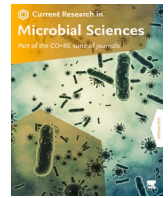


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## The plant endomicrobiome: Structure and strategies to produce stress resilient future crop

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### ABSTRACT

Plants have a microbiome, a diverse community of microorganisms, including bacteria, fungi, and viruses, living inside and on their tissues. Versatile endophytic microorganisms inhabited in every plant part without causing disease and develop endophytic microbiome or endo-microbiome. Plant endo-microbiome are drawn by the nutrient rich micro-environment, and in turn some microbes mutualistically endorse and protect plant from adverse environmental stresses. Plant endo-microbiome interact within well-designed host equilibrium containing xylem, phloem, nutrients, phytohormones, metabolites and shift according to environmental and nutritional change. Plant endo-microbiome regulate and respond to environmental variations, pathogens, herbivores by producing stress regulators, organic acids, secondary metabolites, stress hormones as well as unknown substances and signalling molecules. Endomicrobiome efficiently synthesizes multiple bioactive compounds, stress phytohormones with high competence. The technological innovation as next generation genomics biology and high-throughput multiomics techniques stepping stones on the illumination of critical endo-microbiome communities and functional characterization that aid in improving plant physiology, biochemistry and immunity interplay for best crop productivity. This review article contains deeper insight in endomicrobiome related research work in last years, recruitment, niche development, nutrient dynamics, stress removal mechanisms, bioactive services in plant health development, community architecture and communication, and immunity interplay in producing stress resilient future crop.

### 1. Introduction

Agriculture in the 21st century faces multiple challenges. Population growth is one of the most significant topics at present (Trivedi et al., 2022; Vimal et al., 2024). The current world population of 7.6 billion is expected to reach 8.6 billion in 2030, 9.8 billion in 2050 and 11.2 billion in 2100, according to a United Nations report 2023. Population induced urbanization is foreseen to continue at an accelerating pace with urban areas to account for 70 % of world population in 2050 (FAO, 2009; 2023). To meet the demands of this rising population food production needs to increase by 70 % to feed global hunger and provide food security (FAO, 2009; Singh and Vimal, 2020). This abnormal growth in population and urbanization graph needs food security to be met from existing cultivable lands and under scope of extreme climate change without further deteriorating biodiversity and environmental quality

(French et al., 2021; FAO, 2023). The limitation in cultivable land is crucial because expanding agriculture often leads to deforestation and land use change (Zhang et al., 2021; Trivedi et al., 2022). In addition, conventional agricultural practices reliance on agrochemicals in form of fertilizers, pesticides and growth enhancer agrochemicals (Rane et al., 2022; Yu et al., 2022). These chemicals input grew complained for negative dynamics on soil-crop health and food quality (Edwards et al., 2019; Varshney et al., 2020).

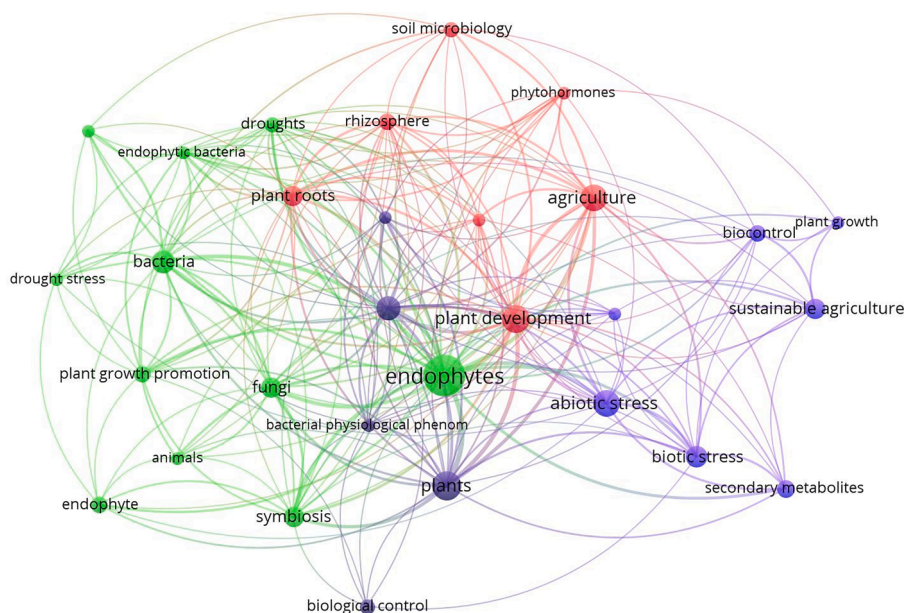
Log term application of agro-pesticides remains in crop system in form of residues and magnify in grains, plants and different living organisms (Rane et al., 2022; Raj et al., 2023). These statements indicated that the further application of chemicals does not offer sustainable enhancement in crop productivity (Chouhan et al., 2021; Tiwari and Bae, 2023). There is need of innovative and sustainable nature-based solutions (NbS) to agriculture, as well as global cooperation and

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**Fig. 1.** The keywords cooccurrence network, obtained from the articles extracted by PUBMED, selecting three keywords: “endophytic” (or “endophyte”), “stress” and “agriculture” in the all-available literature. The resent review is specifically addressed to the publications of the last 5 years (from 2018 to 2023). The network map highlights the most frequency used bibliographic terms to understand the most active research fields that are grouped into three clusters.

policy initiatives to ensure crop productivity and food security for the growing population while preserving the plant for future generations.

Plant associated microorganisms are ubiquitous and support its strength in different ecological zones around the globe (Singh et al., 2020; Peng et al., 2023; Vimal et al., 2024). Plant-microbe interactions have been documented for at least 407 million years (Hardoim et al., 2015). Over the past 25 years, advances in modern genome sequencing technologies have indeed revealed that virtually all non-sterile plants colonized by a diverse microbiome (Qian et al., 2021; Vimal et al., 2023a). This discovery has significantly influenced our perception of the role of microbes in plant health and productivity, both in agricultural and natural ecosystems (Vimal et al., 2017; Copeland and Schulze-Lefert, 2020; French et al., 2021). Microbes significantly play crucial role in host fitness and health, as millions of years of co-evolution exist between soil-plant-microbe interactions in stress management (Liu et al., 2020; Goodwin, 2022). Recent research has highlighted the critical and significant tole of plant endophytic microbes and endomicrobiome services in plant development and productivity (Peng et al., 2023; Vimal et al., 2023b).

Endophyte are organisms that live inside plants without causing any apparent damage to their hosts (Hardoim et al., 2015). Endophytes enjoyed comfort in less competitive zone compared to exophytes (Huang et al., 2022; Ling et al., 2023). It is not always clear, however, if and how these complex endophytic microbial communities affect plant health and functions (Banik et al., 2019; Medison et al., 2022). German botanist ‘Anton de Bary’ recognized as father of plant pathology, invent the term endophytes in 1886 to explain microorganisms that colonize internal tissues of plant parts as roots, stems, leaves and even flower, fruits and seeds (Tiwari and Bae, 2023). Endophytes consists variety of latent pathogens, latent saprophytes, active beneficial and mutualistic bacteria, fungi, and rhizobia (Narayanan and Glick, 2022; Ling et al., 2023). Plants are efficiently acquired, assemble and re-assemble their endophytic microbial partners at different developmental stages as well as environmental conditions (Qian et al., 2021; Nataraja et al., 2022). Endophytes facilitate the successful establishment of symbiotic association with in plant and develop endomicrobiome (Waqar et al., 2023; Chen et al., 2023). Endomicrobiome particularly improved synthesis and secretion of plant growth promoting bioactive compounds for host adaptation under different environmental conditions (Goodwin, 2022;

Ling et al., 2023).

Plant endo-microbiome exhibited both co-operative and competitive interactive outcomes on plant development (Qin et al., 2023). Co-operative endomicrobiome shows synergistic effects on plant while competing microbiome causes detrimental effect (Tiwari and Bae, 2023). Third commensal endo-microbiome has minimal effect on plant growth. The endo-microbiome is typically regulated and developed within the plant niches modulated by the environment and plant defence system (Zhang et al., 2021; Goodwin, 2022). The higher colonization efficacy and stability against abiotic and biotic stress ecologically indicates them as potential solution for environmental management (Khan et al., 2022; Narayanan and Glick, 2022; Chen et al., 2023). Culturable and non-culturable microbiota of colonizing endogenous niche of multiple vegetative and crop plants are profiled by several workers (Kaliaperumal et al., 2023; Song et al., 2023; Vimal et al., 2023b). Each plant part has unique endomicrobiome and part play vital role in inter-generational and intra-generational transfer of microbiome to other plant niches (Goodwin, 2022; Peng et al., 2023).

Multiple studies on plant-endomicrobiome community characterization, functional dynamics and their impact on growth, disease management, abiotic and biotic stress management, water retention and synthesis of beneficial regulating hormones reported with beneficial impact on plant and environmental health (Khan et al., 2012; Deng et al., 2019; Liu et al., 2023). Moreover, beneficial endo-microbiome play dominant role in synthesis of novel metabolites, bio-active molecules as alkaloids, phenols, peptides synthesis, improved nutrient cycling, bio-degradation, bio-remediation and show promising bio-tool for future crop growth stimulator and widely applied in pharmaceuticals, industrial and agro-farming sectors (Thomloudi et al. 2021; Wang et al., 2023).

