.

Purushotham, N., Jones, E., Monk, J., Ridgway, H., 2020. Community structure, diversity and potential of endophytic bacteria in the primitive New Zealand medicinal plant *Pseudowintera colorata*. Plants 9 (2), 156. https://doi.org/10.3390/plants9020156.

Qaim, M., 2020. Role of new plant breeding technologies for food security and sustainable agricultural development. Appl. Econ. Perspect. Policy 42 (2), 129–150. https://doi.org/10.1002/aepp.13044.

Qin, Y., Druzhinina, I.S., Pan, X., Yuan, Z., 2016. Microbially mediated plant salt tolerance and microbiome-based solutions for saline agriculture. Biotechnol. Adv. 34 (7), 1245–1259. https://doi.org/10.1016/j.biotechadv.2016.08.005.

Quambusch, M., Winkelmann, T., 2018. Bacterial endophytes in plant tissue culture: mode of action, detection, and control. Plant Cell Cult. Protoc. 69–88. https://doi.org/10.1007/978-1-4939-8594-4_4.

Ramírez-Puebla, S.T., Servín-Garcidueñas, L.E., Jiménez-Marín, B., Bolaños, L.M., Rosenblueth, M., Martínez, J., Rogel, M.A., Ormeño-Orrillo, E., Martínez-Romero, E., 2013. Gut and root microbiota commonalities. Appl. Environ. Microbiol. 79 (1), 2–9. https://doi.org/10.1128/AEM.02553-12.

Rashid, S., Charles, T.C., Glick, B.R., 2012. Isolation and characterization of new plant growth-promoting bacterial endophytes. Appl. Soil Ecol. 61, 217–224. https://doi.org/10.1016/j.apsoil.2011.09.011.

Ray, T., Pandey, S.S., Pandey, A., Srivastava, M., Shanker, K., Kalra, A., 2019. Endophytic consortium with diverse gene-regulating capabilities of benzylisoquinoline alkaloids biosynthetic pathway can enhance endogenous morphine biosynthesis in *Papaver somniferum.* Front. Microbiol. 10, 925. https://doi.org/10.3389/fmicb.2019.00925.

Raza, A., Razzaq, A., Mehmood, S.S., Zou, X., Zhang, X., Lv, Y., Xu, J., 2019. Impact of climate change on crops adaptation and strategies to tackle its outcome: A review. Plants 8 (2), 34. https://doi.org/10.3390/plants8020034.

Rho, H., Van Epps, V., Kim, S.H., Doty, S.L., 2020. Endophytes Increased Fruit Quality with Higher Soluble Sugar Production in Honeycrisp Apple (*Malus pumila*). Microorganisms 8 (5), 699. https://doi.org/10.3390/microorganisms8050699.

Ribeiro, C.F.A., Silveira, G.G.D.O.S., Candido, E.D.S., Cardoso, M.H., Espinola Carvalho, C.M., Franco, O.L., 2020. Effects of antibiotic treatment on gut microbiota and how to overcome its negative impacts on human health. ACS Infect. Dis. 6 (10), 2544–2559. https://doi.org/10.1021/acsinfecdis.0c00036.

Ringelberg, D., Foley, K., Reynolds, C.M., 2012. Bacterial endophyte communities of two wheatgrass varieties following propagation in different growing media. Can. J. Microbiol 58 (1), 67–80. https://doi.org/10.1139/w11-122.

Rodriguez, R., Redman, R., 2008. More than 400 million years of evolution and some plants still can't make it on their own: plant stress tolerance via fungal symbiosis. J. Exp. Bot. 59 (5), 1109–1114. https://doi.org/10.1093/jxb/erm342.

Rodríguez, C.E., Mitter, B., Barret, M., Sessitsch, A., Compant, S., 2018. Commentary: seed bacterial inhabitants and their routes of colonization. Plant Soil 422 (1), 129–134. https://doi.org/10.1007/s11104-017-3368-9.

Rolli, E., Marasco, R., Vigani, G., Ettoumi, B., Mapelli, F., Deangelis, M.L., Gandolfi, C., Casati, E., Previtali, F., Gerbino, R., Pierotti Cei, F., 2015. Improved plant resistance to drought is promoted by the root-associated microbiome as a water stress-dependent trait. Environ. Microbiol. 17 (2), 316–331. https://doi.org/10.1111/1462-2920.12439.

