



Crop microbiome: their role and advances in molecular and omic techniques for the sustenance of agriculture

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Abstract

Main conclusion This review is an effort to provide in-depth knowledge of microbe's interaction and its role in crop microbiome using combination of advanced molecular and OMICS technology to translate this information for the sustenance of agriculture.

Abstract Increasing population, climate change and exhaustive agricultural practices either influenced nutrient inputs of soil or generating biological and physico-chemical deterioration of the soils and affecting the agricultural productivity and agro-ecosystems. Alarming concerns toward food security and crop production claim for renewed attention in microbe-based farming practices. Microbes are omnipresent (soil, water, and air) and their close association with plants would help to accomplish sustainable agriculture goals. In the last few decades, the search for beneficial microbes in crop production, soil fertilization, disease management, and plant growth promotion is the thirst for eco-friendly agriculture. The crop microbiome opens new paths to utilize beneficial microbes and manage pathogenic microbes through integrated advanced biotechnology. The crop microbiome helps plants acquire nutrients, growth, resilience against phytopathogens, and tolerance to abiotic stresses, such as heat, drought, and salinity. Despite the emergent functionality of the crop microbiome as a complicated constituent of the plant fitness, our understanding of how the functionality of microbiome influenced by numerous factors including genotype of host, climatic conditions, mobilization of minerals, soil composition, nutrient availability, interaction between nexus of microbes, and interactions with other external microbiomes is partially understood. However, the structure, composition, dynamics, and functional contribution of such cultured and uncultured crop microbiome are least explored. The advanced biotechnological approaches are efficient tools for acquiring the information required to investigate the microbiome and extract data to develop high yield producing and resistant variety crops. This knowledge fills the fundamental gap between the theoretical concepts and the operational use of these advanced tools in crop microbiome studies. Here, we review (1) structure and composition of crop microbiome, (2) microbiome-mediated role associated with crops fitness, (3) Molecular and -omics techniques for exploration of crop microbiome, and (4) current approaches and future perspectives of crop microbiome and its exploitation for sustainable agriculture. Recent -omic approaches are influential tool for mapping, monitoring, modeling, and management of crops microbiome. Identification of crop microbiome, using system biology and rhizho-engineering, can help to develop future bioformulations for disease management, reclamation of stressed agro-ecosystems, and improved productivity of crops. Nano-system approaches combined with triggering molecules of crop microbiome can help in designing of nano-biofertilizers and nano-biopesticides. This combination has numerous merits over the traditional bioinoculants. They stimulate various defense mechanisms in plants facing stress conditions; provide bioavailability of nutrients in the soil, helps mitigate stress conditions; and enhance chances of crops establishment.

Keywords Microbiome · Microbial community · Crops · Bioinoculant · Bioformulation · Molecular approach · Omics

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Introduction

The microbial community associated with the crop is referred as crop microbiome. A wide variety of microorganisms are present in the different parts of crops, such as the rhizosphere, phyllosphere, and endosphere. These naturally occurring microbes are the integral part of the crop microbiome, and their functions impact plant growth and productivity (Bargaz et al. 2018; Zope et al. 2019; Sagar et al. 2020a, b, 2022a, b; Khan et al. 2021). The multifaceted network of microbiome is related to various organs of crops, which provides hidden information about functional interaction of plant–microbe. These information help to select potential beneficial microbes for mitigation of stressed agricultural ecosystems and improve crop productivity. However, till date, exhaustive agricultural practices show the dodges in microbial/biotechnology and there is necessity of recent -omics approaches to unfold the complete information of mechanisms of microbiome (Brader et al. 2017; Lemanceau et al. 2017; Khan et al. 2019; Sukmawati et al. 2021).

To achieve the target of increased food demand of growing world population, sustainable improvements are needed in soil quality and fertility, plant growth promotion, biocontrol, stress tolerance, and high yield crop production. The application of plant growth-promoting potential of crop microbiome has been used as the best substitute to synthetic agro-chemicals (Mitter et al. 2016; Basu et al. 2021; Hamid et al. 2021). In these consequences, recent and advanced molecular techniques are applied to reveal information about crop microbiome concerning abiotic and biotic stimulus, plant genetic makeup, and environment. This helps to search for suitable strains or inoculation in stressed conditions (Mitter et al. 2016; Ahmed et al. 2021; Sagar et al. 2020a).

Advances in microbiome practices and molecular and analytical tools, such as microscopic and tagged-imaging techniques, bioinformatics tools, next-generation sequencing, and 'OMICS' technologies, provide deeper insights into the crop-specific microbiome (Nilsson et al. 2018; Rai et al. 2020; Santos and Olivares 2021). These advances also provide insight into the potential of rhizospheric microbes to inhibit soil-borne plant pathogens, information of induced functional genes, functional ecosystem, and their events that contain communication between plants and microbes (Berg et al. 2016; Jansson and Hofmockel 2018). The recent revolutionary application of next-generation sequencing methods, combined with novel microscopic techniques, gives new insight into the accurate microbiome associated with crops in the agricultural land. It also provides unparalleled prospects for transforming microbiomes information into practical applications (Lee et al. 2019).

The crop-microbiome is known to exert various effects on crop growth and yield, disease suppression, and induction of resistance; however, very few crops microbiome are fully explored (Pagano et al. 2017; Zakaria et al. 2019; Rai et al. 2019a). A vast research is devoted toward the investigation and usage of beneficial crop microbes for sustainable plant growth promotion and yield improvements (Si et al. 2018; Sagar et al. 2020a, b; Khan et al. 2020; Ilyas et al. 2020). In this regard, research should emphasize toward deciphering all the aspects of interactions between crops and related microbiota, which includes different parts of crops (soil/rhizosphere, anthosphere, phyllosphere, spermosphere, and troposphere) (Kalam et al. 2020) and their complex signaling (Busby et al. 2017; Lemanceau et al. 2017; Khan et al. 2021).

Studies on crop microbiomes ensure continued food quality and safety regarding the growing population and challenges that adversely affect crop yield due to influencing constraints, like environmental condition, soil and water quality, available soil nutrients, and disease incidences (Shi et al. 2019; Abiraami et al. 2020). The present review highlights the importance and functionalities of the crops microbiome and discusses challenges and concepts regarding applying biotechnological approaches to explore, characterize, and identify crop microbiome.

Structure and composition of crop microbiome

Microbiome profiling of whole crops, different crop organs, and root-associated soils has revealed a diverse and highly dynamic microbial community which is influenced by several environmental factors such as soil type, nutrient and water availability, climate, season, as well as species of crop, different crops' compartment, and developmental stage (Copeland et al. 2015; Robinson et al. 2016). The actual dynamics and functionality define the structure and composition of the crop microbiome. Species-specific crops draw a robust selective gradient regarding microbial species richness that gradually decreases in bulk soil, followed by rhizosphere soil/rhizoplane, and is lowest in the endophytic compartment (Gao et al. 2019). The complex microbial communities' network associated with crops usually comprises archaea, bacteria, fungi, and protists, which benefited crops and performed different ecological balancing functions (Singh et al. 2020). The other parts of crops like the bulk soil or rhizospheric soil, phyllosphere, anthosphere, spermosphere, and troposphere provide habitat for microbiome establishment (Hardoim et al. 2015), and each part associated microbes perform different functions in respect of plant fitness.

Rhizosphere-associated microbial communities

Rhizosphere comprises the soil around the plant roots. Crop roots/rhizoplane/rhizospheric soil provides exclusive ecological niches for the soil microbial community, which competitively colonizes the crop roots and performs plant growth-promoting microbial activity in complex ecosystems (Dubey et al. 2020). The rhizosphere serves as a hot spot for microbial activity and provides opportunities to colonize plant roots. Its uniqueness increased by secreting species-specific crops root exudates that contain amino acids, organic acids, fatty acids, sugars, nucleotides, phytohormones, putrescine, terpenoids, sterols, and vitamins, which communicate signals in the microbiome for active colonization, uptake of transportable nutrients, and water (Kawasaki et al. 2016; Hu et al. 2018). The diversity and composition of the crop microbiome are affected by plant health, plant growth and development, and the magnitude of root exudation (Hartman et al. 2017; Anal et al. 2020). The microbiome participates significantly in soil biological practices, soil carbon sequestration, nutrient cycling through decomposed matter channelization in natural systems, plant growth promotion, pathogen inhibition through the secretory molecule, and plant immunization (Ehrmann and Ritz 2014; Rai et al. 2020). The microbiome of different crops generally comprises various dominant bacterial communities: *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, *Burkholderiales*, *Copiotrophs* *Oligotrophs*, *Planctomycetes*, *Proteobacteria*, *Pseudomonads*, *Sphingobacteriales*, *Verrucomicrobia*, and *Xanthomonadales* (Donn et al. 2015; Fierer 2017).