The last decade brought an extraordinary growth in the interest in plant microbiome studies, from 30 PubMed entries in 2008 to 2997 in 2023. However, very limited studies on plant-endomicrobiome interactions have been conducted. The network cluster map based on PUBMED search of keywords as “endophytic” (or “endophyte”), “stress” and “agriculture” in the all-available literature including title, abstract, keywords, of all bibliographic information in last six years (2018–23) has performed (Fig. 1) using VOS viewer software (“VOS viewer version 1.6.20” 2023). Plant endo-microbiome engineering with potential

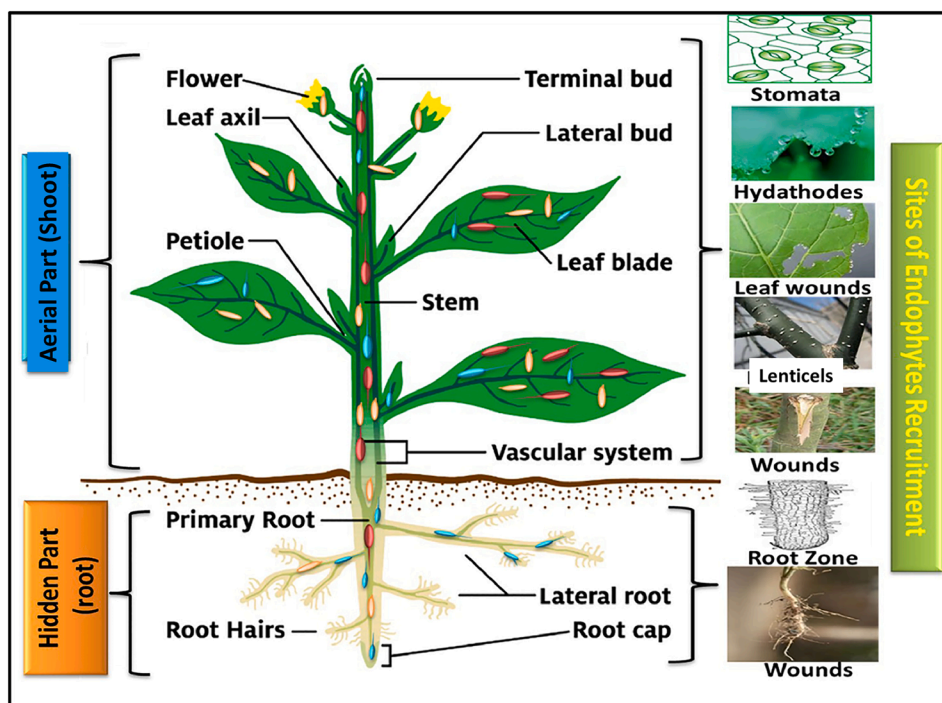


Fig. 2. Different sites of endophytes recruitment in plants from aerial part (shoot) and hidden part (roots).

microbiota and in-depth knowledge on endo-microbiome recruitment, functional niche development, nutrient mobilization, bioactive molecules synthesis, stress phytohormones signalling, community architecture, immunity interplay and long-distance communications have the potential to enhance agricultural productivity (Singh et al., 2020; Vimal et al., 2023a).

Such endomicrobiome services can provide low cost, NbS for climate-resilient sustainable agricultural practices that simultaneously intensifies agricultural output and environmental sustainability. However, critical knowledge gaps appears both in basic, applied and translational research, which constraints the endo-microbiome services in crop development. In this review article, we critically focus on endo-microbiome recruitments, mechanisms, strategies, architecture, functional profiling and immunity interplay to produce stress resilient future crop. Furthermore, present article contains recent in-depth information on (a) plant-endophytic microbiome development and its role in plant growth promotion (b) Plant endomicrobiome recruitment-community structure in different plants (c) Environmental stresses-endomicrobiome mechanisms in alleviation of stress toxicity (d) Plant-endomicrobiome adaptations, genomic and functional profiling elegance for future stress resilient crop plants and (e) Long-distance communication and immunity interplay between plant and microbes.

## 2. Plant domestication-endomicrobiome association for development and stress management

Plant domestication ensures wild plants breeding and development of homogenized cultivable plants genotypes that are widely used by present population for food, feed, and other living purposes (Varshney et al., 2020). Plant domestication has led to the selection and cultivation of specific plant varieties with desirable traits (Singh et al., 2020; Trivedi et al., 2022). Today, domesticated plants are a fundamental part of crop agriculture and provide majority of world's food supply and security (Vimal et al., 2023a). This manmade crop evolution resulted in reduction of crop genetic diversity within cultivated crops and offers a pool of genetic erosion. Host genotype play versatile role in microbiota recruitment and functional dynamics (Canarini et al., 2021; Tiwari and

Bae, 2023; Vimal et al., 2023a). However, in the past years, it is shown that the plant has specific microbial community organization that makes it clearly distinguishable from microbial assemblages that are connected to other life forms (Chouhan et al., 2021).

Plants facilitate and recruit optimal variety of drivers, taxonomically structured communities of microorganisms as bacteria, fungi, protists, nematodes and viruses and develop plant microbiome (Tiwari and Bae, 2023; Vimal et al., 2023a, 2024). The term "plant microbiome" broadly refers to the microbial communities that inhabit every plant part and accessible tissues, specially phyllosphere microbiome (air-plant interface), endosphere microbiome (plant internal tissues), and rhizosphere microbiome (soil-root interface) (Trivedi et al., 2020; Chouhan et al., 2021). The plant endosphere harbours microbial communities that directly affect the physiological features of plants due to beneficial interaction, signalling and without evolving any disease symptoms or damaging the host immune responses (Yuan et al., 2021).

The endomicrobiome community composition, richness, population count and functional dynamics significantly correlated with factors such as plant genotypes, different compartments (e.g., leaves, stems and roots), age and environmental growth conditions (Peng et al., 2023; Vimal et al., 2023a). The peculiar niches dominated by endomicrobiome communities in plant is unique and different from phyllosphere and rhizosphere due to variation in functions, adaptations, responses, competence and specialization (Goodwin, 2022; Ganie et al., 2022). Microbial colonization within the endosphere is not uniform; different parts of the plant, even within the same plant, can host distinct microbial communities (Chouhan et al., 2021; Tiwari and Bae, 2023). This phenomenon is often referred to as microbial niche specialization.

Endophytic microorganisms can be categorized into (a) colonizer and survival endophytes: These endophytes are often found colonizing plant reproductive organs, such as ovules. They have specific adaptations that enable them to establish and survive in these specialized environments. These endophytes might provide benefits to the plant, such as protection against pathogens or improved nutrient uptake, which can be crucial for the successful development of seeds (Meyer and Leveau, 2012; Chouhan et al., 2021). (b) seed endophytes: Endophytes residing within seeds are often characterized as competitors. They need to endure

harsh conditions, including desiccation, high temperatures, and potential exposure to toxins. These endophytes are adapted to compete for limited resources within the seed environment (Abdelfattah et al., 2023). Some seed endophytes might have mechanisms to tolerate or detoxify compounds produced by the plant or other microorganisms in the vicinity (Luo et al., 2019). Endophytic microorganisms can be acquired by plants through both vertical transmission (from parent to offspring via seeds) and horizontal transmission (from the surrounding environment, especially the soil, where plants grow) (Narayanan and Glick, 2022). This dual mode of acquisition significantly contributes to the diversity and composition of endophytic communities within plants (Khan et al., 2012; Chen et al., 2023).

Endophytic microbiome forms close and often mutualistic associations with their host plants, playing crucial roles in plant growth, fitness, and development (Li et al., 2019; Ganie et al., 2022). The secretion of these compounds and the interactions between endophytes and their host plants demonstrate the intricate relationships in natural ecosystems (Ling et al., 2023). Despite the differences in their habitats, certain endomicrobiome populations exhibit shared mechanisms of action in promoting plant growth and enhancing crop immunity (Yuan et al., 2021). Endomicrobiome mediate plant responses by producing Indole-3-acetic acid (IAA) (Kachalkin et al., 2022; Vimal et al., 2023b), 1-amino-1-cyclopropane carboxylic deaminase (ACC deaminase) (Wang et al., 2022; Choudhury et al., 2023), minerals (Scholz et al., 2023), microbial volatile organic compounds (mVOCs) (Massawe et al., 2018; Ling et al., 2023), siderophores for iron chelation (Chouhan et al., 2021; Vimal et al., 2024), pathogen suppression (Thomloui et al., 2021), secretion of secondary metabolites (Thomloui et al., 2021; Kaliaperumal et al., 2023), antioxidants and antioxidant enzymes (Hagaggi and Abdul-Raouf, 2022), osmo-protectants (Peng et al., 2023) and antibiotic and antimicrobial substances (Makhwitine et al., 2023; Song et al., 2023). Endomicrobiome efficiently fix atmospheric Nitrogen (N) and enhance availability to plant tissues (Zhu et al., 2023; Scholz et al., 2023).

Understanding these shared mechanisms highlights the intricate relationship between plants and their associated microbial communities. Deeper knowledge of specific roles and adaptations of these endophytes is essential for plant ecology, as well as for agricultural and conservation efforts. In agriculture, knowledge of beneficial endophytes can be harnessed to improve seed quality and overall plant health. In natural ecosystems, harnessing these interactions contribute to the diversity and adaptation of plant species, playing a significant role in the dynamics of plant populations. The endomicrobiome also offer next generation NbS for improved crop productivity, reduced dependence on chemical inputs, and enhanced immunity and resilience of crops against diseases and environmental stresses.