Rozpądek, P., Domka, A.M., Nosek, M., Ważny, R., Jędrzejczyk, R.J., Wiciarz, M., Turnau, K., 2018. The role of strigolactone in the cross-talk between *Arabidopsis thaliana* and the endophytic fungus *Mucor sp*. Front. Microbiol. 9, 441. https://doi.org/10.3389/fmicb.2018.00441.

Rudgers, J.A., Afkhami, M.E., Rúa, M.A., Davitt, A.J., Hammer, S., Huguet, V.M., 2009. A fungus among us: broad patterns of endophyte distribution in the grasses. Ecology 90 (6), 1531–1539. https://doi.org/10.1890/08-0116.1.

Salehi, M., Moieni, A., Safaie, N., Farhadi, S., 2019. Elicitors derived from endophytic fungi *Chaetomium globosum* and *Paraconiothyrium brasiliense* enhance paclitaxel production in *Corylus avellana* cell suspension culture. Plant Cell, Tissue Organ Cult. 136 (1), 161–171. https://doi.org/10.1007/s11240-018-1503-9.

Salehi, M., Moieni, A., Safaie, N., Farhadi, S., 2020. Whole fungal elicitors boost paclitaxel biosynthesis induction in *Corylus avellana* cell culture. PLoS One 15 (7), e0236191. https://doi.org/10.1371/journal.pone.0236191.

Salehi, M., Farhadi, S., Moieni, A., Safaie, N., Ahmadi, H., 2020. Mathematical modeling of growth and paclitaxel biosynthesis in *Corylus avellana* cell culture responding to fungal elicitors using multilayer perceptron-genetic algorithm. Front. Plant Sci. 11, 1148. https://doi.org/10.3389/fpls.2020.01148.

Santoyo, G., Moreno-Hagelsieb, G., del Carmen Orozco-Mosqueda, M., Glick, B.R., 2016. Plant growth-promoting bacterial endophytes. Microbiol. Res. 183, 92–99. https://doi.org/10.1016/j.micres.2015.11.008.

Sarhan, M.S., Hamza, M.A., Youssef, H.H., Patz, S., Becker, M., ElSawey, H., Nemr, R., Daanaa, H.S.A., Mourad, E.F., Morsi, A.T., Abdelfadeel, M.R., 2019. Culturomics of the plant prokaryotic microbiome and the dawn of plant-based culture media–a review. J. Adv. Res. 19, 15–27. https://doi.org/10.1016/j.jare.2019.04.002.

Schafhauser, T., Jahn, L., Kirchner, N, Kulik, A, Flor, L., Lang, A., Caradec, T., Fewer, D. P., Sivonen, K., van Berkel, W.J., Jacques, P., 2019. Antitumor astins originate from the fungal endophyte *Cyanodermella asteris* living within the medicinal plant *Aster tataricus*. Proc Natl Acad Sci U S A . 116 (52), 26909–26917. https://doi.org/10.1073/pnas.1910527116.

Schlaeppi, K., Bulgarelli, D., 2015. The plant microbiome at work. Mol. Plant-Microbe Inter. 28 (3), 212–217. https://doi.org/10.1094/MPMI-10-14-0334-FI.

Schlegel, M., Queloz, V., Sieber, T.N., 2018. The endophytic mycobiome of European Ash and Sycamore Maple leaves–geographic patterns, host specificity and influence of Ash Dieback. Front. Microbiol. 9, 2345. https://doi.org/10.3389/fmicb.2018.02345.

Schreiner, M., Huyskens-Keil, S., 2006. Phytochemicals in fruit and vegetables: health promotion and postharvest elicitors. CRC Crit. Rev. Plant Sci. 25 (3), 267–278. https://doi.org/10.1080/07352680600671661.

Schultz, B., Boyle, C., 2005. The endophytic continuum. Mycol. Res. 109, 661–686. https://doi.org/10.1017/S095375620500273X.

