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Rhizosphere to rhizosphere hybridization in fruit crops: new perspectives

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The rhizosphere is a dynamic environment in which multiple microbial activities elicit phenotypical, physiological, and molecular crop responses. For a better understanding of the rhizosphere microbiome, researchers are utilizing next-generation sequencing to focus on microbiome regulations with an emphasis on multi-functional microbes. There are two main concepts currently being focused on: identifying microbial antagonists (between beneficial microbes and plant pathogens) from predominant stocks of plant-growth-promoting microbes, preferably with an aim towards bioprospecting soil-plant health; and secondly, developing a more microbially active rhizosphere through a process called rhizosphere hybridization (RH). The present review is focused on some recent studies on the outcome of RH in citrus cultivars, showing renewed functional corridors of the rhizosphere characterized by secondary metabolites providing a load-supporting functional dichotomy through elevated nutrient-supply, activated soil enzyme profiles, and improvements in root- shoot systems and plant defense enzymes. These response trade-offs collectively contributed to higher quality yield coupled with possibly a better shelf life of fruits. The rhizobiome of heritage trees viz., *Azadirachta, Ficus, Dendrocalamus, Populus, Sasa, Acer, Alnus, Quercus*, and *Phyllostachys*, could be effectively used in exercising RH. These observations on RH mean the concept could be expanded in other fruit crops, with an emphasis on developing a robust holobiont (climate-smart suppressive soils and engineering rhizosphere microbiomes for microbially engineered plants) as a part of regenerative agriculture.

KEYWORDS

antagonism, citrus, fruit crops, functional corridor, growth promotion, heritage trees, holobiont, microbial niche

1 Introduction

The soil region adhering to the plant root system, popularly known as rhizosphere, is said to exhibit the greatest microbiome diversity, responsible for changes in the soil bio-physico-chemical properties influenced by root growth and their elevated activity (Pinton et al., 2007). The term "Rhizosphere" was coined by the German scientist Hiltner (1904) from two Greek words i.e. rhiza (root) and sphere (field of influence). There are three broad classifications (Prashar et al., 2013) describing three different tiers of rhizosphere properties: i. root tissues enclosing endodermis and cortical layers (endorhizopshere); ii. the root surface adhering to soil particles and microbes (rhizoplane); and iii. soil immediately adjacent to the root (ectorhizosphere).

Plant roots release various organic compounds through exudation, secretion, and deposition, from seed germination through to the growth of an adult plant, thereby biologically transforming the rhizosphere (Moshiri et al., 2019; Raiesi et al., 2022; Nourgholipour et al., 2022). In this process, plants recruit active microbial communities within the rhizosphere along and within the rootzone (Mousavi et al., 2018). Organic compounds such as water soluble exudates, lysates, dead fine roots, and inorganic ions are made up of gases released by living root systems that are deposited into their surrounding environment and are collectively called rhizodeposition (Whipps and Lynch, 1985). The nature and properties of rhizodeposition increase the nutrient supply in the soil (Solanki et al., 2020). The carbon derived from plants via roots have three different routes of transformation (Cheng and Gershenson, 2007): i. root mass with living or dead root cells; ii. rhizodeposits with plant-derived materials that are effectively transformed by the rhizosphere; and iii. carbon dioxide released by roots and microbial communities. Interestingly, the microbial diversity of the rhizosphere changes in terms of its composition, structure, and function depending on plant developmental and health status, genotypes, and prevailing soil conditions (Zhang et al., 2021a). The rhizosphere microbiota have strong relationships with plant growth and health through nutrient transformation, disease resistance, and substrate metabolism (Wei et al., 2020). Studies on different plants have confirmed that rhizosphere microbiota regulated by breeding and plant domestication play pivotal roles in plant resistance to soil pathogens (Berendsen et al., 2018; Yin et al., 2021). Such complex microbial food webs (referred to as combined trophic interactions) develop in the rhizosphere, linking different microbial communities with environmental conditions and management practices (Jeffery et al., 2010).

Acknowledging the rhizosphere as a unique niche of complex microbial populations that governs soil-plant health-related issues on one hand and sustaining crop production on the other hand (Avis et al., 2008; Singh et al., 2018a) are the two major pillars of sustainable crop production. Conventional plant hybridization ensures plants inherit beneficial genes from both parents, but the influence of such hybridization on the rhizosphere microbiome has not been studied much. This area could potentially aid in identifying promising microbial communities linked to multiple stress tolerance. This kind of attempt also showcases how the plant and microbial gene pool could be integrated synergistically to obtain a microbially engineered plant with an emphasis on developing a hyper-diverse rhizosphere microbiome-driven multiple plant tolerance.

In addressing this important issue, comparative studies (Zhang et al., 2021b; Wang et al., 2023; Xie et al., 2024) on monoculture versus intercropping cultivation patterns of fruit crops have revealed significant differences in the reshaping of microbial communities and the metabolism of both beneficial microbes and microbial antagonists (Lu et al., 2019). Shen et al. (2024) observed how growing almond mushroom (*Agaricus blazei* Murill) intercropped with kiwifruit (*Actinidia chinensis* L.) aided in identifying 95 bacteria genera and 79 soil metabolites. In another study on intercropping sweet potato (*Ipomoea batatas* (L) Lam.) in banana (*Musa nava* Lour.) orchard (Li et al. 2022), soil bacterial, and fungal populations were shown to be significantly higher in intercropped banana (476.0-511.7 and 154.3-198.3 colonies) compared to monocropped banana (397.7-451.0 and 112.0-147.0 colonies). Likewise, studies on Pinto peanut (*Arachis pintoi* L.) intercropped in litchi (*Litchi chinensis* Sonn.) orchard showed improved metabolic activity of advanced bacterial communities, leading to higher potassium supply that correlated to the resistance of litchi root systems to soil borne-diseases (Zhao et al., 2022).These studies provide ample evidence of microbial communities undergoing mutational changes via different trophic interactions when conditioned by root exudates of main crops and intercrops. We propose the term "Rhizosphere Hybridization" (RH) to describe this conceptual framework (Figure 1). RH is a concept that involves combining the microbial diversity of different crop rhizospheres to improve the rhizosphere function of targeted crops for improved plant growth and development. In this paper, efforts were made to collate the work done on the rhizosphere microbiomes of different promising tree plants that could align with RH as well as put forth some future lines of research on the concept.

2 Bibliometric analysis of rhizosphere research

The authors sought to analyze various areas of rhizosphere microbiome research by reviewing publications from varied databases representing Web of Science, Google Scholar, Springer Link, and Wiley-Blackwell databases using keywords such as "rhizosphere", "rhizosphere microbiota", "rhizosphere interactions", and "rhizosphere hybridization". The results showed that 25320 publications on the rhizosphere were published from 2000-2022: 18255 research articles, 2553 review articles, and 4512 publications in the form of book chapters, encyclopedias, and conference abstracts. Of these, a majority of the 12082 publications were dedicated to agricultural and biological sciences. One notable point is that the rhizosphere studies in the subject areas of "Agricultural and Biological Sciences" and "Environmental Science" began in 2010. These results aided in understanding the process of RH and its agronomic impacts on

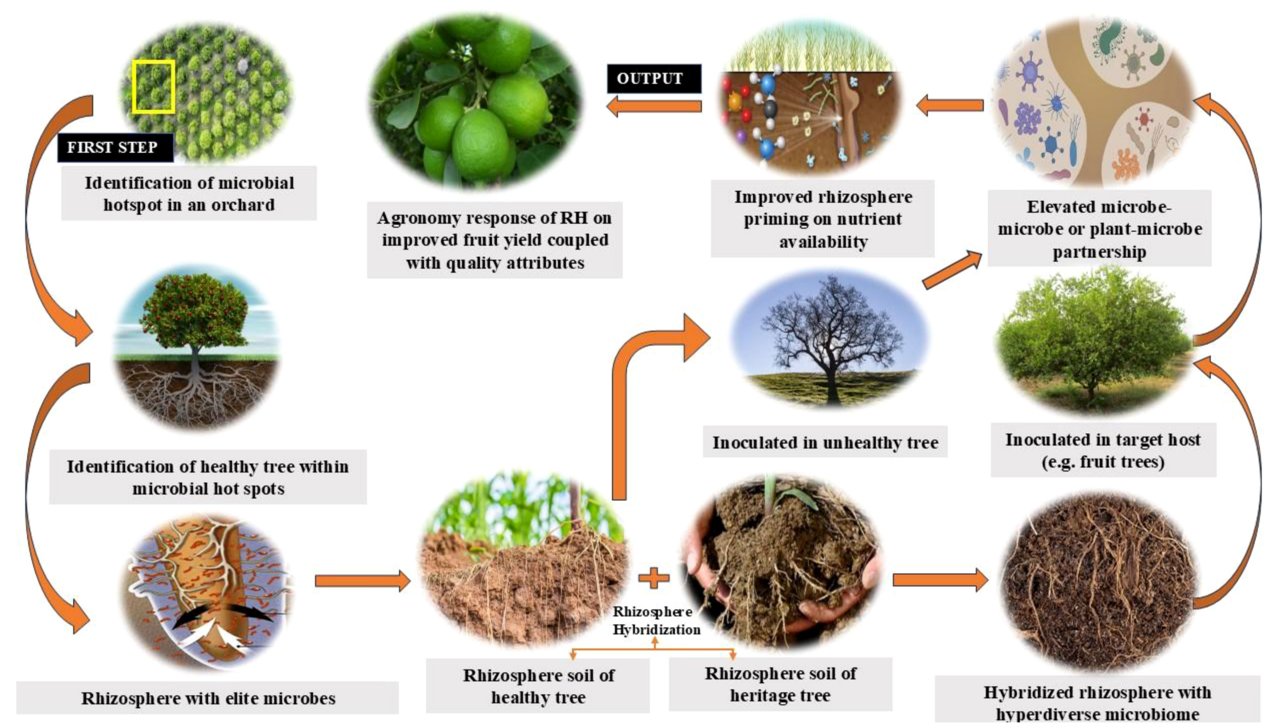


FIGURE 1
Schematic representation of the RH process.