### 3. Plant endomicrobiome recruitment, transmission and community structure in different crop plants

Plants can recruit microbiota from both above-ground and below-ground areas, interacting in various parts and environment (Fig. 2) (Chouhan et al., 2021; Trivedi et al., 2022). The interaction between germinating seeds and the resident soil microbiota is a critical aspect of plant development and overall ecosystem health (Duran et al., 2018; Liu et al., 2020). This interaction primarily takes place in "rhizosphere", which is the soil region directly surround the roots contain enormous food source for microbes as rhizodeposits or root exudates (Korenblum et al., 2020; Chai and Schachtman, 2022). Root zone is exceedingly rich in powerful microbiome army that promotes host plant growth under different environmental conditions (Luo et al., 2019; Zhang et al., 2021). The term "rhizosphere effect" first used by Starkey (1938), refers to a group of multiple events that take place at plant-root-soil interface. These processes leading to gradient dispersion, root exudation, microbial activity, genetic exchange, and nutrient transformation. Rhizosphere microbiome significantly affect plant health through various

mechanisms including nutrient cycling, pathogen suppression, hormonal regulation and stress management (Singh et al., 2020; Vimal et al., 2022).

Horizontal transmission refers to the transfer of microorganisms from one individual or environment to another, as opposed to vertical transmission, which involves the passage of microorganisms from parent to offspring (Luo et al., 2019; Tiwari and Bae, 2023). In the context of microbial colonization of the root endosphere, horizontal transmission occurs via interactions between the plant roots and the rhizosphere (Abdelfattah et al., 2023). The localization of microbiome army in root regions suggests that entry is facilitated by cracks or openings in the root, root hairs, and microbes may enter through root tips (Hawes et al., 2000; Chouhan et al., 2021). Root tips are regions of active growth where new cells are constantly dividing and elongating. These areas provide favourable conditions for microbial colonization and entry (Vimal et al., 2024). *Burkholderia* sp. strain PsJN labelled with green fluorescent protein (GFP) exhibited colonization potential in *Vitis vinifera* shown chronological colonization start on root surfaces, root internal tissues and in xylem vessels of internodes and leaves and in young berries (Compant et al., 2008). Endophytes as *Pseudomonas putida* and *P. fluorescens* colonize the Olive plants through root hairs (Mercado-Blanco and Prieto, 2012). Endophytes tagging with GFP and maize stem injection confirmed systematic movement and colonization in plants, suggested the continuous movement of organisms throughout plant endosphere (Johnston-Monje and Raizada, 2011). Plant health beneficial microbe *Arthrobacter protophormiae* significantly improved root nodulation and mycorrhization activity in *Pisum sativum* and declined NaCl stress through declining ACC oxidase activity and ethylene production (Barnawal et al., 2014).

Endophytes can also be entered in plant aerial tissues via above-ground surfaces, including leaves (phyllosphere), flowers (anthosphere), fruits (carposphere) and stem (laminosphere) (Fig. 2). This provides a broader perspective on the diverse ways microorganisms establish themselves within plant structures. Endophytes can access leaves and stems through various mechanisms, including entry points such as stomata, hydathodes, trichomes, and wounds with the help of rain, soil and pollinators (Fig. 2) (Frank et al., 2017; Zhu et al., 2023). The stomatal route of entry has been studied for plant pathogens, but less so for endophytes (Copeland and Schulze-Lefert, 2020).

Microorganisms present on the surfaces of petals, sepals, and other floral structures may enter these tissues through natural openings or be carried by pollinators. Endophytes can be present on the surface of fruits and may enter the fruit tissues through openings, wounds, or natural openings like lenticels (Chouhan et al., 2021). Microbial aggregates were appears on trichomes, epidermal cell wall junctions and in the vicinity of stomatal complexes. Microbes are able to effectively enter the substomatal chamber through the stomata and colonize the leaf mesophyll's intercellular gaps (Tiwari and Bae, 2023). Beneficial endophyte *Herbaspirillum seropedicae* enters into *Ananas comosus* plant through stomata and promote plant health though nutritional stress management (Baldotto et al., 2011). In sugarcane plants, *Gluconobacter diazotrophicus* entered through stomata, colonize, inhabiting into xylem and develop biofilm (James et al., 2001).

Efficiently colonizers microbes simultaneously travel distance in different organs including anthosphere, phyllosphere, carposphere and caulosphere (Meyer and Leveau, 2012; Vimal et al., 2024). The overlap in community composition between the phyllosphere and the leaf interior suggests that the leaf surface serves as the initial phase of colonization for some foliar endophytes (Copeland and Schulze-Lefert, 2020). This phenomenon underscores the dynamic nature of the interactions between plants and microorganisms (Meyer and Leveau, 2012). Leaf endophytes including microbes are the subset of phyllosphere endophytes. Leaf endophytes most of the times comprises in five major phyla, *Proteobacteria* (90 %), *Actinobacteria* (2.5 %), *Planctomycetes* (1.4 %), *Verrucomicrobia*, and *Acidobacteria* (1.1 and 0.5 %) (Romero et al., 2014; Chaudhary et al., 2022). Endophytes lives inside

**Table 1**

Different endomicrobiome components, biomolecules production activity and effects on plant health and functional dynamics.

S. No.	Host	Endomicrobiome components	Bioactive compounds/Metabolites/Hormones/Antioxidants	Effect on plant health/Functional dynamics	References
1.	<i>Chilo suppressalis</i> (Walker)/ <i>Solanum lycopersicum</i> cv. Hezuo	<i>Beauveria bassiana</i>	$\alpha$ -solanine, 5-O-caffeoylshikimic acid, clerodendrin A, and peucedanin	Pest management	Wang et al. (2023)
2.	<i>Spongia officinalis</i>	<i>Penicillium verrucosum</i>	Averufin	Anti-cancerous activity	Kaliaperumal et al. (2023)
3.	<i>Andrographis paniculata</i>	<i>Lasiodiplodia pseudotheobromae</i>	1-octadecene, erythritol, niacin, oleic acid, phenol, pantolactone, phenyl ethyl alcohol, p-cresol, and tbutyl hydroquinone	Anti-microbial activity	Segaran and Sathiavelu (2023)
4.	<i>Fusarium decemcellulare</i>	<i>M. fortune</i>	12-epicitreoisocoumarinol, eisocoumarinol, citreoisocoumarin, trichophenol A, rigidiusculamide B, fusaristatin A, enniatin H, enniatin I, nectriacid A, nectriacid B, 4-hydroxy-3,6-dimethyl-2 H-pyrane-2-one, macrocarpon C, and $\alpha$ -linoleic acid	Phytopathogen management	Song et al. (2023)
5.	<i>Bacillus halotolerans</i>	<i>Hypericum hircinum</i>	Surfactin, mojavensin, fengycin, 1-dihydroanticiapsin, bacillibactin, bacillaene, and azelaic acid	Ant-microbial activity	Thomloui et al. (2021)
6.	<i>Penicillium chrysogenum</i>	<i>Albizia adianthifolia</i>	Pyrrrolo, cyclotrisiloxane, hexamethyl, cycloetrasiloxane, octamethyl, cyclopentasiloxane, decamethyl, quinoline, propanenitrile, dibutyl phthalate, and silane	Anti-HIV-1 activity	Makhwitine et al. (2023)
7.	<i>Olea europaea</i> L.	<i>Fusarium</i> sp. <i>Alternaria</i> sp. <i>Pyronema domesticum</i>	$\alpha$ -farnesene and p-cymene	Anti-microbial disease susceptibility activity	Gomes et al. (2023)
8.	<i>Oryza sativa</i> L.	<i>Azotobacter</i> sp. Avi2	Develop biofilm areas around root zone	N-fixation activity, nutrient trapping and quorum sensing	Wang et al. (2017)
9.	<i>Glycyrrhiza uralensis</i>	<i>Bacillus cereus</i> G2	Nitrate reductase, nitrite, glutamate synthase, proline, glycine, betaine	Improves N activity and protect from saline stress toxicity	Peng et al. (2023)
10.	<i>Erythrina brucei</i>	<i>Gluconobacter cerinus</i> , <i>Acinetobacter soli</i> , <i>Achromobacter xylosoxidans</i> and <i>Bacillus thuringiensis</i>	P mineralization activity on medium supplemented with aluminium phosphate (Al-P), iron phosphate (Fe-P) and Tri-Calcium Phosphate	Improved <i>E. brucei</i> in both alkaline and acidic soils	Berza et al. (2022)
11.	<i>Kosteletzkya virginica</i>	<i>Trichoderma viride</i>	ACC deaminase	Enhanced plant growth parameters, chlorophyll contents, and antioxidants activities	Wang et al. (2023)
12.	<i>Cathamus oxycantha</i>	<i>Trichoderma gamsii</i> and <i>Fusarium proliferatum</i>	ACC deaminase	Manages plant health under drought stressed plants	Rehman et al. (2022)
13.		<i>Rhizobium</i> sp. WYJ-E13	Cytokinin, anthranilic acid, and l-phenylalanine	Improved plant development	Huang et al. (2022)
14.	<i>Festuca rubra</i> subsp. <i>Pruinose</i>	<i>Diaporthe</i> strain EB4	IAA production	Enhanced tritordeum ( <i>Triticum durum</i> x <i>Hordeum chilense</i> ) and perennial ryegrass ( <i>Lolium perenne</i> ), subjected to salinity stress.	Toghueo et al. (2022)
15.	<i>Rheum emodi</i>	<i>Pelomonas aquatica</i> AIS1S and <i>Solibacillus silvestris</i> DL3R2	Produced IAA and organic acids quercetin, gallic, emodin physcoin and rhein	Improved plant growth at high altitudes under salinity and metal stress conditions.	Somal and Karnwal (2022)
16.	<i>Carthamus tinctorius</i>	<i>Stenotrophomonas maltophilia</i>	Exopolysaccharide production	Upregulated phenolics, flavonoids, carotenoids and SOD, POX, APX and enhanced plant health under Cd toxicity	Hagaggi and Abdul-Raouf (2022)
17.	<i>Glycyrrhiza uralensis</i>	<i>Bacillus cereus</i> G2	Proline, glycine, betaine synthesis and regulate N cycle	Improved relative water content and declined electrolyte leakage, protect membrane system to decline soil salinity	Peng et al. (2023)

the leaves and maintain symbiotic relationship with the host plants.