Sessitsch, A.N.G.E.L.A., Hardoim, P.A.B.L.O., Döring, J., Weilharter, A., Krause, A.N.D.R.E.A.S., Woyke, T.A.N.J.A., Mitter, B., Hauberg-Lotte, L., Friedrich, F., Rahalkar, M., Hurek, T., 2012. Functional characteristics of an endophyte community colonizing rice roots as revealed by metagenomic analysis. Mol. Plant-Microbe Inter. 25 (1), 28–36. https://doi.org/10.1094/MPMI-08-11-0204.

Shade, A., Jacques, M.A., Barret, M., 2017. Ecological patterns of seed microbiome diversity, transmission, and assembly. Curr. Opin. Microbiol. 37, 15–22. https://doi.org/10.1016/j.mib.2017.03.010.

Shahzad, R., Waqas, M., Khan, A.L., Asaf, S., Khan, M.A., Kang, S.M., Yun, B.W., Lee, I.J., 2016. Seed-borne endophytic *Bacillus amyloliquefaciens* RWL-1 produces gibberellins and regulates endogenous phytohormones of *Oryza sativa*. Plant Physiol. Biochem. 106, 236–243. https://doi.org/10.1016/j.plaphy.2016.05.006.

Shahzad, R., Khan, A.L., Bilal, S., Asaf, S., Lee, I.J., 2017. Plant growth-promoting endophytic bacteria versus pathogenic infections: an example of *Bacillus amyloliquefaciens* RWL-1 and *Fusarium oxysporum f. sp. lycopersici* in tomato. PeerJ 5, e3107. https://doi.org/10.7717/peerj.3107.

Shahzad, R., Khan, A.L., Bilal, S., Waqas, M., Kang, S.M., Lee, I.J., 2017. Inoculation of abscisic acid-producing endophytic bacteria enhances salinity stress tolerance in *Oryza sativa*. Environ. Exp. Bot. 136, 68–77. https://doi.org/10.1016/j.envexpbot.2017.01.010.

Shahzad, R., Khan, A.L., Bilal, S., Lee, I.J., 2018. What is there in seeds? Vertically transmitted endophytic resources for sustainable improvement in plant. Growth. Front Plant Sci. 9, 24. https://doi.org/10.3389/fpls.2018.00024.

Shearin, Z.R., Filipek, M., Desai, R., Bickford, W.A., Kowalski, K.P., Clay, K., 2018. Fungal endophytes from seeds of invasive, non-native *Phragmites australis* and their potential role in germination and seedling growth. Plant Soil 422 (1), 183–194. https://doi.org/10.1007/s11104-017-3241-x.

Shi, Y., Yang, H., Zhang, T., Sun, J., Lou, K., 2014. Illumina-based analysis of endophytic bacterial diversity and space-time dynamics in sugar beet on the north slope of Tianshan mountain. Appl. Microbiol. Biotechnol. 98 (14), 6375–6385. https://doi.org/10.1007/s00253-014-5720-9.

Shrivastava, S., Varma, A., 2014. From *Piriformospora indica* to rootonic: a review. Afr. J. Microbiol. Res. 8 (32), 2984–2992. https://doi.org/10.5897/AJMR2014.6928.

Shweta, S., Zuehlke, S., Ramesha, B.T., Priti, V., Kumar, P.M., Ravikanth, G., Spiteller, M., Vasudeva, R., Shaanker, R.U., 2010. Endophytic fungal strains of *Fusarium solani*, from *Apodytes dimidiata* E. Mey. ex Arn (Icacinaceae) produce camptothecin, 10-hydroxycamptothecin and 9-methoxycamptothecin. Phytochemistry 71 (1), 117–122. https://doi.org/10.1016/j.phytochem.2009.09.030.

Shymanovich, T., Faeth, S.H., 2018. Anti-insect defenses of *Achnatherum robustum* (sleepygrass) provided by two *Epichloë* endophyte species. Entomol. Exp. Appl. 166 (6), 474–482. https://doi.org/10.1111/eea.12692.

Siddique, S., Naveed, M., Yaseen, M., Shahbaz, M., 2022. Exploring potential of seed endophytic bacteria for enhancing drought stress resilience in maize (*Zea mays* L.). Sustainability 14 (2), 673. https://doi.org/10.3390/su14020673.