Fungi are an indispensable component of the agro-systems microbiome. the associated group of fungi, such as filamentous fungi, like *Trichoderma* sp. (Li et al. 2015; Rai et al. 2016), *Penicillium* sp. (Babu et al. 2015), endophytic fungi like *Aspergillus* sp., *Trichoderma* sp., *Colletotrichum* sp., *Fusarium* sp., *Cladosporium* sp., *Epicoccum* sp., and *Dendrobium moniliforme* (Chadha et al. 2015; Shah et al. 2019) and mycorrhizal fungi (Turrini et al. 2018) exert beneficial effects on the plant. Some of the dominating fungi negatively influence crop yield by causing disease, for example, *Alternaria* sp., *Colletotrichum* sp., *Fusarium* sp., *Rhizoctonia* sp., *Verticillium* sp., and *Macrophomina* sp. (Tetali et al. 2015; Kashyap et al. 2015).

Phyllosphere-associated microbial communities

The phyllosphere is the region of crop that includes foliar, leaves, and floral parts, offering distinctive epiphytic microbiome habitats. The phyllosphere microbiome comprises various microbes (Rai et al. 2020). The presence of the microbiome in the phyllosphere is regulated by environmental factors (Wallace et al. 2018). The

composition, structure, and dynamics of the phyllosphere microbiome are administrated by immigration, survival, development of the microbial colony from the environment, and physico-chemical properties of the leaf, which affects the health, the quality, and yield of crop plants (Gomes et al. 2018a, b; Yao et al. 2019). Bacterial communities are the most leading and copious microbes in the phyllosphere (Wallace et al. 2018), while pathogenic fungi are comparatively abundant (Kumar et al. 2013a, b; Kashyap et al. 2016). Several researchers reported *Acinetobacter*, *Citrobacter*, *Bacillus*, *Curtobacterium*, *Frigoribacterium*, *Enterobacter*, *Methylobacterium*, *Erwinia*, *Pantoea*, *Pseudomonas*, and *Sphingomonas*, etc. in the phyllosphere or troposphere of grapevine (Zarraonaindia et al. 2015; Kecskeméti et al. 2016). The diversity of cultured yeasts genera *Sporobolomyces*, *Cryptococcus*, *Dioszegia*, *prototypes*, *leucosporidium*, *Rhodotorula*, and *Cystofilobasidium* usually present in the phyllosphere region of various crops (Kucharska et al. 2020). The *Sphingomonads* and *Methylobacteria* were reported as the most dominant genera over the maize leaf microbiome (Wallace et al. 2018).

The phyllosphere microbiome is established by the environment such as soil, water, seed, and air and acclimates to plant tissue, which shapes the community composition. The functional relationship between the different crops and their phyllosphere microbial community is still required to understand different molecular approaches.

Endosphere-associated microbial communities

Endosphere is the internal region of the plant tissues, such as root, shoot, leaves, flowers, and fruits. Endophytic microbes are chief constituents of crop microbiomes that reside within different plant tissues without triggering disease symptoms. Endophytes live symbiotically within the plant tissue or interact with different microbes within the plant tissues, including epiphytes, mycorrhizal fungi, symbionts, pathogens, saprotrophs, etc. (Rai et al. 2020). The entrance of endophytic microbial community inside root tissues frequently happens through either passive mechanism (root cuts or beginning points of lateral roots) or active mechanisms which further spread via xylem vessel to different sections of the crop, such as stem, root, leaves, flower, and fruits (Compant et al. 2010). Crop roots are colonized by a broad range of bacterial endophytes, such as *Actinobacteria*, *Bacteroidetes*, *Firmicutes*, *Proteobacteria*, *Verrucomicrobia*, etc. (Burns et al. 2015; Faist et al. 2016). Edwards et al. (2015) found *Rhizobiaceae*, *Streptomyetaceae*, *Comamonadaceae*, and *Bradyrhizobiaceae* as the dominant families in rice roots. The significance of endophytes comprises a vast and unseen

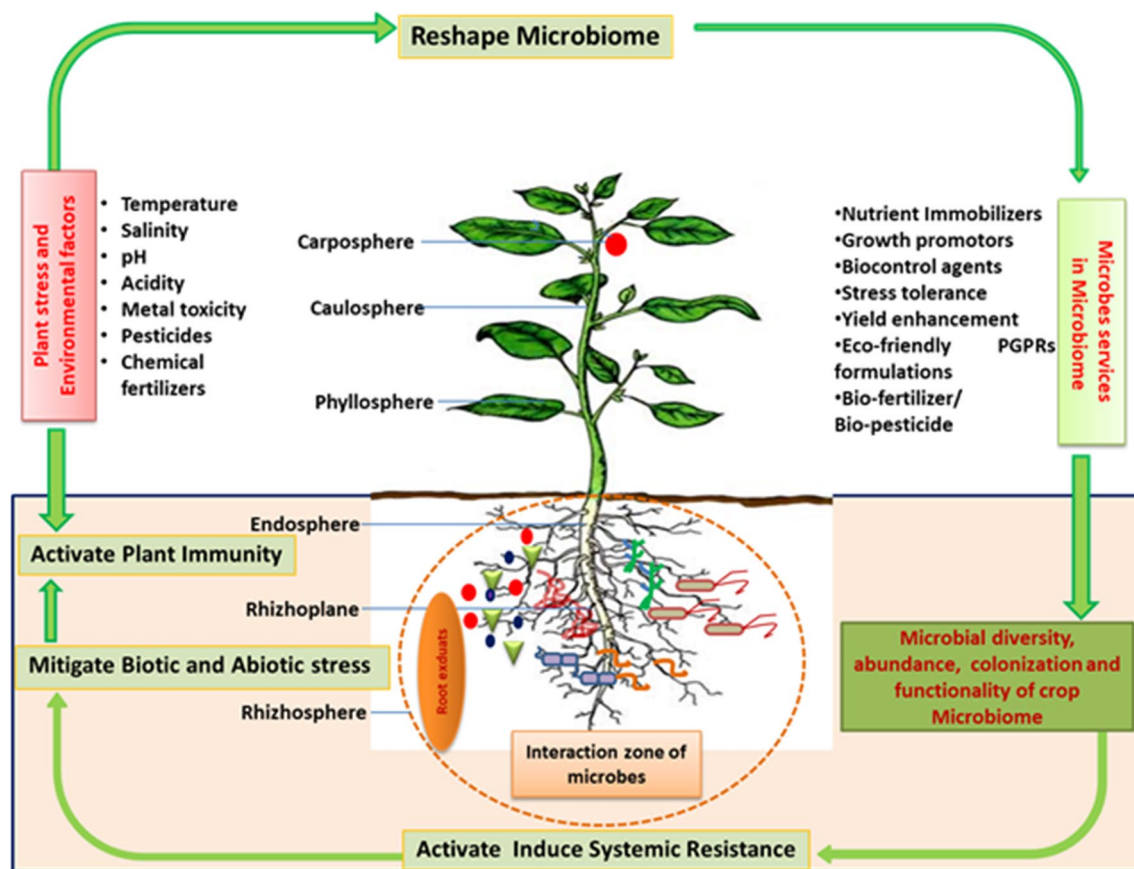


Fig. 1 Crop microbiome and role of associated microbes in the reshaping of microbiome through different functional responses. Mechanism employed by microbes of microbiome to enhance plant

growth, abiotic/biotic stress resistance and improving yield by nutrient uptake under changing climatic

element of fungal biodiversity, and they accomplish different roles in plant development, stimulation of disease resistance responses in the plant, as well as alleviation to biotic or abiotic stresses through the production of antagonistic, antimicrobial, and signaling molecules (Atugala and Deshappriya 2015; Durán et al. 2018; Kapadia et al. 2021). Endophytes affect plant health, growth, and yield by regulating the synthesis of enzymes, phytohormone (Khan et al. 2015), and antimicrobial compounds (Aramsirirujwet et al. 2016; Tian et al. 2017).