The shoot associated endophytes transmitted to the rhizocompartment and dominant component of the newly established root associated microbiomes in *Sedum alfredii* (Crassulaceae) plant. Based on 16S r-RNA gene sequencing tool, the transmitted taxa denoted as *Sterptomycetaceae*, *Nocardioideaceae*, *Pseudonocardioideaceae* which positively correlated with plant growth promotion and metal accumulation (Luo et al., 2019). The eight endophytes isolated from an embryonic tissue of hybrid walnut shoot exhibited high similarity (97–100 %) with *Pseudomonas*, *Brevundimonas*, *Acinetobacter*, and *Roseomonas*, while in a culture-independent method exhibited five independent phyla as *Actinobacteria*, *Bacteroidetes*, *Cyanobacteria*, *Firmicutes*, and *Proteobacteria*. The *Acinetobacter* spp., *Brevundimonas* spp. and *Moraxella* spp. of *Proteobacteria* genera showed a comparatively most abundance of

endophytic bacteria (Pham et al., 2017). These endophytes present in the shoot, and it has the ability to multiply in shoot meristem of newly forming shoot tissue and it passes vertically through seeds (Shahzad et al., 2018). Taken together, these studies suggest that the plants zone play vital role in endophytic microbiome recruitment and community development. Each of these zones represent distinct environment in and around the plant, and play essential role in shaping the plant endo-microbiome and influencing overall plant health.

#### 4. Environmental stresses and endomicrobiome services in stressed crop development

Human activities, particularly those related to industrialization, agriculture, and urbanization, have led to significant anthropogenic-

induced changes on our planet (Vimal et al., 2017; 2018). Air pollutants (SO<sub>2</sub> and N oxides), water pollutants (heavy metals and pesticides) and soil pollutants (industrial chemical and waste) deteriorate environmental quality and sustainability. Climate change led to enhancement of greenhouse gas emissions, primarily carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), and nitrous oxide (N<sub>2</sub>O), are causing global temperatures to rise (Singh and Vimal, 2020; Trivedi et al., 2022). This change in climate patterns has far-reaching effects, including altered precipitation patterns, heatwaves, rising sea levels, and disruptions in agro-ecosystems (Singh et al., 2020; French et al., 2021). Increased CO<sub>2</sub> levels in the atmosphere lead to higher CO<sub>2</sub> absorption by oceans, causing ocean acidification. This has detrimental effects on marine life, particularly organisms with CaCl<sub>2</sub> shells or skeletons, such as coral reefs and shellfish. These anthropogenic-induced changes have dramatic impacts on agro-ecosystems services (Edwards et al., 2019; Chai and Schachtman, 2022). Multiple environmental calamities led to generation of abiotic stresses as drought, salinity, heavy metals, and biotic stresses as pathogens, insects, nematodes and diminish plant health, development and productivity (Narayanan and Glick, 2022; Peng et al., 2023; Vimal et al., 2023b). Soil salinity is an issue of great importance in relation to irrigation and agricultural production in arid and semiarid regions (Vimal et al., 2023a; b). Drought stress is a multidimensional stress and causes changes in the physiological, morphological, biochemical, and molecular traits in plants (Rehman et al., 2022). Temperature stresses as high, chilling and freezing stress disrupt photosynthesis and increase photorespiration thereby altering the normal homeostasis of plant cells (Singh and Vimal, 2020; Vimal et al., 2023a).

Under flooding and waterlogging conditions, plants experience energy and carbohydrate deprivation due to reduced photosynthesis and aerobic respiration (Vimal et al., 2017; 2024). Land use change and mechanical stress as soil compaction causes yield loss range from 20 to 75 % liable to soil texture and sternness of other environmental stresses. Pathogens severely impacted crop health and causes loss of >80 % in affect field (El-Shafey et al., 2021; Kaliaperumal et al., 2023). Overall, crop development under open environmental conditions and unrhythmic climate change led to offer stress equilibrium for plant health and development.

Plant associated microorganisms extensively neutralize the negative impact of environmental, abiotic and biotic stress with different activities as reviewed recently in different studies (French et al., 2021; Vimal et al., 2023a). Plant endomicrobiome play vital role to overcome negative effect of stress toxicity, neutralize stress equilibrium and enhance plant development (Tiwari and Bae, 2023). The beneficial effects provoked by endophytes are phytohormone regulation, metabolites production, nutrient acquisition, detoxification, osmotic adjustment that account for alleviation of stress environment. The multiple remodelling studies associated with endomicrobiome components and different biomolecules synthesis and its effects on plant health and functional dynamics have been illustrated in Table 1. Some of important studies on plant beneficial role of endomicrobiome are depicted in following sub-sections.

#### 4.1. Endomicrobiome-antioxidants, osmo-protectants, and organic acids activities for crop development under stressed conditions

Endomicrobiome associated endophytic microbes significantly declined abiotic and biotic stress toxicity in equilibrium through accumulation of osmolytes, antioxidants compounds and organic acid production (Hagaggi and Abdul-Raouf, 2022; Peng et al., 2023). These biologically active compounds play versatile role in management of plant health and stress management (Vimal et al., 2023b). Plants under stress environment regulated osmotic stress by production of osmolytes as proline, glycine, betaine and soluble sugars. Antioxidants as ascorbate, glutathione and antioxidant enzymes as catalase (CAT), super-oxide-dismutase (SOD), peroxidase (POX), ascorbate peroxidase (APX), mono-dehydro-ascorbate reductase (MDHAR), and

De-hydro-ascorbate reductase (DHAR) etc. significantly declined stress induced excessively produced reactive oxygen species (ROS) in plant cell equilibrium (El-Shafey et al., 2021; Hagaggi and Abdul-Raouf, 2022).

Recently, endophytic microbe *Bacillus cereus* G2 inoculation significantly improved proline, glycine, betaine synthesis, relative water content and regulate N cycle in *Glycyrrhiza uralensis*. In *G. uralensis*, improved relative water content co-related with declined electrolyte leakage, protect membrane system and promote plant growth under salinity stress conditions (Peng et al., 2023). Exopolysaccharide producing *Stenotrophomonas maltophilia* exhibited cadmium (Cd) tolerance and Cd-adsorption potentials and significantly upregulate phenolics, flavonoids, carotenoids and SOD, POX, APX to protect safflower plant from Cd induced toxicity (Hagaggi and Abdul-Raouf, 2022). Salt tolerant endophyte *Bacillus subtilis* SSA4 significantly regulated ascorbate-glutathione cycle and enhanced paddy seedlings growth parameters under 150 mM and 300 mM NaCl toxicity (Vimal et al., 2023b). Three endophytic fungi *Talaromyces versatilis*, *Emericella nidulans* and *Aspergillus niger* significantly enhanced plant biomass, minerals Mg, P, Na, Mn, and Zn, improved CAT, SOD, APX, MDHAR and DHAR activities and enhanced rose-scented geranium plant health under Cd stress (El-Shafey et al., 2021).

Fungal endophyte *Sordariomycetes* sp. EF0801 inoculation significantly improved organic acids as malate, fumarate level in paddy leaves, tartrate, malate, succinate and fumarate in roots and minerals Ca, Mg, P, Fe and Ni in leaves and Ni contents in roots and declined negative effect due to lead (Pb) toxicity (Li et al., 2019). Bacterial strains *Pelomonas aquatica* AIS1S and *Solibacillus silvestris* DL3R2 boosted germination rate, plant health parameters and organic acids production as quercetin, gallic, emodin physcoic, rhein in endangered medicinally important herb *Rheum emodi* that grows at high altitudes under salinity and metal stress conditions (Somal and Karnwal, 2022). Thus, all of these studies demonstrated the potential application of endophytic microbes associated endomicrobiome community dynamics and functional services in plant health development and stress management.

#### 4.2. Endomicrobiome-phytohormone regulation for crop development under stressed conditions

Plant endomicrobiome exert their positive effect on plant health by modulating the levels of essential phytohormones (Kachalkin et al., 2022). Endomicrobiome significantly influence the production, metabolism and signalling pathways of these phytohormones (Tiwari and Bae, 2023). These five essential phytohormones and their role in plant development (a) auxin- involved in cell elongation, root development, and apical dominance (b) cytokinins in cell division and differentiation (c) gibberellins in stem elongation, seed germination, and flowering (d) abscisic acid is associated with stress responses and (e) ethylene regulates various physiological processes, including fruit ripening and stress management. Endomicrobiome regulate every phytohormone content in equilibrium and support overall better plant health. Recently, Toghueo et al. (2022) isolated endophytic fungus *Diaporthe* strain EB4 from native *Festuca rubra* subsp. *Pruinose* roots, a perennial grass adapted to rocky sea cliffs, where soil and nutrients are very limited and inoculated tritordeum (*Triticum durum* x *Hordeum chilense*) and perennial ryegrass (*Lolium perenne*), subjected to two salinity conditions (0 and 200 mM NaCl). The fungal strain significantly produced auxin IAA and modulated the production of IAA in the plant body and enhanced plant health and development.