Sieber, T.N., 2002. Fungal root endophytes. In: Waisel, Y., Eshel, A., Kafkafi, U. (Eds.), Plant Roots: The Hidden Half. Marcel Dekker, Inc, New York, pp. 887–917. https://doi.org/10.1201/9780203909423.ch49.

Silva, F.D.A., Liotti, R.G., Boleti, A.P.D.A., Reis, E.D.M., Passos, M.B.S., Dos Santos, E.L., Sampaio, O.M., Januario, A.H., Branco, C.L.B., Silva, G.F.D., Mendonça, E.A.F.D., 2018. Diversity of cultivable fungal endophytes in *Paullinia cupana* (Mart.) Ducke and bioactivity of their secondary metabolites. PLoS One 13 (4), e0195874. https://doi.org/10.1371/journal.pone.0195874.

Singh, S., Pandey, S.S., Tiwari, R., Pandey, A., Shanker, K., Kalra, A., 2021. Endophytic consortium with growth-promoting and alkaloid enhancing capabilities enhance key terpenoid indole alkaloids of *Catharanthus roseus* in the winter and summer seasons. Ind. Crops Prod. 166, 113437 https://doi.org/10.1016/j.indcrop.2021.113437.

Sobreira, A.C., Francisco das Chagas, L.P., Florêncio, K.G., Wilke, D.V., Staats, C.C., de AS Streit, R., Freire, F.D.C.D.O., Pessoa, O.D., Trindade-Silva, A.E., Canuto, K.M., 2018. Endophytic fungus *Pseudofusicoccum stromaticum* produces cyclopeptides and plant-related bioactive rotenoids. RSC advances 8 (62), 35575–35586. https://doi.org/10.1039/c8ra06824k.

Soliman, S.S., Tsao, R., Raizada, M.N., 2011. Chemical inhibitors suggest endophytic fungal paclitaxel is derived from both mevalonate and non-mevalonate-like pathways. J. Nat. Prod. 74 (12), 2497–2504. https://doi.org/10.1021/np200303v.

Soumare, A., Diédhiou, A.G., Arora, N.K., Tawfeeq Al-Ani, L.K., Ngom, M., Fall, S., Hafidi, M., Ouhdouch, Y., Kouisni, L., Sy, M.O., 2021. Potential Role and utilization of plant growth promoting microbes in plant tissue culture. Front. Microbiol. 12, 649878 https://doi.org/10.3389/fmicb.2021.649878.

Straub, D., Rothballer, M., Hartmann, A., Ludewig, U., 2013. The genome of the endophytic bacterium H. frisingense GSF30T identifies diverse strategies in the Herbaspirillum genus to interact with plants. Front. Microbiol 4, 168. https://doi.org/10.3389/fmicb.2013.00168.

Sujatha, H.S., Murali, M. and Amruthesh, K.N., 2021. Induction of resistance by elicitors of endophytic fungi against early blight disease caused by Alternaria solani in tomato (Lycopersicon esculentum mill.). Plant Cell Biotechnol Mol Biol. 22(27–28), 110–125. https://www.ikpress.org/index.php/PCBMB/article/view/6190.

Sun, S.S., Chen, X.M., Guo, S.X., 2014. Analysis of endophytic fungi in roots of Santalum album Linn. and its host plant Kuhnia rosmarinifolia Vent. J. Zhejiang Univ. Sci. B 15 (2), 109–115. https://doi.org/10.1631/jzus.B1300011.

Teimoori-Boghsani, Y., Ganjeali, A., Cernava, T., Müller, H., Asili, J., Berg, G., 2020. Endophytic fungi of native *Salvia abrotanoides* plants reveal high taxonomic diversity and unique profiles of secondary metabolites. Front. Microbiol. 10, 3013. https://doi.org/10.3389/fmicb.2019.03013.

Terhonen, E., Blumenstein, K., Kovalchuk, A., Asiegbu, F.O., 2019. Forest tree microbiomes and associated fungal endophytes: functional roles and impact on forest health. Forests 10 (1), 42. https://doi.org/10.3390/f10010042.