crops. Only 1661 publications were dedicated to rhizosphere studies published from 2000-2022. Finally, based on the main objectives of the present study focusing on rhizosphere effects and RH, their impact on different crops, and rhizosphere health, 48 research and 14 review papers featuring issues such as fruit crop-based intercropping systems and rhizosphere studies of heritage trees were selected for onward discussion. Such a bibliometric analysis of rhizosphere research facilitated in identifying the gaps in

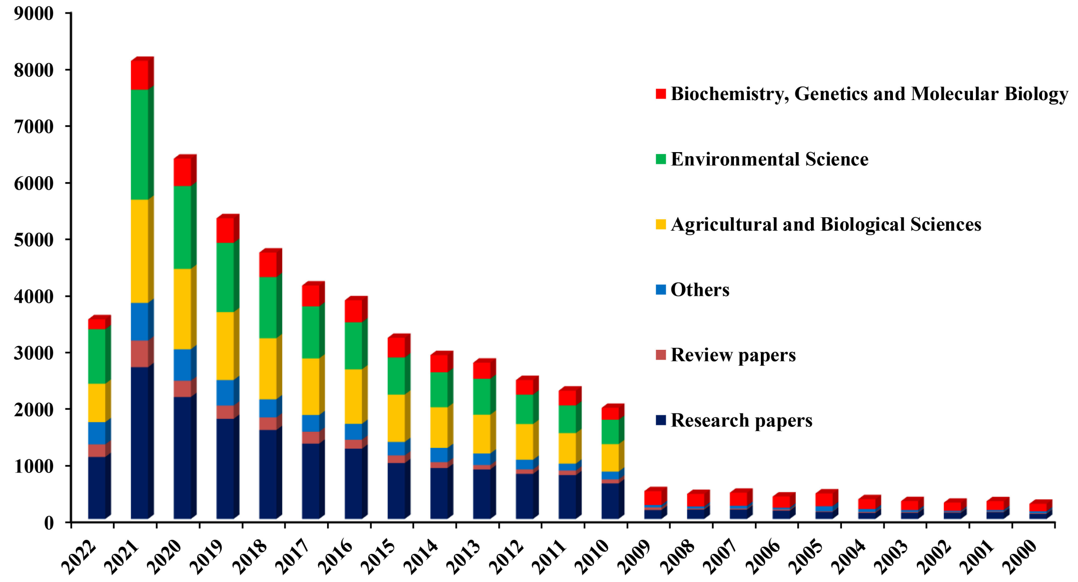


FIGURE 2
Bibliometric analysis of rhizosphere research highlighting the growing dynamics of rhizosphere-related issues over the past 22 years (2000-2022). Rhizosphere microbiome research has been one of the core issues among researchers worldwide.

rhizosphere research (Figure 2) and, at the same time, provided strong clues towards the rising popularity of rhizosphere research worldwide.

3 Rhizosphere, the seat of microbial battle

The rhizosphere is considered a dynamic battlefield between pathogenic and growth-promoting microorganisms, the outcome of which is largely determined by suitable management practices. These “battles” are where all active microorganisms interact among themselves through beneficial (mutualistic), neutral (commensalism), or detrimental (parasitic) relationships. Microbial build-up of the rhizosphere plays a vital role in mediating health and fitness against multiple stresses (Hacquard and Schadt, 2015; Zhang et al., 2021b) and, responsively, the host forms its microbial assemblage (Sasse et al., 2018). Although limited studies have highlighted the rhizosphere microbiomes of tree species (Uroz et al., 2010, 2016; Gallart et al., 2018), knowledge on the links between site factors, composition, and specific microbial niches concerning tree health is still lacking. The rhizosphere ecosystem of fruit trees is based on a fruit tree-soil-microbe relationship (representing the phytobiome) and their interactions with environmental attributes (Table 1).

Among subtropical fruit crops, citrus is one of the most extensively researched worldwide (Srivastava and Hota, 2020). In India, citrus microbiome studies have been undertaken from various angles (Srivastava et al., 2015a), with a particular focus on microbes-mediated soil fertility management (Srivastava and Ngullie, 2009; Srivastava and Malhotra, 2017) to sustain both production (Srivastava and Singh, 2008a) and fruit quality (Shamseldin et al., 2010; Srivastava et al., 2015b), as well as to invesitgate properties (Ngullie et al., 2015). Citrus is a highly nutrient-responsive crop, due to the existence of a strong nutrient sink (Srivastava and Singh, 2008b). However, regulating quality production through exploitation of the citrus rhizosphere microbiome has become a massive challenge (Srivastava and Singh, 2009). Some initial attempts have shown that citrus, like any other fruit crop, transforms the rhizosphere microenvironment according to the prevailing soil fertility gradient (Srivastava and Singh, 2009). These citrus rhizosphere-based microbes showed a strong association with citrus root either alone (Srivastava, 2010) or in combination with organic manure (Srivastava et al., 2002) and/or in combination with chemical fertilizers (Srivastava et al., 2015b). Likewise, changes in rhizosphere properties vis-à-vis fruit crops have been studied, highlighting crops such as strawberries (Kumar et al., 2020), apples (Soliman et al., 2023), citrus (Srivastava et al., 2017), fig (Abid et al., 2022), and pear (Zhang et al., 2020).

3.1 Rhizosphere Microbiome of Heritage Trees

It is common to see an unwarranted decline in the productivity of perennial crops, especially in fruit crops, after attaining peak productivity (Srivastava and Singh, 2009). This is due to the specific rhizosphere environment, popularly known as the “Negative Rhizosphere Effect” (NRE). NRE is commonly observed in crops like tea, apple, peach, and pear (Pandey et al., 2001; Somera and Mazzola, 2022). NRE is often regarded as a “Replant Disease” The underlying reasons for such a rhizosphere-driven decline in productivity is still not understood. Is it a case of the rhizosphere priming on microbial mining or nutrient mining? Sustaining the peak productive life of fruit trees is perhaps the most formidable challenge in agriculture. Researchers worldwide are still working hard to come up with well-conceptualized mechanisms associated with NRE. Modifications in the structural and functional microbial fabric of the rhizosphere due to continuous cropping is often regarded as the root cause of NRE. Sui et al. (2024), while comparing BT (perennial Poplar big trees) and CK (replanting the Poplar seedlings in soil after continuous cropping) groups of Poplar trees, reported no change in *Bacillus* (2.2-2.41%), while *Inocybe* and *Geopora* were 35.3 and 26.2% higher, respectively, in BT than CK groups, suggesting the rhizosphere microbiome was modified in the most effective way to ward off any NRE arising from continuous cropping. Dijkstra et al. (2013) proposed three nutrient-centered hypotheses: i. microbial mining causing a positive rhizosphere priming effect under low soil nutrient availability, ii. preferential substrate utilization inducing a shift in action from decomposing soil organic matter to utilizing rhizodeposition under high soil nutrient availability, and iii. competition causing a negative rhizosphere priming effect due to nutrient-limited microbial growth and decomposition (Weller et al., 2002).

Studies on the rhizosphere microbiome composition of f heritage trees have opened new avenues for identifying and isolating elite microbes with plant growth-promoting potential and antagonistic properties, as well as inoculation into the rhizosphere of targeted fruit crops. Due to their extended life cycle and non-deciduous nature, heritage trees are far less sensitive to biotic and abiotic stresses such as drought, salinity, herbivores, and pathogen attacks (Rodriguez et al., 2019; Zamora Ballesteros et al., 2019; Oliva et al., 2020; Pagán et al., 2022), meaning there is little threat against tree health (Reddy et al., 2013). The occurrence of a strong relationship between a rhizosphere microbiome and plant traits is a prerequisite to plant resistance against soil-borne pathogens (Bora and Bora, 2020a; b) and can be particularly helpful in heritage/forest trees. In a recent study on the rhizosphere microbiome of forest trees, Yu et al. (2022) observed considerable inhibitory effects of bacterial families (such as *Propionibacteriaceae, Phycisphaeraceae*, and *Rokubacteria*) on fungal pathogens of rhizosphere microbiota of seven forest tree species with the differential ability of recruiting key rhizosphere microbes as a function of root exudates. This strengthened the tree-microbial association, with significant differences amongst tree varieties. Hence, optimizing the microbial community of fruit tree rhizospheres with the rhizospheres of heritage trees (e.g. different species of *Ficus, Azadirachta* etc) could be an effective approach for improving growth and yield and developing resistance against soil-borne pathogens in fruit crops.

TABLE 1 Microbial diversity of the rhizosphere associated with different fruit crops: a snapshot.