Kachalkin et al. (2023) reported diversity of cultivable endophytic yeasts from agricultural fruits and unveiled *Aureobasidium pullulans*, *Candida zeylanoides*, *Hanseniaspora uvarum*, *Metschnikowia pulcherrima*, *Meyerozyma caribbica*, *Rhodotorula mucilaginosa* and *Yarrowia galli* in IAA production activity insides fruit tissues and possess reservoir for phytohormonal activities by potential microbiota. Bacterial endophyte *Bacillus amyloliquefaciens* produces ABA, upregulated essential amino acids

and improved endogenous production of salicylic acid in rice plants. The improved level of endogenous phytohormones in paddy plant significantly enhanced growth under salinity stress (Shahzad et al., 2017). *Rhizobium* sp. WYJ-E13 produces cytokinin, anthranilic acid, and l-phenylalanine and efficiently applied as bioinoculants for plant development (Huang et al., 2022).

Bacterial endophyte *Sphingomonas* sp. LK11 isolated from leaves of *Tephrosia apollinea* produces physiologically active as well as inactive gibberellins, and IAA efficiently promoted tomato growth parameters (Khan et al., 2014). Ethylene serves as a crucial signalling molecule in plants, and its production is indeed influenced by various environmental stresses. The biosynthesis of ethylene in stressed plants involves a series of enzymatic reactions, with the precursors S-adenosyl-l-methionine (SAM) and 1-aminocyclopropane-1-carboxylic acid (ACC) playing central roles. The key enzymes catalysing this pathway include SAM synthase, ACC synthase (ACS), and ACC oxidase (ACO). In addition, potential endophytic microbes have the ability to diminish plant ethylene level by producing 1-aminocyclopropane-1-carboxylase (ACC) deaminase that cleaves the ACC compound, a precursor of ethylene (Singh and Vimal, 2020; Rehman et al., 2022; Choudhury et al., 2023). Recently, Rehman et al. (2022) isolated, drought-resistant, ACC deaminase producing endophytic fungi *Trichoderma gamsii* and *Fusarium proliferatum* from xerophyte *Cathamus oxycantha*. Single and dual inoculated with these fungi significantly enhanced *Moringa oleifera* plant growth parameters, total sugars, proteins, lipids, flavonoids, phenols, GA, IAA, SA, antioxidant level and declined ABA and ACC level under drought stress conditions. Endophytic bacteria *Methylobacterium oryzae* CBMB20 and its ACC deaminase knockdown mutants (*acdS*<sup>-</sup>) declined ethylene level by 23 % and efficiently regulated ethylene-induced pathogenesis related signalling in *Capsicum annuum* L. plants under salt stress (Choudhury et al., 2023).

Wang et al. (2022) isolated ACC deaminase positive fungi belonging to different genera from non-invasive perennial halophyte *Kosteletzkya virginica* and found *Trichoderma viride* inoculation significantly enhanced plant growth parameters, chlorophyll contents, and antioxidant activities in wheat and soyabean plants. Furthermore, treatments with *T. asperellum* or *T. viride* strains induced downregulation of ACO and ACC synthase genes expression and declined ethylene production to neutralize salt stress toxicity in inoculated plants. These studies depicted the role of stress induced phytohormonal regulation by indigenous microbiome of plants grown in stress environments and microbiome engineering with potential microbes promote other plant growth, enhanced tolerance to environmental stress and ensures sustainable crop productivity.

#### 4.3. Endomicrobiome-nutrient management for stressed crop development

Plant-endomicrobiome facilitates nutrients availability for plant health by mineral solubilization and atmospheric N fixing services (Zhu et al., 2023; Vimal et al., 2024). Endomicrobiome efficiently improved nutritional dynamics inside plant tissues and manages existing equilibrium under different stress environments. Endomicrobiome gets low oxygen environment inside plant tissues and additionally fix N compared to rhizo-microbiome (Scholz et al., 2023). N level exhibited a critical role in plant biochemistry, being an integral component of many compounds, including chlorophyll, enzymes, amino acids as well as proteins (Duran et al., 2018; Singh and Vimal, 2020).

Rice root endophytic diazotrophic *Azotobacter* sp. Avi2 develop biofilm areas around root zone and form strong association with the host plant. Biofilm reduced O<sub>2</sub> tension from nitrogenase system which is very sensitive to oxygen, enhanced N-fixation activity, nutrient trapping and quorum sensing between microbes (Wang et al., 2017). *Azotobacter* sp. Avi2 significantly enhanced paddy plant growth under *in-vitro* and *in-vivo* conditions under optimized inocula level and recommended over rhizobacteria for plant inoculation (Banik et al., 2019). Endophyte *Bacillus cereus* G2 isolated from roots of *Glycyrrhiza uralensis* efficient

upregulated multiple genes of nitrate reductase, nitrite, glutamate synthase and osmolytes proline, glycine, betaine biosynthesis and facilitates N availability to *Glycyrrhiza uralensis* and protect by osmolytes subjected to saline stress conditions (Peng et al., 2023). When the *Arabidopsis thaliana* roots were co-cultivated with <sup>15</sup>N-labelled endophytic fungus *Piriformospora indica*, enhancement was found in N content in plant leaves under N-starved conditions but not in plants supplied with sufficient N. This study denoted that the *P. indica* participates in plant's metabolomic adaptation against N limitation by delivering reduced N metabolites to the host, thus alleviating metabolic N starvation responses and reprogramming the expression of N metabolism-related genes (Scholz et al., 2023).

Endomicrobiome services significantly enhances bioavailability of water-soluble nutrients, especially phosphorus (P) in the form of phosphate (Castrillo et al., 2017; Chouhan et al., 2021). Mycorrhizal microbiome forms symbiotic associations with plants have long been known to enhance P transport in plants (Nacoon et al., 2020). Microbiome mediated production of organic acids anions as gluconic, malic, citric, oxalic, salicylic and beneneacetic acid efficiently solubilize P in plant available forms. *In vitro* solubilization of tricalcium phosphate [Ca<sub>3</sub>(PO<sub>4</sub>)<sub>2</sub>] (TCP) on petri-plates by microbes exhibited P availability for microbes (Castrillo et al., 2017; Vimal and Singh, 2020). Berza et al. (2022) isolated endophytic microbes as *Gluconobacter cerinus*, *Acinetobacter soli*, *Achromobacter xylosoxidans* and *Bacillus thuringiensis* from *Erythrina brucei* root nodule exhibited excellent P mineralization activity on medium supplemented with aluminium phosphate (Al-P), iron phosphate (Fe-P) and TCP. These microbes showed positiveness for IAA production activity and recommended as efficient microbial inoculants for *E. brucei* in both alkaline and acidic soils.

#### 4.4. Endomicrobiome-secondary metabolites biosynthesis for stressed crop development

Endomicrobiome regulates the metabolites equilibrium inside plant tissue and re-configure plant metabolome that depends on the combination of plant genotypes, root exudates pattern and microbiome recruitment (Liu et al., 2023). Increasing evidence suggests that the plant-endomicrobiome interaction significantly enhanced the plant metabolites production and enhanced plant medicinal and industrial value (Thomlodi et al., 2021; Narayanan and Glick, 2022). Plant metabolites are low molecular weight organic compounds classified into three main categories. Primary metabolites are highly conserved in nature and directly required for plant growth particularly sugars, amino acids and organic acids. Once out into the soil, primary metabolites serve as labile growth substrates that are rapidly consumed by fast-growing generalist microbial populations (Gomes et al., 2023). Secondary metabolites have pinpointed influenced the microbiome by a diverse set of molecules including phenolics, terpenes, coumarins, glucosinolates, benzoxazinoids and different N containing compounds (Narayanan and Glick, 2022; Kaliaperumal et al., 2023). Third are plant hormones that promoted plant metabolism, biochemistry, and physiology in different environments. All these metabolites have significant direct and indirect impacts on the population dynamics and physiological processes of endophytic microbiota (Gomes et al., 2023; Makhwitine et al., 2023).

Root exudates containing more than hundred metabolites and played a pivotal role for endomicrobiome recruitment and its functional activities (Liu et al., 2023). Recently, endophytic fungal bioagent *Lasiodiplodia pseudotheobromae*, isolated from roots of *Andrographis paniculata* produces antimicrobial metabolites as 1-octadecene, erythritol, niacin, oleic acid, phenol, pantolactone, phenyl-ethyl alcohol, *p*-cresol, *t*-butyl hydroquinone and effectively suppressed the mycelium growth of phytopathogens *Fusarium oxysporum*, *Rhizoctonia solani* and *Macrophomina phaseolina* (Segaran and Sathivelu, 2023) under *in-vitro* exponential conditions. Endophyte *Fusarium decemcellulare* F25 isolated from the stem of Chinese medicinal plant *M. fortune* produces beneficial bioactive

Table 2

Hypervariable region sequencing with next generation techniques and endomicrobiome diversity composition in different plants.