Tian, B.Y., Cao, Y., Zhang, K.Q., 2015. Metagenomic insights into communities, functions of endophytes and their associates with infection by root-knot nematode, *Meloidogyne incognita,* in tomato roots. Sci. Rep. 5 (1), 1–15. https://doi.org/10.1038/srep17087.

Tkacz, A., Pini, F., Turner, T.R., Bestion, E., Simmonds, J., Howell, P., Greenland, A., Cheema, J., Emms, D.M., Uauy, C., Poole, P.S., 2020. Agricultural selection of wheat has been shaped by plant-microbe interactions. Front. Microbiol. 11, 132. https://doi.org/10.3389/fmicb.2020.00132.

Tripathi, A., Awasthi, A., Singh, S., Sah, K., Maji, D., Patel, V.K., Verma, R.K., Kalra, A., 2020. Enhancing artemisinin yields through an ecologically functional community of endophytes in *Artemisia annua*. Ind. Crops Prod. 150, 112375 https://doi.org/10.1016/j.indcrop.2020.112375.

Truyens, S., Weyens, N., Cuypers, A., Vangronsveld, J., 2015. Bacterial seed endophytes: genera, vertical transmission and interaction with plants. Environ. Microbiol. Rep. 7 (1), 40–50. https://doi.org/10.1111/1758-2229.12181.

Tshishonga, K., Serepa-Dlamini, M.H., 2019. Draft genome sequence of *Enterobacter hormaechei* strain MHSD6, a plant endophyte isolated from medicinal plant *Pellaea* *calomelanos*. Microbiol. Resour. Announc. 8 (48), e01251–19. https://doi.org/10.1128/MRA.01251-19.

Tyc, O., Putra, R., Gols, R., Harvey, J.A., Garbeva, P., 2020. The ecological role of bacterial seed endophytes associated with wild cabbage in the United Kingdom. Microbiologyopen 9 (1), e00954. https://doi.org/10.1002/mbo3.954.

Ulrich, K., Kube, M., Becker, R., Schneck, V., Ulrich, A., 2021. Genomic analysis of the endophytic *Stenotrophomonas* strain 169 reveals features related to plant-growth promotion and stress tolerance. Front. Microbiol. 12, 1542. https://doi.org/10.3389/fmicb.2021.687463.

Vandenkoornhuyse, P., Quaiser, A., Duhamel, M., Le Van, A., Dufresne, A., 2015. The importance of the microbiome of the plant holobiont. N. Phytol. 206 (4), 1196–1206. https://doi.org/10.1111/nph.13312.

de Vega, C., Arista, M., Ortiz, P.L., Talavera, S., 2010. Anatomical relations among endophytic holoparasitic angiosperms, autotrophic host plants and mycorrhizal fungi: a novel tripartite interaction. Am. J. Bot. 97 (5), 730–737. https://doi.org/10.3732/ajb.0900147.

Venugopalan, A., Srivastava, S., 2015. Endophytes as in vitro production platforms of high value plant secondary metabolites, 873-87 Biotechnol. Adv. 33 (6 Pt 1). https://doi.org/10.1016/j.biotechadv.2015.07.004.

Walitang, D.I., Kim, C.G., Jeon, S., Kang, Y., Sa, T., 2019. Conservation and transmission of seed bacterial endophytes across generations following crossbreeding and repeated inbreeding of rice at different geographic locations. MicrobiologyOpen 8 (3), e00662. https://doi.org/10.1002/mbo3.662.

Wang, C., Wu, J., Mei, X., 2001. Enhancement of taxol production and excretion in *Taxus chinensis* cell culture by fungal elicitation and medium renewal. Appl. Microbiol. Biotechnol. 55 (4), 404–410. https://doi.org/10.1007/s002530000567.

Wemheuer, F., Wemheuer, B., Daniel, R., Vidal, S., 2019. Deciphering bacterial and fungal endophyte communities in leaves of two maple trees with green islands. Sci. Rep. 9 (1), 1–14. https://doi.org/10.1038/s41598-019-50540-2.