Sl no.	Crop details	Diversity of microbes	Remarks	Reference
1.	Mango and Almond (Location: Southern Nigeria)	The mango rhizosphere registered a total bacterial count of 3.9-4.6 x 10^5 CFU g^{-1}, which was comprised of 25% *Bacillus*, 5% *Arthrobacter*, 15% *Corynebacterium*, and 10% *Klebsiella*. Total bacterial count in the almond rhizosphere was observed as 3.9-6.9 x 10^5 CFU g^{-1}, consisting of 25% *Bacillus*, 15% *Corynebacterium*, 5% *Flavobacyerium*, 5% *Streptococcus*, and 5% *Azomonas*.	Population dynamics of different bacterial species depended on specific crop rhizospheres, irrespective of geographical location.	Wemedo and Onolleka (2012)
2.	Mango (Location: Lucknow, Uttar Pradesh, India)	The rhizosphere microbial composition consisted of *Glycomyces*, *Chitinophaga*, *Lysobacter*, *Udaeobacter*, and *Bacillus.*	Organically treated trees harboured higher microbial diversity within the rhizosphere compared to a conventional fertilizer-treated rhizosphere.	Kumar et al. (2021)
3.	Mango (Location: Hainan Province, Southern China)	The rhizosphere consisted of major bacterial phyla, viz., *Chloroflexi* (24.77%) followed by *Proteobacteria* (24.26%), *Actinobacteria* (17.55%), and *Acidobacteria* (15.51%). Dominant fungal phyla included *Ascomycota* (79.38%), *Sordariomycetes* (36.69%), *Eurotiomycetes* (18.96%), *Dothideomycetes* (15.33%), *Basidiomycota* (11.28%), and *Agaricomycete* (9.50%).	Cover cropping influenced the soil bacterial community, altered fungal guilds, enhanced the pathotrophic fungi, and reduced the saprotrophic fungi.	Wei et al. (2021)
4.	Date palm, Mango, and Mandarin (Location: Salheia Destricat, Sharkia Governorate, Egypt)	Date palm + mango registered a much higher rhizosphere fungal diversity (*Aspergillus humicola*, *Aspergillus niger*, *Fusarium* sp, *Gliocladium* sp., *Penicillium* sp., *Phycomycetes fungi*, *Rhizoctonia solani*, *Rhizopus nigricans*), followed by date palm + mandarin and date palm alone in decreasing order with corresponding fungal counts of 118.32 x 10^3 CFU g^{-1}, 16.00 x 10^3 CFU g^{-1}, and 21.17 x 10^3 CFU g^{-1}, respectively.	Intercropping with either mango or mandarin in date palm plantations promoted the microbial diversity by diversifying the agricultural outcome due to variation in root exudate composition.	Abouziena et al. (2010)
5.	Banana (Location: Hainan province, China)	The core microbiome from the disease-suppressive soil was dominated by *Bacillaceae*, followed by *Hyphomicrobiaceae*, *Gaiellaceae*, *Bradyrhizobiaceae*, *Sphingomonadaceae*, *Rhodospirillaceae*, *Paenibacillaceae, Nitrospiraceae*, and *Streptomycetaceae*, representing a total of 121 OTUs covering 21.44% of total microbiome diversity.	*Bacillus amyloliquefaciens* NJN-6 isolated from the suppressive soil proved to be a potential bio-control agent, reducing Panama wilt disease incidence by 68.5%.	Xue et al. (2015)
6.	Banana (Location: Hainan, China)	*Ascomycota* and *Zygomycota* were the most abundant fungal phyla in soil samples of diseased and disease-free rhizospheres, respectively, which consisted of *Fusarium*, *Pseudallescheria*, *Nectriaceae*, *Mortierella*, *Aspergillus*, and *Penicillium* as dominant species. Regarding bacterial phyla, *Proteobacteria*, *Acidobacteria*, *Chloroflexi*, *Firmicutes*, *Actinobacteria*, *Gemmatimonadetes*, *Bacteroidetes*, *Nitrospirae*, *Verrucomicrobia* and *Planctomycetes* were dominant phyla with *Bacillus*, *Lactococcus*, and *Pseudomonas* as major genes.	Diseased soil samples showed higher OUTs than disease-free soil samples, without any significant difference in species diversity. Disease-free soil samples showed higher indices of abundance-based coverage estimator, Chao richness estimator, and Shannon diversity.	Zhou et al. (2019)
7.	Peach (Location: Nebraska, USA)	Rhizosphere microbial diversity was predominantly composed of *Bradyrhizobium* spp., *Steroidobacter* spp., *Saccharibacteria* spp., Gp16., *Actinoplanes* spp., *Rhizobium* spp., *Massilia* spp., *Sphingomonas* spp., *Burkholderia* spp., *Rhizobium* spp., and *Pseudomonas* spp.	Small roots as rhizosphere environments showed a higher abundance of important bacterial taxa compared to primary and secondary roots.	Pervaiz et al. (2020)

(Continued)

TABLE 1 Continued

Sl no.	Crop details	Diversity of microbes	Remarks	Reference
8.	Papaya cv. Golden (Location: Sooretama, Espírito Santo, Brazil)	The organic farming system (*Burkholderia cepacia*, *Burkholdeira vietnamiensis*, *Klebsiella* sp. and *Leclercia* sp) showed a better response than the conventional farming system (*Enterobacter* sp., *Klebsiella* sp., and *Burkholderia vietnamiensis*) with a contrasting microbial diversity comprising bacterial counts of 14–21 x 10^4 CFU g^{-1} and 10–17 x 10^4 CFU g^{-1}, respectively. .	*Klebsiella* sp. and *B. vietnamiensis* inhibited mycelial growth of *Fusarium culmorum* by 76-78% compared to inhibition of mycelial growth of the fungus *Pestalotia* sp. by 62-68%, besides maximum IAA production (180 µg/mL) with *Leclercia* sp.	Melo et al. (2018)
9.	Papaya (Location: Mandya, Karnataka, India)	Microbial diversity was characterized by *Bacillus amyloliquifaciens* (MTCC 10439), *Bacillus cereus* (MTCC 9017), *Erwinia* sp. (MTCC 2760), *Pseudomonas aeruginosa* (MTCC 7904), *Pseudomonas monteilii* (MTCC 9796), and *Pseudomonas marginalis* (MTCC 2758).	These bacteria species showed antifungal activity against *Colletotrichum gloeosporioides* and *Curvularia carica papayae.* However, ethyl acetate fraction of *P. aeruginosa* (MTCC 7904) and *P. monteilii* (MTCC 9796) culture filtrate exhibited complete suppression of mycelial growth of *C. gloeosporioides* at 100 ppm concentration.	Girish and Prabhavathi (2019)
10.	Avocado (Location: San Carlos, USA and Huatusco, Veracruz, Mexico)	The bacterial and fungal diversity was observed to have 888 and 545 OTUs, respectively, in asymptotic plants against 810 and 574 OTUs in symptomatic plants.	Root rot-induced changes in the distribution of bacterial taxa within the community showed an increasing relative abundance of *Pseudomonadales* and *Burkholderiales*, whilst reduced abundance of *Actinobacteria*, *Bacillus* spp., and *Rhizobiales* was predominantly observed.	Solís-García et al. (2021)
11.	Grape (Location: Aldeanueva del Ebro, La Rioja, Olite, Navarre, Spain)	Microbial diversity consisted of *Proteobacteria* (26.1-28.1%), *Actinobacteria* (18.5-24.1%), *Acidobacteria* (13.7-16.4%), *Bacteroidetes* (5.2-6.1%), *Ascomycota* (66.6-69.9%), *Basidiomycota* (11.5-20.1%), and *Zygomycota* (8.9-15.2%).	Comparative abundance of fungal and bacterial microbiota of vineyards showed 82.9% and 58.7% of bacterial and fungal OTUs, respectively, were shared between vineyards, demonstrating the existence of a "core" grape phylogeny, independent of geographical location.	Berlanas et al. (2019)
12.	Apple (Location: Agricultural Research and Extension Center, Winchester, USA)	Microbial diversity of the rhizosphere was defined by Acidobacteria (34.1%), Proteobacteria (14.3%), Planctomycetes (12.5%), Verrucomicrobia (12.1%), and Chloroflexi (9.9%) in decreasing order of their dominance.	Higher abundance of *Acidobacteria*, *Proteobacteria*, and *Planctomycetes* were observed in organic manure-treated rhizosphere, while *Verrucomicrobia* and *Chloroflexi* were most responsive under fertilizer-treated rhizospheres.	Sharaf et al. (2021)

The rhizosphere microbiome of these exemplary fruit trees provide strong clues about their richness in diversity that could be effectively utilized for better outcomes of RH.

As many as 40% of plant photosynthates are reported to be lost by root systems, resulting in a nutrient-enriched rhizosphere that harbors a greater diversity of microbiome (Nannipieri et al., 2007) and has diversified roles in plant growth and development. Soil health with respect to physical and chemical properties depends on the biological activity of the rhizosphere (Srivastava and Singh, 2001) to be involved in the maintenance of soil health and quality. The microbiome diversity within a crop rhizosphere is, therefore, a product of crop variety or cultivar, rootstock-scion combination, age of plant, root architecture, management practices (Srivastava et al., 1994; Gupta et al., 2008), and soil properties (Srivastava and Singh, 2002). Various relationships of different microbial communities within the rhizosphere of a plant take place through the enhancement of plant growth nutrient availability and soil health and the suppression of the pathogenicity of disease-causing pathogens (Pinho et al., 2020).