Multifaceted function of microbes in crop microbiome

Microbes are found to be closely connected with soil and plant functions like soil biogenesis, organic matter degradation, nutrient mobilization, and enhancement in plant yield (Santos and Olivares 2021). The wide varieties of different microbes and healthy plants coexist naturally and develop a complex microbial network that directly influences plant

growth and productivity. Microbes associated with the crop microbiome have an either neutral or beneficial effect on the plants' health that includes augmented nutrient availability/acquisition (van der Heijden and Hartmann 2016; Kannepalli et al. 2021), disease suppression (Hong et al. 2020), high tolerance to abiotic stresses (Agler et al. 2016a, b; Meena et al. 2017; Kour and Sayyed 2019; Nasab and Sayyed 2019), induction of systemic resistance (Reshma et al. 2018), and adaptation to climatic changes and enhanced of the root colonization (Haney et al. 2015; Fallah et al. 2021) (Fig. 1). The rhizospheric and endophytic microbial communities actively participate in different beneficial activities (Cai et al. 2016; Zhu et al. 2016a, b; Sagar et al. 2020a). Several researchers have explored various crops microbiome organization and function in natural and agricultural environments, such as *Arabidopsis thaliana* (Schlaeppli et al. 2014), barley (Bulgarelli et al. 2015), soybean (Rascovan et al. 2016; Jabborova et al. 2020), corn (Lupatini et al. 2017; Kusale et al. 2021), wheat (Chen et al. 2018; Rossmann et al. 2020; Najafi et al. 2021; Kusale et al. 2021), and rice (He et al. 2019; Suriani et al. 2020). Recently developed biotechnological techniques

Table 1 Diversity of microbial community related to different crops and their functions

Crops	Microbial community and identified micro-organisms	Tissue/compartments	Effect of community in crops' microbiome	Applied molecular approaches	References
Cereals crops					
<i>Oryza sativa</i> (Rice)	<i>Rivibacter</i> , <i>Anaeromyxobacter</i> , <i>Roseomonas</i> , <i>Geobacter</i> , <i>Thiobacillus</i> , <i>Clostridium</i> , <i>Desulfobulbus</i> , <i>Sphingomonas</i> , <i>Methylobacterium</i> , <i>Enterobacteriaceae</i> , <i>Alternaria</i> , <i>Hannaella</i> , <i>Pleosporales</i>	Seed, paddy soils	Plant growth promotion and fitness, suppression of pathogen	High-throughput Illumina Miseq Sequencing, GC-MS	He et al. (2019)
<i>Triticum aestivum</i> L. (Wheat)	<i>Pseudomonas</i> , <i>Paenibacillus</i> , <i>Sphingomonas</i> , <i>Fusarium graminearum</i>	Wheat heads	Plant growth improvement and biocontrol	Wheat head microbiome sequencing and analysis of pathogenic as well as beneficial microbes	Chen et al. (2018); Rossmann et al. (2020); Simonin et al. (2020)
<i>Arabidopsis thaliana</i>	<i>Massilia</i> , <i>Flavobacterium</i> , <i>Actinoplanes</i> , <i>Pseudomonas</i> , <i>Janthinobacterium</i> , <i>Sphingomonas</i> , <i>Tetracladium</i> , <i>Mortierella</i> , <i>Paraphoma</i> , <i>Alternaria</i> , <i>Articulospora</i> , <i>Cladosporium</i> , and <i>Plectosphaerella</i>	Root and leaves	Plant growth improvement and biocontrol	Amplicon sequencing and analysis of bacteria and fungi associated with roots and leaves	Bergelson et al. (2019)
<i>Zea mays</i> (Maize)	<i>Actinobacteria</i> , <i>Firmicutes</i> , <i>Proteobacteria</i> , <i>Firmicutes</i> , <i>Rhizobium</i> , <i>Enterobacter</i> , <i>Pseudomonas</i> , <i>Ascomycota</i> , <i>Basidiomycota</i> genera	Rhizospheric soil and root	Plant growth-promoting attributes and plant immune response	High-throughput 16S rRNA pyrosequencing and analysis of operational taxonomic units (OTUs) for microbial diversity and dominant genera assessment, Real-time PCR, Microscopy	Niu et al. (2017); Gomes et al. (2018a, b); Lane et al. (2018); Santos and Olivares (2021)
<i>Cicer arietinum</i> L. (Chickpea)	<i>Firmicutes</i> , <i>Proteobacteria</i> , <i>Actinobacteria</i> , <i>Enterobacter</i> and <i>Pseudomonas</i>	Root	Plant growth promotion and fitness, suppression of pathogen, production of wide range of metabolites	16S rRNA gene sequencing	Brígido et al. (2019)
Vegetable crops					
<i>Lycopersicon esculantum</i> (Tomato)	<i>Pseudomonas</i> , <i>Taumararchaeota</i> , <i>Rhizobium</i> , <i>Proteobacteria</i> , <i>Actinobacteria</i> , <i>Firmicutes</i> , <i>Streptomyces</i> , <i>Euryarchaeota</i> , <i>Ascomycetes</i> and <i>Basidiomycetes</i>	Leaves, stems, root, fruits, seeds, soil (rhizospheric and bulk soil)	Plant growth improvement and biocontrol	Illumina-based 16S rRNA gene sequencing	Lee et al. (2019); Dong et al. (2019); Wen et al. (2020); Morella et al. (2020)

Table 1 (continued)

Crops	Microbial community and identified micro-organisms	Tissue/compartiment	Effect of community in crops' microbiome	Applied molecular approaches	References
<i>Solanum tuberosum</i> (Potato)	<i>Agrobacterium</i> , <i>Stenotrophomonas</i> , <i>Geobacillus</i> , <i>Variovorax</i> , <i>Curtobacterium</i> , <i>Streptomyces</i>	Rhizospheric soil and tuber root	Induction of plant immune response through secreting degrading enzymes, antibiotics, and antimicrobial metabolites	Illumina MiSeq sequencing and analysis, Shotgun metagenomic sequencing and analysis, Quantitative PCR	Shi et al. (2019); Buchholz et al. (2019)
<i>Allium cepa</i> (Onion)	<i>Bacteroidetes</i> , <i>Enterobacteriaceae</i> , <i>Gluconobacter</i> , <i>Proteobacteria</i> , <i>Burkholderia</i> , <i>Acinetobacter</i> , <i>Pseudomonas</i> , <i>Citrobacter</i> , <i>Wickerhamomyces</i> , <i>Nectriaceae</i> , <i>Penicillium</i> , <i>Botrytis</i> , <i>Candida</i> sp., <i>Trichoderma</i> <i>brevicompectum</i> , <i>Streptomyces</i> sp.	Bulbs	Plant growth improvement and biocontrol	16S rRNA and ITS gene sequencing	Yurgel et al. (2018)
<i>Phaseolus vulgaris</i> (Common bean)	<i>Bacteroidetes</i> , <i>Verrucomicrobia</i> , <i>Proteobacteria</i> , <i>Acidobacteria</i> , <i>Actinobacteria</i> , <i>Chloroflexi</i> , <i>Rhizobium</i>	Root region and rhizospheric soil	Biocontrol agents against bacterial and fungal phytopathogen, secreted bioactive compound lipopeptide natured antibiotics, derivatives of phenazine, and antimicrobial metabolites	Operational taxonomic units (OTUs) for microbial diversity and dominant genera assessment	Pérez-Jaramillo et al. (2019); Barelli et al. (2020)
<i>Beta vulgaris</i> L. var <i>saccharifera</i> (Sugar beet)	<i>Pseudomonas</i> sp., <i>Acidobacteria</i> , <i>Bacillus</i> , <i>Actinobacteria</i> , <i>Fusarium</i> , <i>Alternaria</i> , and <i>Colletotrichum</i> sp.	Rhizospheric soil and tuber root	Biocontrol agents against bacterial and fungal phytopathogen, secreted antibiotics, derivatives of phenazine, and antimicrobial metabolites	Illumina MiSeq Sequencing	Huang et al. (2019)
<i>Ipomoea batatas</i> (L.) Lam. (Sweet potato)	<i>Colletotrichum</i> , <i>Fusarium</i> , <i>Verticillium</i> , <i>Chaetomium</i> , <i>Guehomyces</i> , <i>Volutella</i>	Tuber root and rhizospheric soil	Plant growth improvement and biocontrol	ITS gene amplicon sequencing by Illumina MiSeq	Gao et al. (2019)
<i>Daucus sativus</i> (Carrot), <i>Solanum tuberosum</i> (Potato), <i>Brassica napus</i> sp. <i>napobrassica</i> (Neep), <i>Beta vulgaris</i> (Beetroot), and <i>Heliantus tuberosus</i> (Topinambur)	<i>Alphaproteobacteria</i> , <i>Actinobacteria</i> , <i>Gammaproteobacteria</i> , <i>Firmicutes</i>	Rhizospheric soil and root section	Growth-promoting attributes of plant and induction of immune responses of plant, secretion of antibiotics, antifungal secondary metabolites, and degrading enzymes	Ribotyping by Illumina MiSeq Sequencing	Koiv et al. (2019)

Table 1 (continued)