S. No.	Plant	Endomicrobiome diversity composition	Hypervariable region	Techniques applied	References
1.	<i>Oryza sativa</i> L.	<i>Acidovorax</i> , <i>Alcaligenes</i> , <i>Bacillus</i> , <i>Chryseobacterium</i> , <i>Comamonas</i> , <i>Curtobacterium</i> , <i>Delftia</i> , <i>Microbacterium</i> , <i>Ochrobactrum</i> , <i>Pantoea</i> , <i>Pseudomonas</i> , <i>Rhizobium</i> , <i>Rhodococcus</i> , <i>Sphingobacterium</i> , <i>Staphylococcus</i> , <i>Stenotrophomonas</i> , and <i>Xanthomonas</i>	V3-V4	Metagenomic NGS mNGS	Kumar et al. (2021)
2.	<i>Panax ginseng</i> ( <i>Panax ginseng</i> C. A. Mey.)	<i>Ochrobactrum</i> , <i>Cupriavidus</i> , <i>Sphingomonas</i> , <i>Mycobacterium</i> , <i>Muribaculaceae</i> , <i>Methylobacterium</i> , <i>Mycobacterium</i> , <i>Brevundimonas</i> , <i>Lactobacillus</i> , <i>Allorhizobium</i> , <i>Caulobacterium</i>	V5-V7	High-throughput sequencing	Fan et al. (2022)
3.	<i>Gentiana officinalis</i> , <i>G. siphonantha</i>	<i>Rhizobiaceae</i> , <i>Pseudomonas</i> , <i>Novosphingobium</i> , and <i>Pantoea</i>	V4	High-throughput sequencing	Dang et al. (2020)
4.	<i>Mirabilis himalaica</i> (Edgew.)	<i>Streptomyces</i> , <i>Acidibacter</i> , <i>Steroidobacter</i> , <i>Sphingomonas</i> , and <i>Pseudonocardia</i>	V5-V7	Illumina sequencing	Zhang et al. (2023)
5.	<i>Asparagus officinalis</i> L.	<i>Pseudomonas</i> , <i>Pantoea</i> , <i>Virgisporangium</i> , <i>Bradyrhizobium</i> , <i>Actinophytocola</i> , <i>Lechevalieria</i> , <i>Kribbella</i> , <i>Bacillus</i> , and <i>Nocardioides</i>	V5-V7	Illumina MiSeq	Su et al. (2021)
6.	<i>Gentiana officinalis</i> , <i>G. siphonantha</i>	<i>Tetracladium</i> , <i>Cadophora</i> , <i>Cladospira</i> , <i>Calyptella</i> , <i>Ascomycota</i> sp., <i>Efibulobasidium</i> , <i>Alatospora</i> , <i>Pseudomonas</i> , <i>Polyangium</i> , <i>Aetherobacter</i> , <i>Steroidobacter</i> , <i>Terrimonas</i> , <i>mycobacterium</i> and <i>Bacillus</i>	V3-V4	Illumina NovaSeq	Hou et al. (2022)
7.	<i>Panax notoginseng</i>	<i>Conexibacter</i> , <i>Gemmatimonas</i> , <i>Holophaga</i> , <i>Luteolibacter</i> , <i>Methylophilus</i> , <i>Prostheco bacter</i> , <i>Solirubrobacter</i> , <i>Bradyrhizobium</i> , <i>Novosphingobium</i> , <i>Phenylobacterium</i> , <i>Sphingobium</i> and <i>Steroidobacter</i>	V1-V2	Illumina MiSeq	Dong et al. (2018)
8.	<i>Coptis teeta</i>	<i>Mycobacterium</i> , <i>Salmonella</i> , <i>Nocardioides</i> , <i>Burkholderia</i> - <i>Paraburkholderia</i> , <i>Rhizobium</i> , <i>Mycobacterium</i> , <i>Salmonella</i> , and <i>Nocardioides</i>	V3-V4	Illumina MiSeq	Liu et al. (2020)
9.	<i>Olea europaea</i> L.	<i>Parastagonospora</i> , <i>Foliophoma</i> , <i>Candida</i> , <i>Torulaspora</i> , <i>Issatchenkia</i> , <i>Parastagonospora avenae</i> , <i>Foliophoma fallens</i> , <i>Candida</i> , <i>Torulaspora</i> , <i>Issatchenkia</i> , <i>Rhodotorula</i> , <i>Pleosporales</i> ,	ITS-1	Illumina MiSeq	Costa et al. (2023)
10.	<i>Dicoma anomala</i> L.	<i>Pseudomonas</i> , <i>Acenitobacter</i> , <i>Arthrobacter</i> , <i>Bacillus</i> , <i>Bradyrhizobium</i> , <i>Methylobacterium</i> , <i>Sphingobium</i> , <i>Vulcaniibacterium</i>	V3-V4	Illumina MiSeq	Maela et al. (2023)
11.	<i>Epimedium koreanum</i> Nakai	<i>Hydnobolites</i> sp., <i>Setoscyph</i> sp., <i>Ramularia</i> , <i>Sphaerulina</i> sp., <i>Sebacina</i> sp., <i>Exophiala</i> sp., <i>Aspergillus</i> sp., <i>Mortierella</i> sp., <i>Glomas</i> , <i>Aureobasidium</i> , <i>Cerulococci</i> sp., <i>Trichoderma</i> sp., <i>Amphinema</i> sp., <i>Aspergillus</i> sp., <i>Dissoconium</i> sp. and <i>Articulospora</i> sp	V3-V4	Illumina MiSeq	Jiawen et al. (2022)
12.	<i>Camellia sinensis</i> L.	<i>Cladosporium</i> , <i>Strelitziana</i> , <i>Zyoseptoria</i> , <i>Pseudeurotium</i> , <i>Pseudoramichloridium</i> , <i>Penicillifer</i> , <i>Trichoderma</i> , <i>Paraconiothyrium</i> , <i>Melanconiella</i> , and <i>Saccharomycopsis</i>	ITS1	Illumina HiSeq	Wu et al. (2020)
13.	<i>Salicornia europaea</i> , <i>Suaeda maritima</i> , and <i>Camphorosma annua</i>	<i>Hydrogenophaga</i> , <i>Altererythrobacter</i> , <i>Paracoccus</i> , <i>Jonesia</i> , <i>Pelagibacterium</i> , <i>Rhizobium</i> , <i>Luteimonas aestuarii</i> , <i>Oceanisphaera</i> , <i>Azoarcus</i> , <i>Pseudomonas</i> and <i>Oceanisphaera</i> sp.	V3-V4	Illumina MiSeq	Dragojevic et al. (2023)

metabolites as 12-epicitreoisocoumarinol, eisocoumarinol, citreoisocoumarin, trichophenol A, rigidiusculamide B, fusaristatins A, enniatin H, enniatin I, nectriacid A, nectriacid B, 4-hydroxy-3, 6-dimethyl-2 H-pyrane-2-one, macrocarpon C, and  $\alpha$ -linoleic acid and inhibit the growth of phytopathogen causes anthracnose of banana (*Collectotrichum musae* ATCC 31244) under *in-vitro* agar diffusion assay (Song et al., 2023).

Kaliaperumal et al. (2023) isolated novel anticancer bioactive metabolite averufin from *Penicillium verrucosum* sponge-derived endophytic fungi from *Spongia officinalis* and suggested for clinical trials. Whole genome sequence of endophytic bacteria *Bacillus halotolerans* Hil4, isolated from leaves of medicinal plant *Hypericum hircinum*, exhibited secondary metabolite biosynthetic gene clusters (BGCs), produced metabolites as surfactin, mojavensin, fengycin, 1-dihydroantipain, bacillibactin, bacillaene, and azelaic acid significantly declined disease incidence (70 %) and disease severity index (25.5 %) against the Gray-Mold postharvest disease on grape berries and cherry tomatoes (Thomludi et al., 2021). Endophytic fungus *Beauveria bassiana* upregulated metabolites activities as  $\alpha$ -solanine, 5-O-caffeoylshikimic acid, clerodendrin, peucedanin related with alkaloid, flavonoids biosynthesis and tryptophan metabolism pathways. Additionally, gene silencing of UDP-glucose:sterol glucosyltransferase, a gene involved in  $\alpha$ -solanine synthesis, indicated that *B. bassiana* efficiently inhibit the herbivore pest whitefly *Bemisia tabaci* by  $\alpha$ -solanine (Wang et al., 2023).

Shabban et al. (2023) reported *Aspergillus* sp. strain FVL2 efficacy of producing novel metabolites 7-demethyl-neosulochrin, fumigaclavine I, *N*-benzoyl-tryptophan supported the discovery of novel secondary metabolites producing efficacy of *Aspergillus*. Liu et al. (2023) obtained thirteen bioactive secondary metabolites with diverse C skeletons, including a novel polyketide with unique 5,6-dihydro-4H, 7H-2,

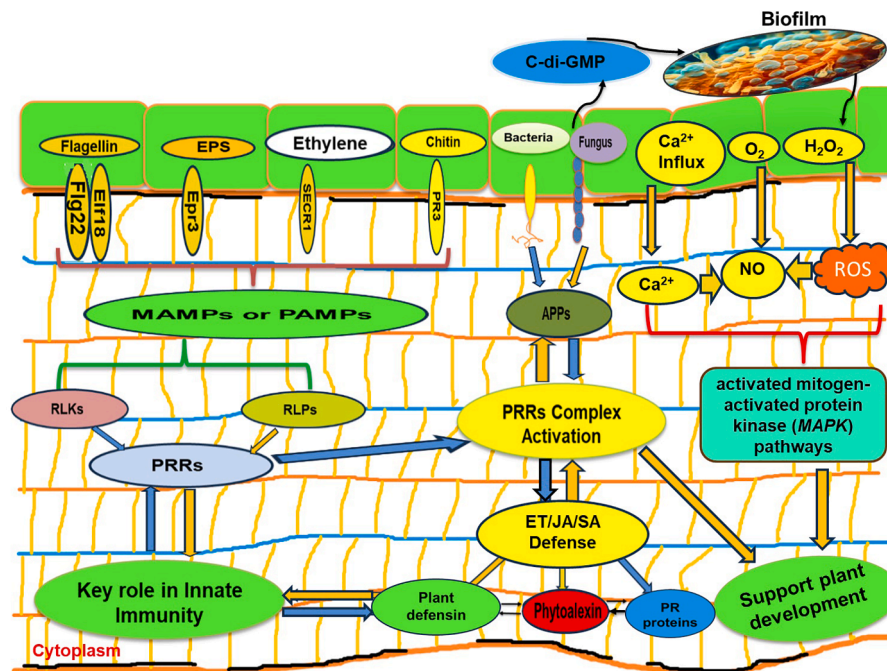
6-merthanopyrano [4,3-d] dioxocin-7-one ring system and three unreported polyketides structures from endophytic fungus *Neocamarosporium betae*, isolated from desert plant *Suaeda glauca* (*Chenopodiaceae*) and *Nitraria roborowskii* (*Zygophyllaceae*). This study confined the hypothesis that endophytic fungi in desert drought stress environment possibly produce novel bioactive metabolites to protect and promote plant health in stress conditions. Therefore, considering the potential of secondary metabolites as a natural resources for medicinal and industrial applications, there is an urgent needs to adopt alternative approaches as cell suspension culture, and metabolic engineering of plant-microbiome; in respect to the later, the manipulation of plant endomicrobiome to mediate the production of valuable metabolites.