4 Crops with unique rhizosphere properties

Soil microbial activities and their population dynamics are significantly affected in the presence of living roots, popularly known as the "rhizosphere effect", which regulates the accumulation pattern of different nutrients and ecosystem functioning in terrestrial ecosystems (Yuan et al., 2020). Interestingly, the phylogenetic distance of plant hosts and associated bacterial communities are closely related (Lei et al., 2019). Sinha et al. (2009) proposed the rhizosphere properties rhizosphere microbial index, dehydrogenase, basal soil respiration/microbial biomass carbon ratio, electrical conductivity, phenol oxidase, and active microbial biomass carbon as the most critical in defending the rhizosphere of tree species such as *Aegle marmelos, Azadirachta indica, Bauhinia bauhinia, Butea monosperma, Eugenia jambolana, Moringa oleifera, Dalbergia sissoo, Tamarindus indica, Morus alba, Ficus religiosa, Eucalyptus* sp., and *Tectona grandis.*

The rhizobiome of tree species such as banyan (*Ficus benghalensis* L.), bamboo (*Dendrocalamus strictus* (Roxb.) Nees), Neem (*Azadirachta indica* A. Juss), which possess inherent abilities for high biomass production, higher microbial activity, and broad geographic adaptability makes them preferable choices as bio-inoculants (Table 2). But, an in-depth investigation of microbial diversity and functions to identify multi-functional microbes followed by co-evolutionary changes as a result of the introduction into the rhizosphere of target crop(s) is imperative to redefine the microbial networking of new rhizospheres, called "hybridized rhizosphere". Evidence for such novel possibilities can be easily drawn from crop-specific rhizosphere microbiome traits and their reshaping in response to crop management inputs. Nimoni and Pongslip (2009) observed a large number of indole acetic acid (IAA) forming bacterial diversity in *Ficus religiosa*. Isolation and characterization of isolates showed 91% similarity with *Rhizobium* spp. *Brevibacterium*, an endophytic bacterium, isolated and characterized from the rhizosphere of *F. religiosa*. Studies on the efficacy of synthesizing IAA in *Raphanus sativus* by inoculating the bacterial species isolated from 18 soil and 10 new isolates from the roots of *Brassica oleracea* showed an elevated response on root and shoot development than the control. These observations showed the potential of inter-rhizosphere microbiome interactions at different trophic levels toward better crop response.

Peter and Pandey (2014) collected the rhizosphere samples of bamboo and isolated two strains of *Pseudomonas* spp. out of a total of 22 isolates. The morphological and biochemical tests confirmed the isolates as *P. fluorescence* (59% diversity) and *P. auruginosa* (40.9% diversity). The abiotic stress tolerance activity showed that these two species thrived up to 10°C at a wide pH range of 5-9, having a tolerance level of salt concentration from 2–6 ppm. *P. fluorescence* and *P. auruginosa* were also observed to inhibit *Fusarium oxysporum, Rhizoctonia solani*, and *Alterneria solani* by 59.5-64.3%, 42.0-45.9%, and 50.0-52.5%, respectively. Kanse et al. (2015) isolated six phosphate-solubilizing fungi, tentatively identified based on colony morphology as *Talaromyces, Aspergillus*, and *Rhizobium*. One isolate, SLS8, based on 8s RDNA sequence, was confirmed as *T. funiculosus*, showing maximum phosphate-solubilizing ability compared to others. The study also suggested *T. funiculosus* SLS8 as a promising inoculant (seed inoculant) for maintaining good soil phosphate levels in saline soil.

Soil respiration is an indirect measurement of the autotrophic microbial load of soil, which in turn is an indicator of ecological sustainability. In a study on *in-situ* measurement of soil respiration by Prasad and Baishya (2019), the highest annual soil respiration was observed under the canopy of *F. religiosa* (18.72 μmol CO_2 m^{-2} s^{-1}year) and lowest under A. indica (4.58 μmol CO_2 m^2/s/year) during rainy and winter seasons, respectively. Different tree species showing a decreasing order of soil respiration were observed to be *F. religiosa* > *A. lebbeck* > *P. juliflora* > *V. leucophloea* > *M. pinnata* > *C. fistula* > *A. indica*. The higher soil respiration under the canopy of native over non-native species further suggested the importance of the interactive effects of soil moisture and temperature in the ecosystem of heritage trees that could be used well in the process of RH. The uniqueness of rhizosphere properties in terms of microbial diversity and functions needs to be upscaled to utilize RH successfully.

4.1 Rhizosphere properties of citrus (as a case study)

Soil microorganisms in the citrus rhizosphere play a decisive role in improving soil ecology through changes in soil properties, thereby helping improve the nutrient supply chain for the betterment of citrus growth and development (Srivastava and Malhotra, 2017; Srivastava and Singh, 2002; Ortas, 2012). In response to the rhizosphere as a biological indicator for soil fertility, soil microorganisms are major contributors to defining the production sustainability of citrus orchards (Srivastava et al., 2008). Citrus trees are considered highly dependent on arbuscular mycorrhizal (AM) symbiosis as citrus roots are characterized by short and poorly distributed root hairs (Graham and Syvertsen, 1985). Van Heerden et al. (2002) reported an abundance of various

TABLE 2 Nature and properties of rhizosphere microbiomes of different worldwide wild forest species.

Sl No	Tree species	Potential rhizospheric microbes	Reference
1.	Bo tree (*Ficus religiosa* L)	Abundance of *Deinococcus ficus* sp. *nov*., a Gram-positive, non-motile, non-spore-forming, rod-shaped, and aerobic bacteria possessing high survival under UV light at 243 nm.	Lai et al. (2006)
2.	Bamboo (*Dendrocalamus strictus* (Roxb.) Nees)	Bacterial isolates were observed as Gram negative, rod-shaped aerobic and non-endospore forming in nature.	Niveditha et al. (2008)
3.	Bo tree (*Ficus relegiosa* L.)	Distribution of ten plant-growth-promoting rhizobacteria, out of which eight strains showed the ability to produce IAA and siderophores and solubilize zinc and potash.	Shilpkar et al. (2009)
4.	Eastern cottonwood (*Populus deltoids*)	Rhizosphere bacterial communities (*Proteobacteria*, *Acidobacteria*, and *Verrucomicrobia* in increasing order) and fungal communities (*Ascomycetes* within *Pezizomycotina* and *Basidiomycetes* within *Agaricomycotina* in decreasing order) showed contrasting distribution patterns.	Gottel et al. (2011)
5.	Bo tree (*Ficus religiosa* L.)	Different microbial communities viz., *Rhizobium*, *Azotobacter*, and Yeast were observed to be more abundant compared to other microorganisms during the pre-monsoon period.	Pathak and Keharia (2013)
6.	Bamboo (*Sasa borealis* L.)	An abundance of *Phyllostachys bambusoides, Phyllostachys nigra* var. *henonis, Sasa borealis*, and *Phyllostachys nigra f. punctate* were predominantly observed.	Lee and Whang (2014)
7.	Banyan tree (*Ficus benghalensis* L.)	Distribution of seven Gram-positive, endospore-forming, and rod-shaped endophytic bacterial strains (*Bacillus subtilis* and *Bacillus amyloliquefaciens*) was observed.	Rodge et al. (2016)
8.	Neem (*Azadirachta indica* A.Juss)	As many as six microbes viz., *Aspergillus* sp., *Fusarium* sp., and *Penicillium* sp., were observed in abundance with *Aspergillus niger* displaying the maximum anti-microbial activity against *E. coli*.	Rani et al. (2017)
9.	Banyan (*Ficus benghalensis*), Cluster fig (*Ficus racemose*), and Bo (*Ficus religiosa*)	Predominant distribution of seven endophytic fungi viz., *Aspergillus*, *Trichophyton*, and *Coccidioides* species belonging to the Eurotiomycetes sub-class were observed.	Jariwala and Desai (2018)
10.	Sugar maple (*Acer saccharum* Marsh)	Plant-associated bacterial communities were dominated by different phyla viz., *Proteobacteria*, *Acidobacteria*, *Actinobacteria*, and *Bacteroidetes*; the main fungal taxa were *Ascomycota.*	Wallace et al. (2018)
11.	Formosan alder (*Alnus formosana* Burkill)	Resistance against drought and salt stress was observed with the inoculation of specific Frankia strains.	Lee and Tsai (2018)
12.	Neem (*Azadirachta indica* A.Juss)	Abundance of *Azotobacter paspali* and *Azotobacter vinelandii.*	Hala and Ali (2019)
13.	Oak tree (*Quercus*)	*Proteobacteria*, *Actinobacteria*, and *Acidobacteria* as well as *Basidiomycota*, *Ascomycota*, and *Zygomycota* were observed as the main colonizers within the oak rhizosphere.	Pinho et al. (2020)
14.	Moso bamboo (*Phyllostachys edulis* L.)	Presence of *Flavobacterium*, *Bacillus*, and *Stenotrophomonas* facilitated higher absorption of nitrogen.	Yuan et al. (2021)

- The rhizosphere microbiome of these forest species could be introduced into the rhizosphere of targeted fruit crops with an objectivity of expanded microbiome diversity to enhance crop response.

fungi in the citrus rhizosphere, consisting of *Aspergillus fumigatus, Absidia corymbifera, Penicillium diversum, Emericella nidulans, Rhizomucor pusillus, Paecilomyces variotii, Thermomyces lanuginosus*, and *Talaromyces thermophilus*. Some arbuscular mycorrhizal fungi (AMF), including *Glomus, Gigaspora, Entrophospora, Scutellospora*, and *Acaulospora* species, have been reported to occur frequently in citrus orchards (Wu and Srivastava, 2012). In a fungal diversity study of *Citrus unshiu* Marc. trees grafted on *Poncirus trifoliata*, Sun et al. (2017) reported 579 and 566 operational taxonomic units (OTUs) of fungi in plant roots and rhizosphere soil, respectively. Out of these, 462 OTUs intersecting between the roots and rhizosphere soil of citrus indicated that plant roots are favorable sites for the growth and development of those fungi rather than rhizosphere soil. Considering the phylum, *Ascomycota* was the dominant fungal species in soil and roots. Kohli et al. (1997) reported that microbial populations in soil play a crucial role in increasing the fruit yield of Nagpur mandarin with plant-available nutrients. The correlation values of *Azotobacter* count (r = 0.692, p= 0.01), ammonifiers (r= 0.512, p= 0.01), and phosphate-solubilizing bacteria (r = 0.618, p= 0.01) showed a stronger connection with fruit yield than plant-available nitrogen (r = 0.489, p= 0.01), phosphorous (r= 0.316, p= 0.05), and potassium (r= 0.321, p= 0.05) in soil, signifying the potential of the population density of microbes as a bio-indicator of elevated fruit yield.