Crops	Microbial community and identified micro-organisms	Tissue/compartiment	Effect of community in crops' microbiome	Applied molecular approaches	References
<i>Spinacia oleracea</i> Linn. (<i>Spinach</i>), <i>Brassica napus</i> L. (<i>Rape</i>), <i>B. oleracea</i> var. <i>italica</i> (<i>Broccoli</i>), <i>Apium graveolens</i> var. <i>dulce</i> (<i>Celery</i>), and <i>B. oleracea</i> var. <i>botrytis</i> (<i>Cauliflower</i>) <i>Brassica rapa</i> (Cabbage)	<i>Firmicutes</i> and <i>Proteobacteria</i>	Rhizospheric soil and root section	Suppression of pathogens, enhancement in plant growth and fitness, releasing hydrolytic enzymes and secondary metabolites	Phospholipid fatty acid (PLFA) analysis, PCR-DGGE	Zhang et al. (2010)
	<i>Actinobacteria</i> , <i>Firmicutes</i> , <i>Proteobacteria</i> , <i>Bacteroidetes</i> , <i>Acidobacteria</i> , <i>Gemmatimonadetes</i> , <i>Ascomycetes</i> , <i>Basidiomycetes</i>	Root and rhizospheric soil	Growth-promoting attributes of plant and induction of immune response in plant	Biolog™ MicroPlates and 454 pyrosequencing	Liu et al. (2018)
<i>Cichorium endivia</i> (Lettuce)	<i>Bacillus</i> , <i>Xanthomonas</i> , <i>Pseudomonas</i> , <i>Enterobacter</i> , and <i>Moraxella</i>	Leaves, root section, rhizospheric and bulk soil	Plant growth promotion and plant defense	Terminal restriction fragment length polymorphism (TRFLP), Matrix-assisted laser desorption/ionization time-of light mass (MALDI-TOF MS), spectrometry and ribotyping	Frohling et al. (2018)
(Eggplant)	<i>Acidobacteria</i> , <i>Cyanobacteria</i> , <i>Bacillus</i> , <i>Planctomyces</i> , <i>Chaetomium</i> , <i>Acremonium</i> , <i>Fusarium</i> , <i>Aspergillus</i>	Root and rhizospheric soil	Growth-promoting attributes of plant and suppresses the growth of phytopathogens	High-Throughput Illumina MiSeq Sequencing	Ghani et al. (2019)
Fruits					
<i>Vitis vinifera</i> (Grapevine)	<i>Paenibacillus</i> spp., <i>Bacillus</i> spp., <i>Pseudomonas</i> spp., <i>Sphingomonas</i> spp	Rhizospheric soil and Root section	Growth-promoting attributes of plant and suppression of phytopathogens	Ribotyping and ITS high-throughput amplicon sequencing (HTAS), quantitative Polymerase Chain Reaction (qPCR)	Berlanas et al. (2019)
<i>Fragaria x ananassa</i> (Strawberry)	<i>Bacillus</i> , <i>Flavobacterium</i> , <i>Mycobacterium</i> , <i>Caulobacter</i> , <i>Novosphingobium</i> , and <i>Pseudomona</i>	Rhizospheric soil and section of root	Growth-promoting attributes of plant and stimulation of plant immune response, secreting hydrolytic enzymes, antibiotics, and antimicrobial metabolites	Ribotyping on the Illumina MiSeq platform	Deng et al. (2019)

Table 1 (continued)

Crops	Microbial community and identified micro-organisms	Tissue/compartiment	Effect of community in crops' microbiome	Applied molecular approaches	References
<i>Musa</i> spp (Banana)	<i>Chloroflexi</i> , <i>Firmicutes</i> , <i>Proteobacteria</i> , <i>Nitrospirae</i> , <i>Acidobacteria</i> , <i>Gemmatimonadetes</i> , <i>Bacteroidetes</i> , <i>Planctomycetes</i> , <i>Verrucomicrobia</i> , <i>Ascomycota</i> and <i>Zygomycota</i>	Fruit	Induction of Plant immune response through secreting hydrolytic enzymes, antibiotics, and antifungal metabolites	Amplicon generation and Illumina MiSeq sequencing	Xue et al. (2015); Zhou et al. (2019); Vepstaitė-Monstavičė et al. (2018); Hong et al. (2020)
<i>Citrus limonium</i> (Lemon)	<i>Proteobacteria</i> , <i>Actinobacteria</i> , <i>Bacteroidetes</i> , <i>Cyanobacteria</i> and <i>Firmicutes</i> ,	Rhizospheric soil and section of root	Plant growth enhancement and biocontrol	Ribotyping	Zhang et al. (2017); Padhi et al. (2019)
<i>Malus robusta</i> Reh (Apples), <i>Pyrus betulaeifolia</i> Bge. (Pears), <i>Katy apricot</i> (Apricots), <i>Longguan</i> (Cherries), <i>Prunus davidiana</i> (Peaches), <i>Kyoho grape</i> (Grapes), <i>Zhonghe</i> (Walnuts)	<i>Proteobacteria</i> , <i>Gemmatimonadetes</i> , <i>Bacteroidetes</i> , <i>Ambiguous</i> , <i>Lysobacter</i> , <i>Nitrospira</i> , <i>Mortierella</i> , <i>Geomyces</i> , <i>Chaetomium</i> , <i>Alternaria</i> , <i>Fusarium</i> ,	Rhizospheric soil	Plant growth and defense mechanism analysis, rhizosphere microenvironment, physico-chemical properties of soil, enzymatic secretions within the community-level and physiological profiling of members	Ribotyping	Si et al. (2018)
Medicinal crops/spices (Ginger)	<i>Cladosporium</i> , <i>Bradyrhizobium</i> , <i>Kaistobacter</i> , <i>Rhodanobacter</i> , <i>Tetracladium</i> , <i>Rhodoplanae</i> , <i>Cryptococcus</i> , <i>Lecanicillium</i> ,	Rhizospheric and bulk soil, stem,	Showing plant growth-promoting attributes, secretion of antibiotics, hydrolytic enzymes and antifungal secondary metabolites	Ribotyping	Liu et al. (2017)
<i>Anethum graveolens</i> (Dill), <i>Allium schoenoprasum</i> (Chives), <i>Ocinum basilicum</i> (Basil), <i>Mentha spicata</i> (Mint), <i>Rosmarinus officinalis</i> (Rosemary)	<i>Actinobacteria</i> , <i>Lentisphaerae</i> , <i>Leaves Proteobacteria</i> , <i>Firmicutes</i> , <i>Bacteroidetes</i> , <i>Acidobacteria</i> ,	Leaves	Induction of plant immune responses, production of antibacterial and antifungal secondary metabolites	Amplicon generation and Illumina MiSeq sequencing	Jackson et al. (2015)
<i>Curcuma longa</i> L. (Turmeric)	<i>Bacillus</i> , <i>Pseudomonas</i> , <i>Clavibacter</i> , <i>Azotobacter</i> , <i>Azospirillum</i> , <i>Arthobacter</i> , <i>Burkholderia</i> , <i>Enterobacter</i>	Rhizome	Stimulation of plant defense, production of antibacterial and antifungal secondary metabolites, enhanced plant growth	16S rRNA gene Amplicon sequencing	Kumar et al. (2017)

can explore the diversity and functions of crop microbiomes (Table 1).

Nutrient mobilization

The major biogeochemical cycles (nitrogen, carbon, sulfur, and phosphorus) are vital constituents of an ecosystem. They are interlinked to geological, chemical, and biological processes, such as N₂ fixation, photosynthesis, soil fertility, and organic matter decomposition that establish a sustainable environment (Finzi et al. 2011). The microbial community of different crops plays a dynamic role in managing soil nutrient cycling through enhanced mobilization and uptake of nutrients to plants. In another report, fungal communities are dominant in biodegradation that helps in plant nutrition improvement in plant biomass (Khan et al. 2016; Sarkar et al. 2021). Several researchers reported nutrient mobilization and solubilization of insoluble minerals via fortification of a single or group of microbes, i.e., Arbuscular Mycorrhizal Fungi (AMF) solubilize phosphate and improve the bioavailability of P to the plants (Sharma et al. 2016; Giovannini et al. 2020; Bastami et al. 2021). Inoculation of a mixture of AM fungi, *Penicillium* spp., and native microbial community encouraged positive effects on nutrition and development in legumes and cereals, rhizobia with AMF (Wang et al. 2011), or even with the tripartite inoculation (three different organisms) with AMF-*Rhizobium*-P-solubilizing fungus (Meng et al. 2015; Zhu et al. 2016a, b). Researchers have focused on isolation, characterization, and development of multifunctional microbial consortia that include free-living nitrogen-fixing (NF) with higher capabilities to enhance efficient nitrogen (N) uptake and thus plant growth and yield (Vassilev et al. 2015; Morella et al. 2020). For instance, coinoculation with *Pseudomonas aeruginosa* GRC2 and *Sinorhizobium meliloti* RMP with chemical fertilizers, including urea and phosphate fertilizers, caused nutrient mobilization, growth improvement, and productivity in *Brassica juncea* (Maheshwari et al. 2010). Likewise, the interest in developing microbial consortia quenches the thirst for nutrient cycling and sustainable agriculture by exploring the different microbiome. The inoculation with NF bacteria and native microbial community of *Azospirillum* spp., *Azotobacter* spp., *Sinorhizobium* spp., and *Burkholderia* spp. significantly enhanced yields in various essential agriculture crops (Shoghi-Kalkhoran et al. 2013). Exopolysaccharide (EPS) producing microbes recover soil structure and aggregation (in stress conditions), as result of that the process of entrapping and mobilization of nutrients increased as well as enhanced water retention capacity observed (Rashid et al. 2016; Acosta-Motos et al. 2020). Exploring crop microbiome and associated microbial community involved in multifunctional plant growth

mechanisms and their motivated research help develop microbial consortia (Rai et al. 2020).