## 5. Plant-endomicrobiome adaptations, genomic and functional profiling elegance for stressed crop development

Practically, all the living organisms on planet earth interact with one another in different ways, and they all coexist as a community (Copeland and Schulze-Lefert, 2020; Qian et al., 2021). Ecological theories advocated that the microbial communities are designed by a multifaceted interaction of four fundamental eco-evolutionary processes as (a) microbial recruitment-communities influenced by abiotic and biotic factors (b) dispersal-microbial movement between communities (c) ecological drift-stochastic variation in growth and death (d) diversification-genetic variation. However, microbial recruitment, movement, ecological drift and immunity positively affected the microbial diversity in respective microbiome (Cordovez et al., 2019; Yuan et al., 2021).

The plant is providing an environment for microorganisms with different ecological niches, interconnected at the spatial and temporal





**Fig. 3.** Endophytes mediated immunity evolving different MAMPs/PAMPs and components of cell wall. Endophytes interface with host immune signalling components by developing receptor proteins, effectors, phytohormones, cytosolic calcium, reactive oxygen species and strengthen immune response of plants to pathogens and facilitates niche development. Abbreviations: exopolysaccharides (EPS), microbial associated molecular patterns (MAMPs), pathogen-associated molecular patterns (PAMPs), receptor-like kinases (RLKs), receptor-like proteins (RLPs), pattern recognition receptors (PRRs), apoplastic proteins (APPs), ethylene (ET), jasmonic acid (JA), salicylic acid (SA), cytosolic calcium (Ca<sup>2+</sup>), reactive oxygen species (ROS).

scale (Anten and Vermeulen, 2016; Canarini et al., 2021). However, plants grow in an open environment influenced from external (environment) and internal (developmental) factors, resulting in a dynamic system of adaptive responses of physiological processes (Ganie et al., 2022). Microorganisms can be shifted to the crop hosts via the vertical transmission from parent plants and seeds, as well as horizontal transmission from complex environment as soil microbial seedbank, adjoining plants, insects and animal interaction (Edwards et al., 2021; Abdelfattah et al., 2023). Thus, existence in the plant may need microbial population to be highly adaptable on community and cellular level.

The shifts in endophyte communities can be attributed to several factors, and one key factor is the ability of individual endophyte species to adapt to changes in the plant environment (French et al., 2021). Different endophytes may possess varying mechanisms for coping with environmental stressors, such as changes in temperature, nutrient availability, phytohormones, metabolites or other conditions (Deng et al., 2019; Choudhury et al., 2023). Some endophytes may thrive in specific environmental conditions, while others may struggle to survive or reproduce under altered circumstances (Hagaggi and Abdul-Raouf, 2022). As a result, the relative abundance of different endophyte species within a community may change in response to environmental shifts (Khan et al., 2012). Additionally, interactions between endophyte species within the community can also contribute to observed shifts. These interactions may include competition for resources, mutualistic relationships, or even antagonistic interactions. For example, one endophyte species may produce compounds that inhibit the growth of competing species or enhances the fitness of the host plant, leading to changes in the overall composition of endophyte communities (Hordoim et al., 2015). Next generation genome sequencing, metagenomic profiling of microbiota exhibited endomicrobiome diversity and functional dynamics are dynamic and transform during plant parts and development stages (Liang et al., 2024) as well as in environments (Copeland and Schulze-Lefert, 2020; Wang et al., 2023) in multiple plants.

Different studies have reported endomicrobiome architecture in

different plants in recent years with different next generation high throughput sequencing tools stretching hypervariable region (V1-V9) have been illustrated in Table 2. Recently, Zhang et al. (2023) collected *Mirabilis himalaica* from five different locations in China and studies bacterial diversity with 16S r-RNA V5-V7 hypervariable region with Illumina sequencing in different plant parts. The *Proteobacteria* and *Actinobacteria* were the dominant phyla in all the samples, while the dominant genera changed based on the different tissues and varies with physicochemical properties. The *Streptomyces*, *Acidibacter*, *Steroidobacter*, *Sphingomonas*, and *Pseudonocardia* were the dominant genera in plant core endomicrobiome. These microbial community dynamics were significantly correlated with nutritional status N, P, K, soil organic matter and environmental conditions. Costa et al. (2023) examined endophytic community in the phyllosphere of the different olive (*Olea europaea* L.) cultivars target ITS1 region with Illumina Mi Seq and reported *Ascomycota* was the richest and most abundant phylum, followed by *Basidiomycota*, genus *Parastagonospora*, *Foliophoma*, *Parastagonospora*, *Foliophoma*, *Candida*, *Torulasporea*, *Issatchenkia* *Parastagonospora avenae*, *Foliophoma fallens*, *Candida*, *Torulasporea*, *Issatchenkia*, *Rhodotorula*, and *Pleosporales* were found in phyllosphere and some of them have potentially antifungal activity against the different pathogens including causal agent of anthracnose.

Jiawen et al. (2022) reported foremost genera *Glomas*, *Aureobasidium*, *Hydnobolites* sp., *Setoscyph* sp. *Ramularia*, *Sphaerulina* sp., *Sebacina* sp., *Exophiala* sp., *Aspergillus* sp., *Mortierella* sp. *Cerulococci* sp., *Trichoderma* sp. *Amphinema* sp., *Aspergillus* sp., *Dissoconium* sp. and *Articulospora* sp. in Korean plant *Epimedium koreanum* Nakai, analyses V3-V4 region with Illumina Mi Seq. The variance inflation factor showed that the nutritional factors as soluble salt, whole nitrogen, alkaline lysis N, P, K and environmental factors were significantly and positively associated with dominant microbiota *Sebacina* sp. Hou et al. (2022) studied microbial diversity in *Gentiana officinalis* and *G. siphonantha* association with secondary metabolite with Illumina NovaSeq tool and found *Tetracladium* and *Cadophora* were dominant fungal genus in *G. officinalis* and *G. siphonantha* samples, respectively. While *Pseudomonas* was

dominant bacterial genus in two closely related species, with relative abundances were 8.29 and 8.05 %, respectively. Secondary metabolite loganic acid was positively correlated with endophytic fungi, while gentiopicoside, swertiamarine and sweroside were significantly positively correlated with endophytic bacteria in both species.

Dragojević et al. (2023) examined the endo-rhizosphere of indigenous succulent halophytes *Salicornia europaea*, *Suaeda maritima*, and *Camphorosma annua* from the natural salt marshes of *Slano Kopovo* (Serbia) sequencing V3-V4 region with Illumina MiSeq. The genus diversity comprises with *Hydrogenophaga*, *Altererythrobacter*, *Paracoccus*, *Jonesia*, *Pelagibacterium*, *Rhizobium*, *Luteimonas aestuarii*, *Oceanisphaera*, *Azoarcus*, *Pseudomonas* and *Oceanisphaera* sp. Additionally, isolated strains (65 %) belong to halotolerant genera *Halomonas*, *Kushneria*, and *Halobacillus* tolerated salinity level (3 %–25 %) and exhibited in-vitro plant growth promotory actives as IAA, Biofilm formation, nutrient solubilization and ACC Deaminase activity. Thus, growing all evidence suggests that the nutritional dynamics and environmental factors played vital role in endomicrobiome recruitment, interplay, diversity and functional homeostasis. Plant-endomicrobiome signalling significantly encourages bioactive metabolites, phytohormones, stress regulators and antimicrobials activities inside plant equilibrium. However, there are still several gaps and challenges in this research area, as effective endomicrobiome for specific growth promoting activity is difficult due to their immense diversity, species specificity and variable population. Addressing, these challenges require interdisciplinary research with advanced next generation tools as well as omics technologies, enabling researchers to better understand their functions and interactions in plant ecosystems.

## 6. Plant-endomicrobiome long-distance communication and immunity interplay for stressed crop development

Endophytic microbes are capable of infecting plant tissues by evading the plant's immune response (Yuan et al., 2021). This ability to circumvent the plant's defence mechanisms is crucial for establishing a successful endophytic relationship (Liang et al., 2024). Endophytes may contribute to the plant's ability to withstand environmental stressors such as drought, pathogens, or other adverse conditions (Vimal et al., 2023a). Plants have mechanisms for selectively allowing microbial colonization. This selectivity involves the recognition of beneficial microbes and the initiation of symbiotic relationships while finding off potential pathogens. The plant's selective allowance of microbial colonization involves the expression of phenotypic genes and the release of metabolic signals (Saijo et al., 2018; Choudhury et al., 2023). These signals play a role in guiding the development of endophyte structures within the plant tissues. Metabolic signals released by the plant serve as communication cues for endophytic microbes (Narayanan and Glick, 2022). These signals can influence the behaviour and function of the endophytes, contributing to a harmonious interaction that benefits both the plant and the microbes.