He et al. (2002) reported that soil microbial biomass nutrients viz., microbial biomass carbon, (Cmic 1.62-3.16 mg/kg), microbial biomass nitrogen, (Nmic 19.0-35.2 mg/kg), and microbial biomass phosphorous, (Pmic 20.2-42.3 mg/kg) constituted only 1.61-2.60%, 1.2-2.5% and 2.4-8.4% of total organic carbon, respectively, in citrus orchards in Zhejang province, China. The phosphorous-solubilizing capacity of *Bacillus subtilis, Bacillus polymyxa, Trichoderma viridi*, and *Aspergillus terreus* found on citrus growing belts of India is reported to be 13.30-81.68% P_2O_5 through insoluble tricalcium phosphate (Bhattacharya et al., 1999). Not only the bacterial species but also the mycorrhiza species like *Glomus caledonium*, *Glomus mosseae*, and *Glomus clarum* are abundantly observed in citrus growing belts of Italy (Palazzo et al., 1992). In eastern Spain, *Glomus mosseae* and *Glomus intraradices* are commonly observed mycorrhizal fungi in citrus rhizosphere soils, which can be inoculated back into soils through agronomic practices like crop rotation with aromatic plants viz., *Thymus vulgaris, Lavandula vera, L. angustifolia*, and *Rosmarinus officinalis* (Camprubi and Calvet, 1996a, b). In Japan, citrus orchards are reported to be richly abundant in *Gigaspora*, *Scutellospora*, and *Glomus* AM fungi (Ishii and Kadoya, 1996). Bhattacharya et al. (1999) reported that the *Glomus population* was higher in the juvenile phase (1-5-year-old orchards) as compared to the reproductive stage (5-10-year-old orchards).

Ngullie et al. (2015) evaluated 15 citrus varieties, namely four limes/lemons, three mandarins, and eight sweet oranges, at the pre-bearing stage on Alfisol. The trend in the growth of canopy volume of different citrus cultivars supported the changes in bacterial count ($CFUg^{-1}$) of 7.3 x 10^8, 4.9 x 10^6, 4.5 x 10^6, and fungal count ($CFUg^{-1}$) of 7.7 x 10^7, 3.1 x 10^5, and 2.2 x 10^5 in limes/lemons, sweet oranges, and mandarins, respectively. Similarly, soil microbial biomass nutrients were also observed to be higher in lime/lemons as compared to sweet oranges and mandarins, indicating the greater affinity of lime/lemon rhizosphere to reproduce microbial biomass and maintain a better nutrient pool of soil. Citrus rootstocks having greater root volume reflected their vigorousness crop phenology in terms of canopy volume, a pre-requisite for ensuring higher fruit yield. The response of different fruit crops to microbial inoculation in terms of parameters related to soil fertility changes and crop response established their strong responsive nature (Table 3).

Of late, culture-independent metagenomic studies aided the identification of newer microbial species and established a strong foundation for developing artificially constructed microbial communities known as artificial microbial consortia or synthetic communities (SynComs) using core microbiomes to recreate more robust structures and functions of the microbiome and representing different microbial niches. A great advantage of SynComs studies lies in the fact that members can be added, eliminated, or substituted as needed (Vorholt et al., 2017), in addition to elucidating spatial microbial interactions (Amor and Bello, 2019). Two main approaches are usually employed to artificially select the microbiomes: top-down (modifying the existing microbiome) and bottom-up (starting from individual microorganisms to build engineered microbiomes). In the top-down approach, selected environmental variables (e.g., pH, temperature, and redox potential) are used to manipulate the existing microbiome through ecological selection (Lawson et al., 2019). Although this approach is widely used for bioremediation (Atashgahi et al., 2018) and wastewater treatment (Demarche et al., 2012), it has the disadvantage of working with a complex community. In contrast, the bottom-up approach offers the biggest advantage of simplifying microbial interactions by building artificial communities from pre-selected individual organisms (Raaijmakers and Kiers, 2015).

Microbial taxa that are highly connected and more influential on the community in a pre-existing or artificially constructed microbiome are given maximum preference (Banerjee et al., 2018) for microbial screening followed by isolation and whole-genome sequencing to determine their functional capabilities (Kong et al., 2022). Consequently, their role in regulating the growth and function of other members of the microbiome can be effectively exploited to enhance specific desired functions. Such a concept of assembling SymComs is quite different from known and well-studied bacteria. Hence, it is possible to increase the number of desired bacterial strains while decreasing the number of undesired strains (Cloutier et al., 2023; Ma et al., 2022; Kugarajah et al., 2023) using the strong functional relationship between plant metabolites and the bacterial community diversity of the rhizosphere. In one of the recent incubation studies spanning 28 days, three different plant metabolites, namely benzoxazolinone, gramine, and quercetin, were added to the soil (Schutz et al., 2021) and showed that the bacterial diversity was significantly reduced by the first two metabolites only. Consequently, plants producing one or more of these metabolites are suggested to have a specific effect on the soil bacterial community.

5 Agronomic and microbial response of RH (our experiences)

While chemical or synthetic fertilization can improve fruit yield and quality, long-term use has failed to sustain the same yield expectancy due to erosion in soil carbon stock, culminating in the emergence of multiple nutrient deficiencies. Such unprecedented loss of soil fertility is likely to bring changes in microbial communities within the rhizosphere (Srivastava et al., 2008), coupled with reoriented production dynamics. Artificially, the rhizosphere could be reconstructed depending upon the need of the plant to enhance physiological efficiency through rhizosphere engineering, popularly known as RH. This is synonymous with creating an artificial environment for plant growth-promoting microorganisms to provide another protective layer against the pathogenic microbes (Rhizosphere fortification). By and large, trees react and acclimate to antagonistic soil environments, and this can happen through different strategies, including changes in root exudation and rhizo-deposition, which bring variable changes in rhizosphere soil properties (Gargallo-Garriga et al., 2018).

RH is a relatively recent introduction to rhizosphere research to modify rhizosphere ecology and create an environment for plant growth-promoting microbes to positively influence plant agronomy (Keditsu and Srivastava, 2014). The concept of RH is, therefore, put forward to demonstrate the value-added benefits of nutrient-microbe-plant synergy, in addition to the expected dynamism to microbial diversity in harmony with a wide range of fruit crops (Srivastava et al., 2015b, 2021). Studies were carried out in the past (Cheke et al., 2018a; b) on the inoculation response of rhizosphere soils of three perennial

TABLE 3 Associative responses of fruit crops with microbial inoculants reported through worldwide literature.