Plant growth promotion

The participants of the crop microbiome exert positive, neutral, and negative effects on plant growth and development through direct or indirect mechanisms. The direct mechanisms of plant growth promotion by PGPR are mediated through the production of phytohormone, nitrogen fixation, and mineral solubilization (Rai et al. 2019a; Manasa et al. 2021; Nithapriya et al. 2021). Several researchers reported colonization of diverse bacterial communities associated with soybean and wheat that displayed growth-promoting properties of plants were *Arthrobacter* sp., *Bacillus* sp., *Erwinia* sp., *Pseudomonas* sp., *Paraburkholderia* sp., and *Pantoea* sp. (Rascovan et al. 2016; Sagar et al. 2018). Several researchers described the role of *Trichoderma* sp. in releasing different bioactive compounds like antioxidants, phytohormones, enzymes, and plant elicitors like phytoalexins and phenols. They found that these elicitors help improve tolerance to abiotic stress and root proliferation (López-Bucio et al. 2015; Rai et al. 2020). Mycorrhizal fungi are the other best example of microbiome-associated microbes that stimulate plant growth and support through diverse mechanisms (Zhu et al. 2016a, b).

Disease management

The plant mycobiome serves as a defensive shield to counter plant pathogens (Agler et al. 2016a, b) through direct encounter or indirect interactions via different mechanisms, such as parasitism, competition for space/nutrients, and initiation of systemic resistance in response to biotic and abiotic stresses (Santos and Olivares 2021). The severity of disease incidence in the crops is influenced by various elements, such as crop susceptibility, the population size of the pathogen, environmental condition, and biotic factors of crop microbiome that determine the outcome of the interaction between crop and pathogen (Brader et al. 2017). Some plant pathogens produce phytotoxic compounds and phytohormones that affect host plant growth (de Vrieze et al. 2018). The beneficial microbial community of the crop microbiome suppresses activities of pathogens and disease management (Hopkins et al. 2017; Berg and Koskella 2018) through different mechanisms like the production of antibiotics, cell wall-degrading enzymes, pathogen-related proteins, siderophores, volatile compounds, modulating plant hormones level, and stimulating systemic resistance of plant (Santhanam et al. 2015; Durán et al. 2018; Rai et al.

2020). In particular, some bacterial genera like *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Streptomyces*, *Paraburkholderia*, *Pantoea*, and *Paenibacillus* have been recounted for suppression of pathogen (Gómez-Expósito et al. 2017; Schlatter et al. 2017; Sagar et al. 2020a). Trivedi et al. (2017) recognized three bacterial taxa belonging to *Acidobacteria*, *Firmicutes*, and *Actinobacteria* that controlled the invasion of *Fusarium* wilt and inhibited phytopathogen. Durán et al. (2018) recounted the role of the endosphere bacterial community against *Gaeumannomyces graminis* by producing a wide range of secondary metabolites. Several studies (Contreras-Cornejo et al. 2016; Zeilinger et al. 2016) revealed that filamentous fungi mitigate biotic stress while improving plant life growth and health in various agriculture crops.

Stress tolerance

Abiotic stresses are the major restrains for sustainable agricultural and crop yield. Changing climatic conditions pose drought, salinity, acidity, low/high temperature, the addition of heavy metals, and deprivation of nutrients (Meena et al. 2017). Plants frequently cope with these adverse environmental situations by changing or re-programming metabolic mechanisms (Santos and Olivares 2021). A microbial's inherent metabolic and genetic capability makes them suitable for abiotic stress and induces local and systemic responses (Yuan et al. 2019; Rai et al. 2020). In this order, the crop microbiome is more explored to combat these ecological stresses (Shahzad et al. 2017).

Salt tolerance

Soil salinity adversely affected the growth parameters of crops and reduced productivity. Though, the negative effect of high salt concentration in the soil can be reduced through several mechanisms, such as the production of phytohormones, antioxidants, ACC deaminase, and osmoprotectant by microbiome-associated microbes and induces plant resistance (Shahzad et al. 2017). Yuan et al. (2019), the rhizospheric microbiome facilitates stress-tolerant capability and promotes germination and development/growth of *Hibiscus hamabo* in salinity conditions. Tian et al. (2017) reported a diverse group of bacteria from the endophytic microbiome of tomato root that promoted plant growth by producing phytohormone (IAA and cytokinin). Rascovan et al. (2016) documented that the rhizospheric microbiome of wheat and soybeans are proficient in producing ACC deaminase and IAA. Mark Ibekwe et al. (2017) observed the influencing impact of salinity on the soil and rhizospheric microbiome of spinach that altered the diversity of the microbial community.

During the summer season, spinach displayed a high relative richness of *Flavobacteriaceae*, while the rainy season revealed the dominance of the *Halomonadaceae* family. Recently, Sagar et al. (2020a) documented the role of antioxidant enzymes and ACC deaminase producing *Enterobacter* sp. PR14 in alleviating salinity stress and enhancing the growth of rice and millets in saline soils. Kusale et al. (2021) found that *Klebsiella variicola* isolated from the wheat rhizosphere produced organic acid, phytase, siderophore, ACC deaminase, and antioxidant enzymes like superoxide dismutase, catalase, and glutathione oxidase under salinity stress conditions. In another study, EPS producing microbes have gained significant attention because of their stress tolerance potential and showed enhanced productivity of crops. The exact mechanism employed by EPS producing microbes to form a biofilm sheath around the roots of plants and ameliorate salinity induced oxidative stress (Saha et al. 2020). Sultana et al. (2020) concluded that significant increase in productivity of rice under salinity stress was observed by EPS producing microbes, namely *Bacillus aryabhatai*, *Achromobacter denitrificans* and *Ochrobactrum intermedium*. They efficiently solubilize phosphates and fix nitrogen, thus facilitating nutrients to salinity stressed plant and protect from oxidative stress.

Drought tolerance

Drought is another foremost limiting factor that adversely affects crop microbiome and productivity. Fitzpatrick et al. (2018) demonstrated that drought influences and transformed the composition and diversity of rhizospheric microbiomes in *Actinobacteria*. Besides osmotic stress, the movement of nutrients and the presence of oxygen in the soil are restricted, hindering plant growth (De Vries et al. 2020). Production of natural EPS during drought conditions is a well-known characteristic of microbes. EPS are found to be beneficial in soil humification and aggregate formation, enhanced water holding capacity, quorum sensing, and establishing microbial diversity in crop microbiome (Arora et al. 2020; Ilyas et al. 2020). Santos-Medellín et al. (2017) established that rice crop restructured their rhizospheric microbiome during drought stress and observed an abundance of *Actinobacteria* and *Chloroflexi* phyla and reduction in the *Acidobacteria* and *Deltaproteobacteria* phyla under drought stress. Niu et al. (2018) observed significant increase in colonization of bacteria in root hairs and growth of foxtail millet under drought stress, due to EPS producing *Pseudomonas fluorescens* (D11, DR7) and *Enterobacter hormaechei* (DR16). Ilyas et al. (2020) and Khan et al. (2020) found *Bacillus subtilis* and *Azospirillum brasilense* produce osmolytes (proline and sugar) and stress-induced

phytohormones (IAA, GA, and cytokinin) help in increased the growth parameters of wheat.