Plants have evolved a sophisticated innate immune system to sense and recognize invading microorganisms and efficiently trigger defence accounts (Fig. 3) (Bazin et al., 2020). Plants recognizes microbial appearance on its surface with detection of conserved microbial or pathogen-associated molecular patterns (MAMPs or PAMPs), as bacterial flagellin and fungal chitin, through transmembrane pattern recognition receptors (PRRs) (Lu et al., 2010; Deng et al., 2019). When PRRs on the plant cell surface recognize molecular patterns, it triggers a series of intracellular signalling cascades leading to PAMP-triggered immunity (PTI). PTI is a broad-spectrum defence response that helps protect the plant from a wide range of potential pathogens (Hacquard et al., 2017). PTI activation leads to the induction of various receptor like kinases (RLKs), receptor like proteins (RLPs), activation of mitogen-activated protein kinase (MAPK) cascades (Trda et al., 2014). However, pathogens and microbes can overcome the first layer by suppressing PTI signalling or evading recognition of PRRs by secreting virulence effectors.

Some pathogens can secrete effector molecules to suppress PTI. In response, plants have evolved resistance through polymorphic NB-LRR proteins (processing nucleotide-binding and leucine rich repeat domains), resulting in hypersensitive reaction to limit the pathogens multiplication and this specific defence response known as effector-triggered immunity (ETI) (Hacquard et al., 2017).

Recently, Yuan et al. (2021) reported that the PRRs has also needed for ETI. PTI and ETI have significantly improved the status of defence signalling pathways including changes in ion fluxes, enhanced cytosolic  $Ca^{2+}$  and production of reactive oxygen species and activated mitogen-activated protein kinase (MAPK) pathways. Leading synthesis of nitric oxide, ethylene, salicylic, jasmonic acid, antimicrobial compounds, pathogenesis-related (PR) proteins, and stomatal regulation, callose deposition, and transcriptional and metabolomics reprogramming contributed to the plant's defence arsenal (Calvo et al., 2014). However, growing evidences suggests that there are many more complex pathways of plant-microbiome immunity interactions that exists in plants and yet to be discovered.

Lipopolysaccharides (LPS) is a component of the outer membrane of Gram-negative bacteria (Singh and Vimal, 2020). Plants can detect LPS as a MAMP, triggering responses that are often associated with the establishment of beneficial relationships with certain bacteria (Sasse et al., 2018). Plant distinguishes microbial derived chitin oligosaccharides, exopolysaccharides (EPS) leading to activation of defence and establishment of beneficial interactions (Genre et al., 2013). The ability of plants to recognize specific MAMPs allows them to discriminate between beneficial and pathogenic microbes (Hacquard et al., 2017). This recognition is crucial for the establishment of symbiotic relationships, such as mycorrhizal associations and nitrogen-fixing nodules formed with certain bacteria (Genre et al., 2013). Upon ligand binding, the PRRs may recruit co-receptors or associate with additional proteins to form receptor complexes. These co-receptors enhance the sensitivity and specificity of the recognition process (Calvo et al., 2014). The ligand-bound PRRs and co-receptors form complexes, creating a molecular signalling platform on the cell surface. This complex formation is a critical step in transducing the extracellular signal to intracellular signalling cascades as  $Ca^{2+}$  influx play vital role in downstream process; MAPK activation leads to the phosphorylation of target proteins and phytohormone signalling play pivotal roles in regulating plant interactions (Pfeilmeier et al., 2016; Bazin et al., 2020). The 22-aminoacid epitope in N terminal part of flagellin, is highly conserved in wide range of bacteria as *Bacillus subtilis* have recognized by plants (Deng et al., 2019). FLAGELLIN-SENSING 2 (FLS2) receptors initiate heterodimerization between its co-receptors BRI1-ASSOCIATED KINASE (BAK1) and BAK1-LIKE (BKK1). These co-receptors phosphorylate their interacting receptors-like cytoplasmic kinase BOTRYTIS-INDUCED KINASE (BIK1) and regulate PTI signalling (Segonzac and Zipfel, 2011). BIK1 has phosphorylated and subsequently trans-phosphorylated FLS2/BAK1 complex and transmit flagellin signalling and activate intracellular signalling cascades (Lu et al., 2010). BIK1 is designated as an essential component in MAMPs signal transduction and induced systemic resistance in plants. Beneficial microbes produce a large number of MAMPs and trigger host-microbe long distance communication as well as immunity (Hacquard et al., 2017).

Indeed, there is a high degree of overlap between symbiotic signalling and immune signalling in plants. This overlap is often facilitated by cross-regulations within host PRRs pathways. Microbial polysaccharides, cyclic glucans, are important signals for microbial interactions within plants. Additionally, some VOCs targets key points and activate downstream metabolic pathways by domino effect and MAMPs source for plant microbe interaction (Massawe et al., 2018; Sasse et al., 2018). Hence, not all endophytes can form a decisively advantageous symbiotic association in hosts. This recognition depends on plant type, endophyte genotype, physiological environment and play significant role in immunity interplay and long-distance communication between endophytic microbes for stress management. Proposed model exhibiting

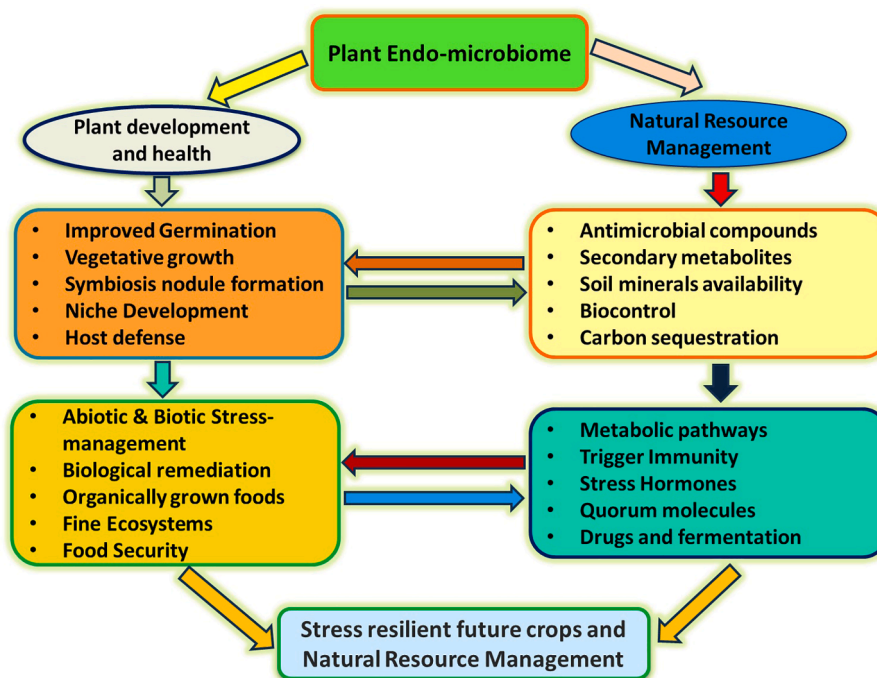


Fig. 4. Proposed model exhibiting the plant endomicrobiome services in stress resilient future crops and NbS.

the plant endomicrobiome services in stress resilient future crops and NbS is shown in Fig. 4.

## 7. Conclusion

The plant endosphere serves as an eclectic and dynamic habitat for microbes to occupy in order to proliferate and create a beneficial endomicrobiome inside different plant parts, offer NbS to conserve the nature, natural resources to improve plant performance. Still, there are big gaps regarding the recruitment, lifestyle, mechanisms and immunity interplay in plant-endomicrobiome services. In this review, we have summarized the nascent corpus of scientific evidence regarding the role of plant endomicrobiome structure and strategies to produce stress resilient future crop. However, deeper understanding of indigenous plant-endomicrobiome interplay and functional dynamics is needed for implementation from laboratory to field scale to restore and regenerate the complexity and diversity of different agro-ecosystems. Multiple microbial communities architecture and functional dynamics hypothesises and proven in last few years, but we don't still completely understand which physico-biological conditions enrich specific microbiota development. Improved understanding of characteristics and dynamics of endomicrobiome mediated bioactive molecules, signalling, immunity interplay as well connections between endomicrobiome, environmental, physiological factors play vital role in microbiome engineering. In addition, we must investigate the divergent *in-planta* activities, connecting colonization, population diversity, signalling in different plant tissues and at different plant growth stages with activity levels, in order to completely comprehend the role and contribution of endomicrobiome to support plant performance, functioning and immunity in different environments. The emerging genomics and omics insight tools in association with chromatography, synthetic biology, genome editing, metabolic engineering, machine learning and data designing provide an opportunity to develop efficient engineered microbiome for particular plant species. Transdisciplinary and active cooperation between agriculturists, microbiologists, biochemists, bioinformaticians, and big data analysts are necessary for the development of engineered plant endomicrobiome to produce stress resilient future crop.

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## CRediT authorship contribution statement

**Shobhit Raj Vimal:** Conceptualization, Data curation, Formal analysis, Writing – original draft. **Jay Shankar Singh:** Writing – review & editing. **Ashwani Kumar:** Writing – review & editing. **Sheo Mohan Prasad:** Supervision.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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