Sl No	Crop	Microbial species	Experimental details	Response attributes	Reference
1	Mandarin (*Citrus reticulate* Blanco) cv. Baladi	Humic acid + *Bacillus megaterium* var *Phosphatircum*	Sandy soil, Beheria Governorate, Egypt	Increase in recovery from dry root rot of diseased trees, reduction in colonization of *Fusarium solani*, and improvement in yield and fruit quality.	El-Mohamedy and Ahmed (2009)
2	Rough lemon (*Citrus jambhiri* Luch)	Azospirillum-AM fungi consortium (*Funneliformis mosseae*, *Gigaspora margarita*, and *Acaulospora laevis*).	Typic Ustochrept, with alkaline (pH 8.1) and EC (0.36 dSm^{-1}), Punjab, India.	Improvement in seed germination, seedling growth, root growth, and organic carbon along with plant available P and K.	Singh et al. (2018b)
3	Sweet orange (*Citrus sinensis* Osbeck) CV.Washington navel	*Pseudomonas fluorescens* (strain 843)	Silty clay soil, Delta Nile Valley, high pH (8.9) and EC (3.28 dsm^{-1}), at Al–Menoufia Governorate, Egypt.	Increased fruit yield and fruit physico-chemical attributes and reduced population growth of nematode, *Tylenchulus semipenetrans.*	Shamseldin et al. (2010)
4	Mandarin (*Citrus reticulata* Blanco) cv. Balady	50% compost (N-equivalent)- 250 ml of biofertilizer mixture (*Bacillus circulans* (4 x 10^{7} cfu ml^{-1}) *Bacillus megaterium* (6 x 10^{7} cfu ml^{-1}) *Azotobacter chroococcum* (5 x 10^{5} CFU mL^{-1}))- 5 kg of natural mineral compound ore tree^{-1} year^{-1}.	Clay loamy soil, EC 0.32 dsm^{-1}and pH 7.97, of El Kalubia Governorate, Egypt	Improvement in fruit yield and fruit quality (increase in fruit size, peel thickness, juice weight %, T.S.S: acid ratio, vit. C, and decrease in fruit acidity), total bacteria count (*Bacillus circulans, Bacillus megaterium*, and *Azotobacter chroococcum*), and plant available nitrates, collectively leading to better crop response.	El-Shazly et al. (2015)
5	Mandarin (*Citrus nobilis* Lour. × *Citrus deliciosa* Ten.) cv Kinnow	AM fungi *Glomus manihotis- Glomus mosseae- Gigaspora gigantia.*	Alkaline loam soil with moderate fertility, New Delhi, India	Increase in plant height, canopy volume, leaf area, and number of new shoots plant^{-1}, in addition to improvement in leaf nutrient concentration in index leaves and fruits.	Shamshiri et al. (2012)
6	Mandarin (*Citrus reticulata* Blanco) cv. Balady	*Azotobacterchroococcum-Azospirillum liposerum- Bacillus megaterium- Bacillus circulans* (250 g tree^{-1} year^{-1}).	Soil characteristics pH 7.91 and EC 1.11 dSm^{-1}, Assiut University, Egypt	Increase in 27.1% yield, 9.09% leaf N, 20.62% leaf P, and 42.85% leaf-K over control treatment.	Mohamed et al. (2009)
7	Swingle citrumelo (*Citrus paradisi* Macfad cv. Duncan × *Poncirus trifoliata* (L.) Raf.)	Bacillus spp (Isolates BM16 and CPMO4) at 10^{7} CFU mL^{-1}	Seedlings were grown under unsterilized growth medium of vegetable origin, Sylvio Moreira Citriculture Centre, Brazil.	Increase in seedling height, number of leaves, stem diameter, shoot, and root dry mass at 150-days after germination.	Giassi et al. (2016)
8	Acid lime (*Citrus aurantifolia* Swingle)	*Azotobacter chrococcum*	Sandy soil, alkaline pH, high EC, Jhalawar, Rajasthan, India	Increase in seedling height, number of leaves, root:shoot ratio, leaf area, seedling biomass, chlorophyll content, and leaf nitrogen content.	Yadav et al. (2012)
9	Grapefruit (*Citrus paradisi* Macfad) cv. Duncan	*Pseudomonas geniculata* strain 95 (10^{8} CFU mL^{-1}) isolated from Valencia orange.	Ustipsamment (Sandy soil, acidic pH), Lake Alfred, Florida	Reduction in symptoms of canker and expressed salicylic acid- signalling pathway and increase in ROS of treated plant.	Riera et al. (2018)
10	Olive (*Olea europaea*) cv. Zard	*Pseudomonas fluorescens* (1.7×10^{8} Cells mL^{-1}), *Bacillus subtilis* (2×10^{8} Cells ml^{-1}), and mycorrhizal powder inoculum (Arbuscular mycorrhizal fungi, *Rhizophagus irregularis*) (10^{5} Cells gr^{-1} propagule)	Silty loam calcareous soil, EC 2.42 dSm^{-1}, pH 8.85, Fars province, Iran	Increased fruit length, diameter, flesh thickness, fresh weight, dry weight, yield per tree, and oil quality compared to chemical fertilizers.	Tadayon et al. (2025)
11	Apple (*Malus domestica* Borkh)	*Bacillus velezensis* FZB42 or *Pseudomonas* sp. RU47	Loamy sand soil, pH 5.6, soil organic carbon 17 gkg^{-1}, Ellerhoop, Germany	Inoculants reduced relative abundance of *Enterobacteriaceae* in the apple replant disease (ARD) rhizoplane and increased phytoalexin content in roots than ARD soil	Hauschild et al. (2024)

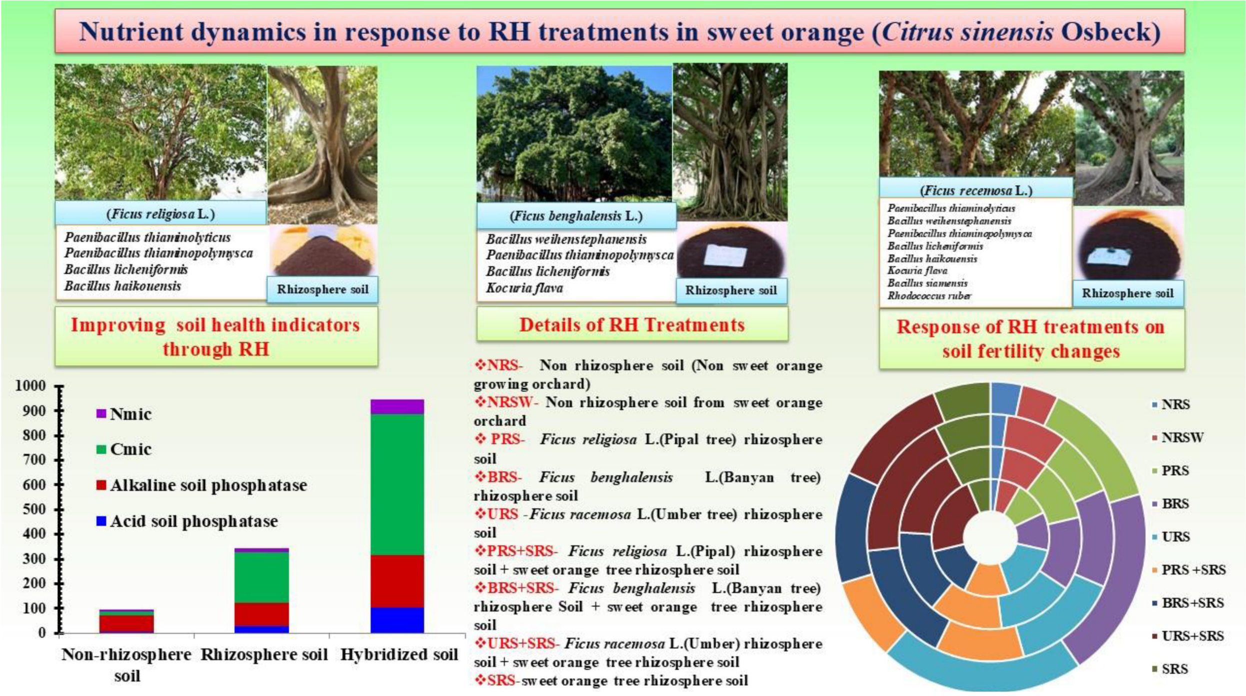
(Continued)

TABLE 3 Continued

Sl No	Crop	Microbial species	Experimental details	Response attributes	Reference
12	Grape (*Vitis vinifera* L.)	*B. velezensis* (1.8×10^9 CFU/mL) *and B. velezensis* (1.5×10^9 CFU/mL); *B. megaterium* (1.3×10^9 CFU/mL); *P. aryabhattai* (1.3×10^9 CFU/mL); *R. aquatilis* (1.6×10^9 CFU/mL)	pH 6.21, soil organic matter 25.37 gkg^{-1}; Nanning, China	*Bacillus velezensis* 18, *B. velezensis* 20, and *Rahnella aquatilis* 5 emerged as consistently effective performers over the two-year period, demonstrating the ability to optimize growth and yield.	Shi et al. (2024)
13	Pomegranate (*Punica granatum* L.)	*Pseudomonas fluorescens* and *Glomus mosseae*	Silty loam soil, pH 7.9, soil organic carbon 0.8%, Gorgan, Iran	The combined use of *P. fluorescens* and *G. mosseae* improved quality production of pomegranate under salinity stress.	Ziatabar Ahmadi et al. (2024)
14	Mango (*Mangifera indica* L.)	*Consortium of Glomus mosseae, G. fasciculatum and Gigaspora margarita*	*In vitro* in-ovulo embryo cultured plantlets of mango genotypes for biohardening; IARI, New Delhi, India	All AMF-treated plants showed increased vegetative growth, chlorophyll content, proline content, and total phenol content, hence proving their efficacy in mitigating adverse effects of transplanting shock and enhancing survival.	Singh et al. (2017)
15	Plantain (*Musa paradisiaca* L.)	*Arthrobacter* sp., *Bacillus* spp., *Sinomonas* sp., *Paenibacillus* spp.,and *Kosakonia radicincitans DSM16656, Beauveria, Trichoderma,*	Acidic soil derived from weathered volcanic rocks, low cation exchange capacity, Akonolinga, Cameron	Significant improvements in acid phosphatase and urease activity in plantain rhizosphere, in addition to control of crop pests and diseases	Olougou et al. (2024)
16	Guava (*Psidium guajava* L.)	Phosphorus-solubilizing bacteria (PSB) @ 10 ml/plant + *A. chroococcum @ 10 g/plant*	pH 6.7; EC 0.23 dSm-1, 0.4% OC, 251.3 $kgha^{-1}$ $KMnO_4$-N, 32.4 $kgha^{-1}$ Olsen-P, 76.8 $kgha^{-1}$ NH_4OAc-K, Solan, India	Increased the yield efficiency and quality attributes like TSS and Ascorbic acid content of the guava by improving microbial population and micronutrient concentration.	Ashwini et al. (2022)
17	Papaya (Carica papaya L.) cv. Surya	FYM + Vermicompost + AMF + PGPR Mix + *Pseudomonas fluorescens*	Laterite soil, pH 4.92; 275 kg/ha $KMnO_4$-N, 15 kg/ha Olsen-P, 165 kg/ha NH_4OAc-K; Kerala, India	Increased the yield and qualitative aspect of fruits including carotenoid, ascorbic acid, and total sugar	Bindu and Renjan (2024)
18	Litchi (*Litchi chinesis* Sonn.) cv.	AM fungi + *Azotobacter chroococcum* (2:1)	pH 6.9, EC 0.21 dSm^{-1}; 5.8 g/kg OC, 135.7 $mgkg^{-1}$ $KMnO_4$-N, 9.2 $mgkg^{-1}$ $NaHCO_3$-P, 11.4 $mgkg^{-1}$ NH_4OAc-K; *Azotobacter chroococcum* (12.2 × 10^6 $CFUg^{-1}$), *Pseudomonas* sp. (8.6 × 10^5 $CFUg^{-1}$) and K-mobilizers (9.1 × 10^4 $CFUg^{-1}$); Himachal Pradesh, India	Increased resident microbe survival, total chlorophyll content, and root:soil ratio in seedlings. *A. chroococcum* increased microbial biomass 2.59% more than the untreated control. Acidic phosphatases, dehydrogenases, and alkaline phosphatases also increased in the rhizosphere.	Kumar et al. (2024)