Tolerance to toxic metals

Metal contamination harmfully affects the agro-ecological environment and human health (Thakare et al. 2021). Several recent studies revealed the effect of toxic metal ion stress, its tolerance and signaling mechanism on the plant microbiome, and a novel phytomicrobial strategy for metal stress mitigation (Tiwari and Lata 2018; Sagar et al. 2020a). It has been demonstrated that metal contamination limited the quality of water, soil, microbial community, and crops (Ayangbenro and Babalola 2017). The bioaccumulation of metals in plants causes retardation in growth, physiological processes, and metabolism (Dusengemungu et al. 2021). Patel et al. (2016a, b) demonstrated the role of PGPR in improving plant growth in wheat under heavy metal stress. Sayyed et al. (2019) demonstrated the role of siderophore producing *Achromobacter* sp. in growth promotion in groundnut and reported its tolerance wide variety of heavy metal ion. Akhtar et al. (2021) demonstrate *Bacillus cereus* heavy metal (Cr^{+3}) tolerance potential that can be used for plant growth as well as phytostabilisations of *Brassica nigra* in chromium contaminated soils. Similarly, Hassan et al. (2017) observed that plant growth-promoting rhizobacteria (*Bacillus cereus* and *Pseudomonas moraviensis*) could alleviate toxicity of metals (Cu, Cr, Co, Cd, Ni, Mn, Pb) and promote the growth of wheat under saline condition. Tripathi et al. (2015) suggested that *Trichoderma*-inoculated chickpea could alleviate As stress through the As-methylation process.

Approaches and application of microbiome

However, due to inadequate knowledge of plant-associated microbiome composition, diversity, and functionality, recently developed approaches need to explore up to depth. The modern molecular approaches, such as -omics/metabolomics approaches (genomics, epigenomics, transcriptomics, metatranscriptomics, proteomics, and metabolomics), system biology, nano-biology, and rhizho-engineering, are exploited to identify the functional microbial communities with plant and soil as well as exploited different ability of microbes for different purposes (Aguar-Pulido et al. 2016; Foo et al. 2017; Castle et al. 2018). In this order, Ahmed et al. (2018) demonstrated metagenomic profiling of saline soil microbiome to explore community structure and novel genetic elements of uncultivable microbes, can provide information about osmoadaptation mechanisms. The literature shows numerous success stories of the use of metabolomics technique to explore metabolic functions of plant/microbe in soil (Hu et al. 2018; Zhao et al.

2019; Bertola et al. 2021). Bernardo et al. (2019) used metabolomics and showed mycorrhizal fungi inoculated wheat plant is able to tolerate water stress through modulation of oxidative stress and increased production of phytohormone. Hence, metabolomics approach helps in re-programming of metabolites in crop microbiome to mitigate stress, and explore physiology and metabolic pathways of plant that became functional during stressed environment. Similarly, Starke et al. (2019) revealed complete protein profile of soil using metaproteomic profiling and showed functional genomics approach to explore the metabolic active microbes in soil/crop microbiome. This information could be a valuable indicator for understanding the involvement of specific dominant group of microbes involved in crop improvement and stress tolerance (Abiraami et al. 2020). The microbial biodiversity of soil microbiome, using metagenomic high-throughput screening, has identified genes that play their role in stress resistance and bioremediation (Chandran et al. 2020). Bonini et al. (2020) explored phytohormone and secondary metabolites profiling using metabolomics, when sweet pepper plants have been inoculated with biostimulants. The authors reported enhanced plant and fruit yields, elevated production of phytohormone, and secondary metabolites. In another study, proteomics sequencing has been carried out to study the enzymatic activity and metaproteome of the rhizosphere when biostimulants applied to maize seeds (Mattarozzi et al. 2020). This approach is used to understand crop effects and help to designing of future bioformulations for stressed mitigation in plant and crop productivity. Nan et al. (2022) investigate microbial diversity of saline-alkali soil, using high-throughput sequencing technique for better understanding of the mechanisms and micro-ecology of soil/plant microbiome. Thus, the implication of evolving approaches involved in search of novel micro-organisms having enhanced nutrition availability, plant's growth promotion, biocontrol, and disease resistance ability that is currently acknowledged as bioformulations in crop microbiomes (Pascale et al. 2020).

Recent modern approaches and its application overcome the conventional constraints and explore host/microbe-derived molecules responsible for the network communication, keystone species, analyze metabolic mechanisms of plant-microbe nutrient exchange, and enhanced crop yield and fitness in different ecological conditions (Song et al. 2020; Trivedi et al. 2020). Several applications of microbiome studies were applied, viz., next-generation sequencing and multilocus barcode approaches for investigation of microbial diversity in crop microbiome, search of novel species with multifarious function, development of bioformulation, nano-formulations from host/microbe-derived molecules, and synthetic administration of microbes with beneficial function in crop

microbiome with the help of rhizo-engineering (Santos and Olivares 2021; Glick and Gamalero 2021).

Constraints/limiting factors

Crop microbiome comprises wide group of micro-organisms that execute selection of the communities to reshape the structure, maintain composition of microbiome, and perform different functions. A number of factors are contributed to maintain the composition of crop microbiome, like plant density, genotype of host, climatic conditions, mobilization of minerals, soil composition and type, agricultural practices, nutrient availability, interaction between nexus of microbes, and interactions with other external microbiomes (e.g., soil fungi and bacteria), (Nilsson et al. 2018). These complex microbiome micro-organisms are strongly influenced by factors like host, interaction of microbes in microbiome, and environmental conditions (Dastogeer et al. 2020). Host factor effect the crop microbiome, comprises crop species, host genotype, developmental stage and age of host, host secreted exudates and metabolites, and host immune system (Wagner et al. 2016; Agler et al. 2016a, b; Cai et al. 2017). Microbial factor that shaping the crop microbiome structure and modulate microbiome functioning includes microbe-derived compounds, intra- and inter-species interaction, and keystone species (Banerjee et al. 2018; Schlechter et al. 2019). Another most driving factor of crop microbiome is environmental elements, such as, soil composition, type, and pH, farming practices, and climatic factors (Agler et al. 2016a, b; Estendorfer et al. 2017). The dynamics and function of microbiome has stimulated to explore these constrains, their effect on microbiome, and how recent approaches overcome these problems.

Molecular and omic techniques in the exploration of crop microbiome

The crop microbiome is a complex nexus of plant–microbe interaction, which comprises almost 99% non-cultivated, uncharacterized microbes that are still unrevealed. A broad range of molecular approaches has been applied to quantify, identify, detect, and reveal the mechanism of pathogenic microbes associated with the rhizosphere, phyllosphere, and endosphere. The traditional approaches were centered on cultivated microbes and morphological identification-based techniques used to explore the plant mycobiome. However, the limitation of traditional methods is time-consuming, lengthy, pure culture-dependent, and requires extensive knowledge of classical taxonomy. These factors make them unable to enumerate pathogen population and inability to accurately quantify the disease-causing mechanism of the pathogen, which forces to search some alternative techniques (Rai et al. 2020; Santos and Olivares 2021). The detection,

diagnosis, and identification of the hidden role of crop microbiome need sensitive, rapid, and précised methods (Rai et al. 2020). These limitations and innovative findings of microbiome research have led to the development of new molecular and omics techniques combined with novel microscopic methods for improved, accurate, and reliable insights into crop microbiome (Nilsson et al. 2018) (Table 2, Fig. 2).

The advanced molecular techniques, metagenomics, transcriptomics, proteomics, metabolomics, imaging techniques with analytical tools, and high-throughput sequencing studies explored the root colonization by microbes that provide evidence about the fluctuations in expression of up-regulated plant genes to stress conditions (Rai et al. 2020). Further studies have concentrated on rhizospheric microbes, though very little information is gathered about the interaction between phyllosphere and endophytic microbes. The phyllosphere microbe is commonly explored through culture-dependent approaches. Similarly, most endophytes are not culturable, but their function directly affects plant fitness through different mechanisms. That is why, molecular techniques have been essential for identification (Kumar et al. 2013a, b) and confirmed that many endophytes coexist with other functional groups in the microbiome. In this consequence, endophytes' ecological and functional roles in maintaining microbiome structure, richness, organization, and diversity are vital for plant development and existence (Rai et al. 2020; Santos and Olivares 2021). Rapid progress in oligonucleotides sequencing technologies and comparative "OMICS" approaches, such as genomics, proteomics, transcriptomics, and metabolomics, now assists us to explore the mycorrhizal association with crops, reconnecting taxonomic and phylogenetic profiles and their exclusive functions in respect of plant growth (Meena et al. 2017).