Whitaker, B.K., Reynolds, H.L., Clay, K., 2018. Foliar fungal endophyte communities are structured by environment but not host ecotype in *Panicum virgatum* (switchgrass). Ecology 99 (12), 2703–2711. https://doi.org/10.1002/ecy.2543.

Willer H., Trávníček J., Meier C., Schlatter B., 2021. The World of Organic Agriculture Statistics and Emerging Trends 2021 Willer H, Trávníček J, Meier C, Schlatter B (Eds.) Research Institute of Organic Agriculture (FiBL) and IFOAM – Organics International. https://www.fibl.org/fileadmin/documents/shop/1150-organic-world-2021.pdf.

Woźniak, M., Grządziel, J., Gałązka, A., Frąc, M., 2019. Metagenomic Analysis of Bacterial and Fungal Community Composition Associated with *Paulownia elongate* × *Paulownia fortunei*. BioResources 14 (4), 8511–8529. https://doi.org/10.15376/biores.14.4.8511-8529.

Xia, Y., Sahib, M.R., Amna, A., Opiyo, S.O., Zhao, Z., Gao, Y.G., 2019. Culturable endophytic fungal communities associated with plants in organic and conventional farming systems and their effects on plant growth. Sci. Rep. 9 (1), 1–10. https://doi.org/10.1038/s41598-018-38230-x.

Xiang, D., Wei, W., Wan, Y., Wu, X., Ye, X., Peng, L., Zhong, L., Wu, Q., Zou, L., Zhao, G., Zhao, J., 2021. Polysaccharide Elicitor from the Endophyte *Bionectria sp*. Fat6 Improves Growth of Tartary Buckwheat under Drought Stress. Phyton 90 (2), 461. https://doi.org/10.32604/phyton.2021.011724.

Yang, H., Ye, W., Ma, J., Zeng, D., Rong, Z., Xu, M., Wang, Y., Zheng, X., 2018. Endophytic fungal communities associated with field-grown soybean roots and seeds in the Huang-Huai region of China. PeerJ 6, e4713. https://doi.org/10.7717/peerj.4713.

Yang, Y., Zhao, H., Barrero, R.A., Zhang, B., Sun, G., Wilson, I.W., Xie, F., Walker, K.D., Parks, J.W., Bruce, R., Guo, G., 2014. Genome sequencing and analysis of the paclitaxel-producing endophytic fungus *Penicillium aurantiogriseum* NRRL 62431. BMC Genet 15 (1), 1–14. https://doi.org/10.1186/1471-2164-15-69.

Yu, X., Yang, J., Wang, E., Li, B., Yuan, H., 2015. Effects of growth stage and fulvic acid on the diversity and dynamics of endophytic bacterial community in *Stevia rebaudiana* Bertoni leaves. Front. Microbiol. 6, 867. https://doi.org/10.3389/fmicb.2015.00867.

Zhang, Q., Acuña, J.J., Inostroza, N.G., Mora, M.L., Radic, S., Sadowsky, M.J., Jorquera, M.A., 2019. Endophytic bacterial communities associated with roots and leaves of plants growing in Chilean extreme environments. Sci. Rep. 9 (1), 1–12. https://doi.org/10.1038/s41598-019-41160-x.

Zimmerman, N.B. and Vitousek, P.M., 2012. Fungal endophyte communities reflect environmental structuring across a Hawaiian landscape. Proc. Natl. Acad. Sci. 109 (32), 13022–13027. https://doi.org/10.1073/pnas.1209872109.

Žiarovská, J., Medo, J., Kyseľ, M., Zamiešková, L., Kačániová, M., 2020. Endophytic bacterial microbiome diversity in early developmental stage plant tissues of wheat varieties. Plants (Basel) 9 (2), 266. https://doi.org/10.3390/plants9020266.

Zou, K., Liu, X., Hu, Q., Zhang, D., Fu, S., Zhang, S., Huang, H., Lei, F., Zhang, G., Miao, B., Meng, D., 2021. Root endophytes and *Ginkgo biloba* are likely to share and compensate secondary metabolic processes, and potentially exchange genetic information by LTR-RTs. Front. Plant Sci. 1370. https://doi.org/10.3389/fpls.2021.704985.