heritage trees, namely *Ficus racemosa* L. (Common name: Umber tree), *Ficus benghalensis* L. (Common name: Banyan tree), and *Ficus religiosa* L. (Common name: Pipal tree), into the rhizosphere of sweet orange trees (*Citrus sinensis* Osbeck). The inoculation response of *F. recemosa* showed the best response on rhizosphere properties of sweet orange trees, associated with a net increase of 18.0 g kg^{-1} Walkley-C, 62.2 kg ha^{-1} $KMnO_4$-N, 19.0 kg ha^{-1} Olsen-P, and 95.6 kg ha^{-1} NH_4OAc-K, in addition to a 2.34 times increase in microbial biomass nitrogen (Nmic), 4.23 times increase in microbial biomass carbon (Cmic), and 2.81 times increase in soil alkaline phosphatase over rhizosphere of sweet orange trees alone. The magnitude of these responses was, however, significantly lower when compared with the rhizosphere of *F. recemosa* alone, with an increase in Walkley-C by 11.2 g kg^{-1}, $KMnO_4$-N by 32.2 kg ha^{-1}, Olsen-P by 11.2 kg ha^{-1}, and NH_4OAc-K by 28.2 kg ha^{-1}, in addition to 1.34 -folds, 2.23-folds, and 1.62-folds increase in Nmic, Cmic, and soil alkaline phosphatase, respectively. Hence, microbially hybridized soil proved to be biologically highly active for better agronomic crop response (Figure 3). Later, another mode of RH (Dzuvichu et al., 2023) was studied by inoculating the rhizosphere of highly productive Khasi mandarin (*Citrus reticulata* Blanco) trees into lesser productive trees; after two seasons, significant improvements in fruit yield and soil fertility changes were observed (Table 4). The Rhizosphere III treatment observed significantly higher bacterial and fungal counts of 38 X 10^5 and 32 X 10^4 CFU g^{-1} soil, respectively, compared to other rhizosphere treatments, recording bacterial counts of 08 X 10^{4-}38 X 10^5 CFU g^{-1} soil and fungal counts of 04 X 10^{3-}22 X 10^4 CFU g^{-1} soil. These microbial changes with Rhizosphere III treatment were associated with 1.54 times (10.68 Mg ha^{-1}) higher fruit yield compared to other rhizosphere treatments (6.93-9.73 Mg ha-1) as a function of significantly higher soil nutrients pool maintained with the Rhizosphere III treatment. Against the backdrop of such observations, how shall we identify the microbial hot spots featuring the development of elite microbial spp. within an orchard and rationalize the spatial distribution of microbes to optimize fruit yield without sacrificing the quality? These RH-based observations paved the way for the inoculation of soil rhizospheres or endosphere microbes for elevating micronutrient concentration in various plant parts viz., roots, leaves, and fruits (Ku et al., 2019), to sustain production on a long-term basis.

Hota et al. (2021a), in their comprehensively planned study, successfully developed a hybridized soil (BbNByR) by using the rhizospheres of banyan (*Ficus benghalensis* L), neem (*Azadirachta indica* A.Juss), and bamboo (*Dendrocalamus strictus* (Roxb.) Nees) trees inoculated into rhizosphere of acid lime as the host fruit tree. This treatment showed significantly higher shoot growth parameters (30.4 cm seedling height, 3.0 mm seedling diameter, 5.8 branches $seedling^{-1}$, and 38.9 leaves seedling $^{-1}$) and root growth parameters (14.5 cm taproot length and 17.3 number of secondary roots seedling $^{-1}$) over single rhizosphere effect of the control treatment involving host tree alone (Table 5). Synonymous to a hybridized rhizosphere response, the microbial consortium



❖NRS- Non rhizosphere soil (Non sweet orange growing orchard)
❖NRSW- Non rhizosphere soil from sweet orange orchard
❖ PRS- *Ficus religiosa* L.(Pipal tree) rhizosphere soil
❖BRS- *Ficus benghalensis* L.(Banyan tree) rhizosphere soil
❖URS -*Ficus racemosa* L.(Umber tree) rhizosphere soil
❖PRS+SRS- *Ficus religiosa* L.(Pipal) rhizosphere soil + sweet orange tree rhizosphere soil
❖BRS+SRS- *Ficus benghalensis* L.(Banyan tree) rhizosphere Soil + sweet orange tree rhizosphere soil
❖URS+SRS- *Ficus racemosa* L.(Umber) rhizosphere soil + sweet orange tree rhizosphere soil
❖SRS-sweet orange tree rhizosphere soil

FIGURE 3
Diagrammatic representation on response of RH in sweet orange (*Citrus sinensis* Osbeck) grafted on Rangpur lime (*Citrus limonia* Osbeck) rootstock for improved rhizosphere health indicators (microbial biomass nitrogen, Nmic; microbial biomass carbon, Cmic; alkaline soil phosphatase; and acid soil phosphatase) and soil fertility changes (the inner most circle represents organic carbon, followed by $KMnO_4$-N, Olson-P, and NH_4OAc-K as we move on from the inner circle). Hybridized soil (URS + SRS) involving inoculation of rhizosphere of *F. recemosa* (URS) into the rhizosphere of sweet orange trees (SRS) proved to be far superior over either of the two alone. Source: Based on data generated through studies by Cheke et al. (2018a, b) and Srivastava et al. (2021).

TABLE 4 Yield response of RH in Khasi mandarin (*Citrus reticulata* Blanco) grown on acid Alfisols.

Treatments	Microbial population (CFU g^{-1} soil)		Leaf nutrients concentration							Fruit yield (Mg ha^{-1})
	Bacterial count.	Fungal count.	Macronutrients*			Micronutrients**				
			N	P	K	Fe	Mn	Cu	Zn	
Rhizosphere-I	$08x10^4$d	$04x10^3$d	2.13bc	0.06b	1.12c	209.2	81.1d	10.1d	19.4cd	6.93d
Rhizosphere-II	$32x10^4$c	$18x10^3$c	2.03d	0.06b	1.01d	216.2	92.3c	11.2c	20.0c	8.53c
Rhizosphere-III	$67x10^5$a	$32x10^4$a	2.34a	0.10a	1.72a	218.4	115.3a	18.4a	24.2a	10.68a
Rhizosphere-IV	$38x10^5$b	$22x10^4$b	2.21b	0.08ab	1.52b	204.2	102.8b	13.3b	22.2b	9.73ab
SEm ±	1.60	1.80	0.03	0.01	0.03	4.73	1.73	0.33	0.46	0.80
CD (P=0.05)	4.20	6.70	0.10	0.04	0.10	NS	5.2	1.00	1.40	1.11

* and ** expressed in percentage and mg kg^{-1} dry matter, respectively. SEm and CD stand for standard errors of means and critical difference, respectively. Different alphabets denote significant differences amongst treatments using Duncan's Multiple Range Test.

Treatment involving the inoculation of rhizosphere soil (Rhizosphere-III) of healthy trees into the rhizosphere of another set of low-producing trees of Khasi mandarin showed changes in soil microbial load, leaf nutrients composition, and fruit yield, significantly higher than rest of the other treatments. Such responses suggested the role of microbial hot spots within the same orchard in the presence of elite microbes. However, we could not carry out studies on changes in culture-independent microbes to obtain more insights about such responses featuring RH.

Source: Dzuvichu et al. (2023).

(*Paenibacillus alvei* Cheshire and Cheyne (MF113275), *Micrococcus yunnanensis* Cohn (MF113274), *Bacillus pseudomycoides* Nakamura (MF113272), *Aspergillus flavus* Link (MF113270), and *Acinetobacter radioresistens* Nishimura (MF113273)) displayed a much greater magnitude of response in mature acid lime trees through an increase in microbial biomass load of the rhizosphere, thereby adding additional rhizosphere resilience by reducing the mortality of new seedlings/buildings once planted in a new field (Hota et al., 2021b).