The culture-dependent technique comprises the sequential process, the first isolation of organisms into the pure culture, characterization based on morphology and biochemical utilization, and then taxonomic identification through gene-based or whole-genome sequencing, but most culture-independent microbes are ignored due to their not or sluggish growth appearances in culture (Nesme et al. 2016; Rai et al. 2020; Santos and Olivares 2021).

Numerous advanced molecular techniques have been upgraded; this includes direct amplification of oligonucleotide from the bulk soil/rhizospheric soil, characterization of microbial genus and species, multilocus barcode approaches, live function analysis of microbes inside plant tissues through GFP tagged confocal imagining, endophytic microbiome visualization by fluorescence in situ hybridization and microscopy (Hardoim et al. 2015), and next-generation sequencing (Berg et al. 2016; Nesme et al. 2016; Rai et al. 2020). To fingerprint the leading microbial species at diverse taxonomic levels, functional single-strand

Table 2 List of recently used molecular techniques that exploited for assessments of microbial communities of diverse crops

Molecular technique	Host plant	Microbial community	Degree of discrimination	Application	References
Conventional PCR	Chilli, Brinjal	<i>Sclerotium rofskii</i> , <i>Colletotrichum capsici</i>	Diversity analysis by using 16S rRNA and ITS region	Species-specific primer-based PCR Technique	Kuzdralinski et al. (2017)
Random amplified polymorphic DNA (RAPD)	Tomato, Chilli, Rhizospheric Soil	<i>Fusarium</i> , <i>Elsinoë</i> , <i>Trichoderma</i> , <i>Colletotrichum</i> , <i>Bacillus</i> , <i>Pseudomonas</i> , <i>Azotobacter</i>	Microbial diversity analysis	Analysis of molecular diversity	Rai et al. (2016); Kashyap et al. (2016); Brader et al. (2017)
Restriction fragment length polymorphism	Pathogen affected leaves, root, stem	<i>Pythium myriotylum</i>	Distinction between nonpathogenic and pathogenic	Phylogenetic analysis	Gómez-Alpizar et al. (2011)
Microsatellites	Tomato, Potato, Brinjal, Paddy, Wheat	<i>Ascochyta rabiei</i> , <i>Macrophomina phaseolina</i> , <i>Ceratocystis fimbriata</i> , <i>Sclerotinia subarctica</i> S. <i>sclerotiorum</i> , <i>Puccinia graminis</i> , <i>P. trititina</i> , <i>Alternaria</i> sp., <i>Rhizoctonia</i> sp., <i>Fusarium</i> spp., <i>Fusarium avenaceum</i> , <i>Colletotrichum</i> spp	Interspecific diversity analysis of phytopathogenic fungi and construction of genetic map through fingerprinting method	Taxonomic and population genetics studies, and population analysis	Kumar et al., (2013a, b); Faist et al. (2016); Rai et al. (2019b)
Denaturing Gradient Gel Electrophoresis (DGGE)	Rhizospheric Soil	<i>Alternaria</i> sp., <i>Rhizoctonia</i> sp., <i>Fusarium</i> spp., <i>Colletotrichum</i> spp	Avirulent/Virulent isolates, culture-independent microbes characterization, identification and validation	Investigation of SNPs and microsatellites, mutation	Manici et al. (2017); Orlewska et al. (2018)
Multiplex amplification/PCR	Sugarcane, Onion	<i>F. oxysporum</i> f. sp. <i>cepae</i> , <i>Alternaria</i> spp., <i>Colletotrichum</i> sp., <i>F. oxysporum</i> f. sp. <i>lycopersici</i> , <i>Ralstonia solanacearum</i> , <i>Phytophthora Infestans</i> ,	Vegetative compatibility groups (VCGs), closely related species, and races	Identification of pathogen, Formae species /races	Armanhi et al. (2016)
Padlock probe hybridization-multiplex PCR (PLPs)	Tomato, Onion, Potato	<i>Rhizoctonia</i> sp., <i>F. graminearum</i> , <i>F. culmorum</i> , <i>Fusarium</i> spp., <i>Alternaria</i> spp., <i>Colletotrichum</i> spp	Populations/species, species-specific gene expression	Differentiation of long oligonucleotide molecules with known sequences and allelic variation	van Doorn et al. (2007)
Quantitative real-time PCR (qRT-PCR)	Tomato, Potato, Cereals, Wheat, Rhizospheric Soil	<i>Fusarium oxysporum</i> , <i>F. solani</i> , <i>Alternaria</i> spp., <i>Colletotrichum</i> spp., <i>Phytophthora Infestans</i> ,	Uncultivable microbes identification	Assessment of abnormalities in the genome, analysis of expression of genes at particular stress condition, Recognizing unidentified microbes of phytochrome, identifying beneficial and phytopathogenic microbes and insect larvae	Nielsen et al. (2012); Berlanas et al. (2019)
DNA Barcoding	Potato, Brinjal, Spinach, Beetroot, Mustard,				Schoch et al. (2012)

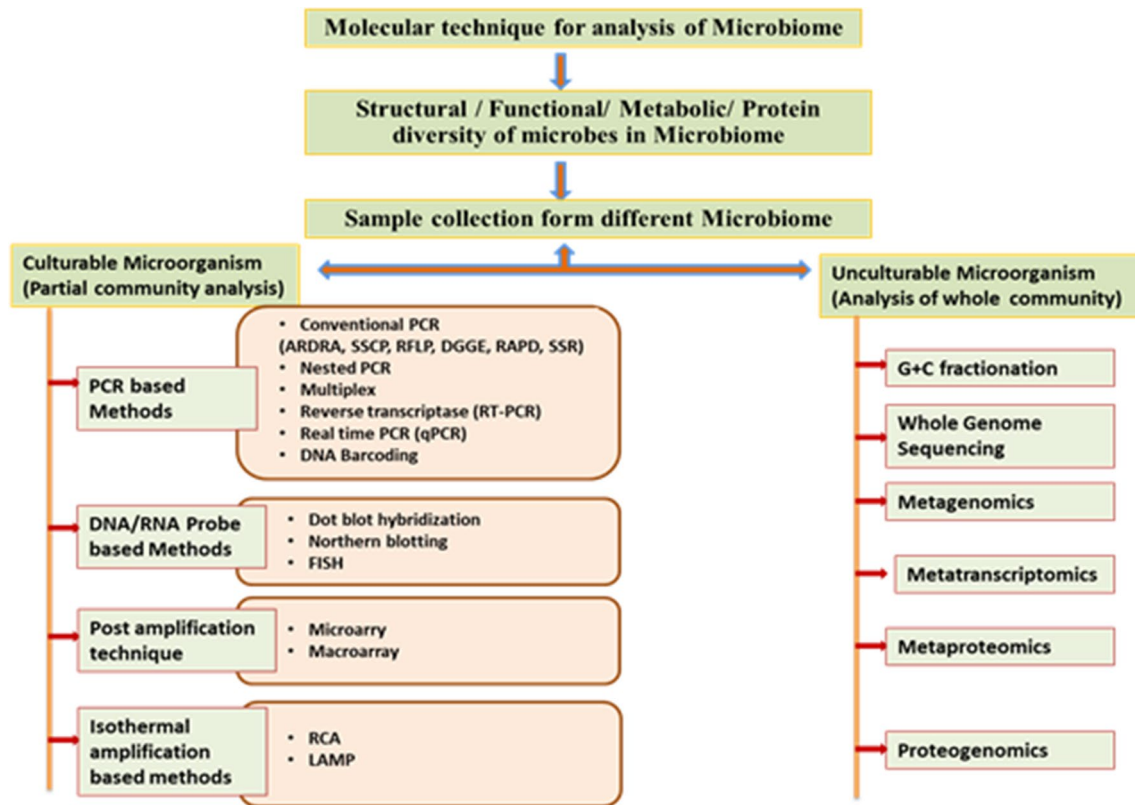


Fig. 2 Illustration of different molecular techniques to explore the crops microbiomes and representing diversity, functionality, abundance and shifts according to changing seasons. New metagenomic

and transcriptomic approaches helps to identify uncultivable microbial genes that expressed in plants during biotic and abiotic stress tolerance

conformation polymorphism (SSCP), or denaturing gradient gel electrophoresis (DGGE). Quantification of microbial biomass from different plant tissues can be attained by real-time PCR techniques that are significantly influenced by the cell number, size, and type and a group of fungus and necessitate wide-ranging calibration for pure cultures of each species (Tellenbach et al. 2010).

The innovation of evolving molecular technologies helps gather knowledge about the culture-independent microbial species, but those microbes' ecological associations and nutritional modes are still thought-provoking for scientists (Tedersoo and Nilsson 2016). Oligonucleotide sequencing methods evolved from sequencing single specimens to parallel. Sanger sequencing helped explore the unseen mycobiota and its richness, structure, functioning, and significance. NGS technologies continue to progress, and the third-generation sequencing more precisely and provides more extraordinary read lengths than earlier generations (Song et al. 2015; Rhoads and Au 2015; Nilsson et al. 2018). This review concisely discusses the application of recently developed molecular techniques that interpret the study of the microbial community associated with different crops regarding taxonomic profiling and their role in exploring

microbiome structure, component, function, signaling mechanism, and ecosystem functioning.

Approaches of crop microbiome and sustainable agriculture

A major challenge for sustainable agriculture is to fulfill global food demand with increasing population; simultaneously, the farmers face unpredictable climatic changes, nutritionally depleted and contaminated soils, poor agricultural practices, reducing pesticides and chemical fertilizers, and water scarcity. The explored crop microbiomes are the best alternative for sustainable agriculture in this scenario. The crop microbiome provides niches and nutrients, while the beneficial microbes promote plant growth, nutrition, and abiotic and biotic stresses mitigation. In this order, several researchers have been investigating the structure, function, and influencing factors of the crop microbiome; as a result, they explored the complex relation of plant–microbe interactions, signaling molecules, and biotic and abiotic constraints approaches that reshape microbiome through recent advanced techniques. The advanced biotechnological

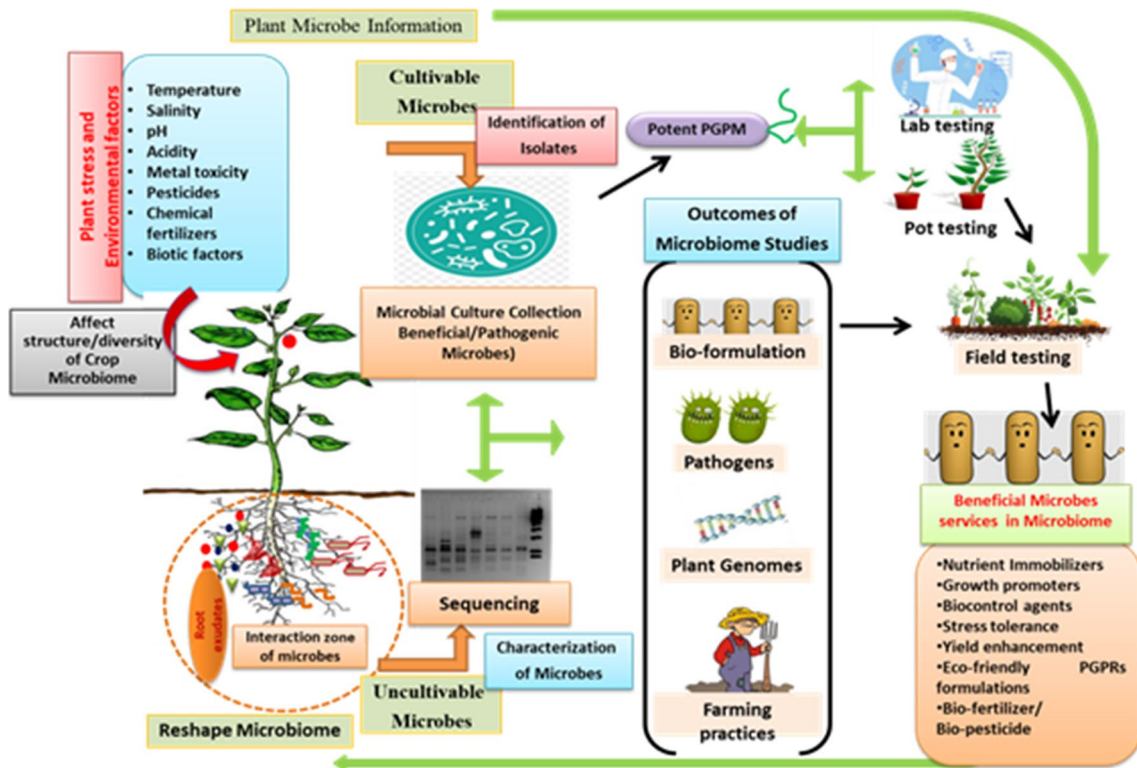


Fig. 3 Application of different biotechnological approaches that implement knowledge of microbiomes into useful biological products

approaches such as DNA and RNA sequencing, comparative genomics, transcriptomics, proteomics, and metabolomics gathered information about the crop microbiome that modulate the structure, functioning, influencing factors, signaling molecules, and mechanisms of microbiomes; further, this knowledge will be applied to reshape the microbiome for sustainable agriculture.

The key findings of microbiome studies demonstrate the role of beneficial microbes, biotic and abiotic elements that regulate the structure, richness, and biodiversity of crop microbiomes through biotechnological approaches. These approaches amalgamate culture-dependent/independent techniques to characterize microbiome-associated community to single isolate, pathogenic to beneficial and validated the effects of beneficial microbes either single or in combination as bioinoculants in different plant species (Fig. 3).

The plant microbiome can be explored by biotechnological approaches, isolates by cultivation-dependent techniques, and culture-independent isolates by sequencing of oligonucleotides, which suggests the profile of the complete associated microbes of the microbiome. If showing a beneficial effect on plants, these microbes are further used as bioformulations/bioinoculants, either single or in a combination of isolates. These two methodologies must be joined together to recognize, isolate, and characterize the chief participants of the microbiome, who

will have their practical skills tested in greenhouse and field experiments.

Crop microbiome combined with nano-particles can be used as nano-biofertilizers and nano-biopesticides. Nano-biofertilizers and nano-biopesticides are now getting attention in the agricultural sector of developing countries. Nano-particles stimulate various defense mechanism in plants facing stress conditions. The use of nano-particles has numerous merits due to their high surface area, high solubility, and low molecular weight. Nano-biofertilizer is produced through the combination of nano-particles and biofertilizers. It is the technique in which biofertilizers are encapsulated within a suitable nanomaterial. They release the nutrients in the soil in a controlled manner and reduce the side effects of environmental stresses. They decrease the use of chemical fertilizer, improve the availability and uptake of the nutrients, are eco-safe, and are cost-effective (Eliaspour et al. 2020; Pudake et al. 2019). It was observed that nano-particles have a direct and indirect effect on plant–microbe interaction; direct mode includes the availability of nutrients in the rhizosphere, while indirect mode way includes the stimulating effects on bacterial strains (Timmusk et al. 2018). It was reported that the use of only 75 ppm CeO₂-nanocomposite significantly enhanced the length of *Trigonella foenum-graecum*. Therefore, the use of very little amount gave pronounced results (Mary

et al. 2022). Nano-biofertilizer has the dual properties of bioinoculants and nano-particles that enhance the chances of crops establishment. They maintain the delivery of nutrients at the target destination (Elnahal et al. 2022;) and help in combating metal phytotoxicity (Fatima et al. 2020).

Conclusion and future prospects

The adverse effect of rapid climate change, soil degradation, and ecosystem imbalance has affected agricultural yield and posed a global threat to food security. Crop microbiomes are the best alternative for sustainable agriculture and ecosystem management in this scenario. The crop microbiome is highly diverse, complex, and shaped by multiple factors responsible for community assembly, microbial interactions, and functioning. The restless research in the last few decades drags new focus on investigating and exploring crop microbiome. This review examined the nexus of crop microbiome, their management, and advanced technologies to overcome the constraints in their functioning. The diversity, complexity, functionality, and precise mechanism of the signal exchange process, root exudation, microbial colonization, and secretion for disease suppressive metabolites are revealed at an advanced level with the help of combined approaches, such as biochemical, molecular, imaging, and "omics" approaches. In this order, the search for potential microbes to increase plant growth, fitness, stress resilience, soil fertility, and the development of microbial formulations/inoculants is on-demand. Despite the various functions of bioformulations, several constraints, including shelf-life, specific function in reshaping the microbiome, and survival of inoculated strain(s), are still a question for its application in the real farming system. Therefore, multi-omics approaches may lead to a search of potential microbes to develop effective microbial consortia that reshape and regulate the function/growth of other members of the crop microbiome. The emerging models' development (SynComs-Synthetic microbial communities and "Culturomics"-Culture-based methods) that perform successfully in the field favor sustainable agricultural practices and plant breeding approaches (Saad et al. 2020; Mitter et al. 2021). The development of advanced multi-omics approaches driving the understanding of plant-associated functional genes. It describes how these essential microbial genes and pathways that mediate pathogenic, beneficial, and commensal host interactions are relevant information for developing potential formulations and delivery approaches in the field. Microbiome engineers implement this information to design and establish long-lasting inoculants in the microbiome to support bioformulations developing agencies and sustainable agriculture.

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