Studies on microbe-mediated rhizosphere fortification in acid lime (Hota et al., 2020a, b, 2021b) showed that the application of vermicompost combined with a microbial consortium increased the canopy volume, improved leaf phenotypical features, and enhanced fruit yield and fruit quality parameters (such as juice content, TSS, and acidity). These observations showed that the process of RH in acid lime improved the yield and quality, as well as qualitatively improving the carrying capacity of hybridized rhizosphere with value-added efficient microbial traits. Root exudates stimulate the microbial community in the rhizosphere by providing soil microbes with the desired nutrient forms and easily degradable energy sources from root exudates and dead root cells (Kaksonen et al., 2006). The microbial diversity of heritage trees like *Ficus* (Rodge et al., 2016), Neem (Biswas et al., 2016), and Bamboo (Tu et al., 2014) have been studied in-depth to replicate their behavior in a conducive environment. Thus,

TABLE 5 Evaluation response of different treatments of RH on agronomic performance of acid lime (*Citrus aurantifolia* Swingle).

RH treatments	Seedling height (cm)	Seedling diameter (mm)	Number of branches seedling $^{-1}$	Number of leaves seedling^{-1}	Tap root length (cm)	Number of secondary roots seedling^{-1}
T_1, Control	61.7hi	5.3ij	4.0gh	60.1j	23.2j	18.5i
T_2, MC	83.2cd	6.5de	7.0cd	88.4de	32.8d	30.8de
T_3, AlRW	76.9e	6.9cd	8.1bc	89.0d	31.6de	31.1cd
T_4, BbR	85.3bc	7.2bc	9.0ab	95.5bc	36.0bc	32.1c
T_5, BbRW	67.6gh	6.2fg	4.6fg	71.6gh	28.5gh	25.6g
T_6, NR	70.7fg	5.9hi	6.6de	75.9g	30.3fg	25.6g
T_7, NRW	65.6 fg	6.0gh	5.1f	65.8i	26.4hi	22.3h
T_8, ByR	86.9ab	7.5b	9.0ab	97.3ab	36.3ab	33.6ab
T_9, ByRW	72.4ef	6.3ef	6.8d	82.2f	31.3ef	29.5ef
$T_{10,}$ BbNByR	92.1a	8.3a	9.8a	99.0a	37.7a	35.8a
CD (P=0.05)	7.1	0.5	1.0	4.9	2.8	2.5

MC, microbial consortium; AlRW, water extract of acid lime rhizosphere; BbR, rhizosphere soil of bamboo; BbRW, water extract of bamboo rhizosphere; NR, rhizosphere soil of neem; NRW, water extract of neem rhizosphere; ByR, rhizosphere soil of banyan; ByRW, water extract of banyan rhizosphere, and BbNByR, rhizosphere soil of bamboo, neem, and banyan. CD stands for critical difference. Different alphabets denote significant differences amongst treatments using Duncan's Multiple Range Test. Treatment T_{10} (combination of the rhizosphere soils of bamboo, neem, and banyan tree) produced the best response on root-and shoot growth-related parameters over the other RH treatments.

Source: Hota et al. (2020a, 2021a).

rhizosphere properties defined in terms of the microbial pool have a strong influence on plant growth depending upon the diversity and evenness of different microbial communities within the rhizosphere of different tree species (Figure 3).

Various interactions among diverse microbial communities promote key processes associated with plant growth and soil health. Some soils are naturally suppressive to many soil-borne pathogens, although this suppression relates to agro-pedological features of the soil. In most agro-systems, the biological components are primarily important in disease suppression, paving the way for biological control of plant pathogens to be brought into the ambit of sustainable issues relating RH (Weller et al., 2023). A typical beneficial response is achieved with the 'mycorrhiza-helper-bacteria', a term coined by Garbaye (1994) for those bacteria widely known to stimulate mycelial proliferation of mycorrhizal fungi. Soil microorganisms are known to synthesize molecules capable of increasing the root exudation, which, in turn, stimulate mycorrhizal mycelia abundance in the rhizosphere (Wu and Srivastava, 2012). The establishment of the mycorrhizal fungus in the root cortex is known to change many key processes associated with plant physiology (Zou et al., 2016). These key functions comprise the mineral nutrient composition of plant tissues, hormonal balance, and the patterns of carbon allocation to different plant parts (Srivastava et al., 2021). Microbial communities are known to play key roles in soil carbon stabilization by incorporating organic carbon into their cellular materials and products, are stabilized by mineral associations and supply enzymes catalyzing the decomposition and transformation of plant and soil carbon (Kögel-Knabner, 2002), even though organic matter is ultimately decomposed microbially (Srivastava et al., 2015a; Srivastava, 2010).

Research on the microbiome of hybridized soil still needs to establish to what extent major microbial communities function as a collective entity, since biofilm formation in the rhizosphere is an important trait that prevents microorganisms from being detached from plant roots by various natural processes (Velmourougnane et al., 2017). Do such hybridized soils develop biofilms? Biofilms consist of syntrophic communities of microorganisms where cells stick to each other in a self-produced matrix of extracellular polymeric substances (Rana et al., 2021). Such a matrix provides the structural and functional protection through which microbes chemically link with each other by quorum sensing and function as one unit (Tan et al., 2015; Vlamakis et al., 2013). In soils, microbial communities such as bacteria and fungi develop biofilms on abiotic surfaces such as ore (minerals), water-air interfaces, and dead organisms (Rekadwad and Khobragade, 2017). In recent years, biofilmed biofertilizers (BBs) (biofertilizers containing microbial communities capable of forming biofilms) have emerged as a new inoculant strategy to improve biofertilizer efficiency and sustain soil fertility amid detrimental nutrient mining over time (Sharma et al., 2023). The idea behind BBs is that biofilm formation creates a more suitable environment for microorganisms to compete with resident organisms and negotiate with the heterogeneity of biotic and abiotic factors in soil (Unal et al., 2019).

5.1 Soil enzymes and RH

RH facilitates the development of a physiologically more active rhizosphere. Therefore, the processes and reactions taking place within the rhizosphere are influenced by the stage of root development, diversity and functionality of rhizosphere microorganisms, degree of root-microorganism association, and profile of rhizosphere enzymes— key driving factors responsible for creating rhizosphere environments conducive to positive crop responses. The enzymes are more concentrated in the rhizosphere than in bulk soil, as the rhizosphere soil is richer in organic-C substrates (Gianfreda, 2015). The balance of microbial activities, especially enzymes activities, is, therefore, responsible for the development of resilient soil health. The enzymes that are present in the rhizosphere, both through their interactions with plants and their functions in decomposition of organic compounds coupled with nutrient cycling, play a crucial role in ecological fitness and functioning of the host plant (Nannipieri et al., 2012). Furthermore, activities of rhizosphere enzymes (Table 5) are valuable indices of changes taking place in the microbial functioning within the rhizosphere soil (Gianfreda, 2015). In addition, various management practices also dictate the rhizosphere enzymatic profile of different fruit crops (Table 6).

5.2 RH and holobiont paradigm

Over the years, important components defining the rhizosphere function such as soil, microbes, and plants have been extensively studied in isolation, including pathogenic or symbiotic microbial interactions. Ecological approaches have only recently been developed, possibly in relation to the emergence of molecular tools and, to a lesser extent, understanding of the complex environment of the rhizosphere (Lundberg et al., 2012). In this situation, the plants and associated microbes are no longer seen as individual but rather as an association, a part of a phytobiome. Hence, the holobiont paradigm (a physiological unit of plant-microbe associative relationship) has emerged in the plant world (Zilber-Rosenberg and Rosenberg, 2008; Rosenberg et al., 2010; Vandenkoornhuyse et al., 2015), with microbes playing a key role in plant adaptation to changing environments. Crucially, the holobiont should be viewed as the unit of selection in the evolutionary process (Rosenberg et al., 2010) and, as a consequence, modification of any component of the holobiont could have a cascading effect on other components. A recent study demonstrated that the domestication of plants has affected the fabric of microbial communities, both within the rhizosphere or endosphere (Pérez-Jaramillo et al., 2016). Viewing the plant as a superorganism—representing an independent ecosystem—add a new dimension to efforts to engineer the rhizosphere microbiome, exploit the microbial gene pool, and develop microbially engineered plants. Any breakthroughs in the near future should take into account the plant-associated numerical diversity of microbial communities and their function. Hence, a better knowledge of

TABLE 6 Changes in enzymatic activities of rhizosphere soil of different fruit crops in response to soil managements practices.

Crop	Enzyme	Experimental details	Results	Reference
Mango *(Mangifera indica)* L.	Dehydrogenase	Effect of farmyard manure, vermicompost, mulching, microbial inoculants (*Azotobacter*, PSM, and *Trichoderma harzianum*), and substrates (N, P, K)	Higher activity of dehydrogenase in vermicompost, microbial inoculants and mulching treatments	Adak et al. (2014)
Trifoliate orange	Substrate β-glucosidase, catalase, peroxidase, and phosphatase, with a decrease in activity of polyphenol oxidase	Effects of arbuscular mycorrhizal fungus (*Funneliformis mosseae)* on glomalin-related soil protein production and soil enzyme activities	Increase in activity of substrate β-glucosidase, catalase, peroxidase, and phosphatase, but a decrease in activity of polyphenol oxidase	Wu et al. (2015)
Apple *(Malus domestica)*	Urease, phosphatase, and invertase	Effect of corn-apple rotation on enzyme activity in rhizosphere soil of apple trees	Continuous cropping of apple reduced soil enzyme activities	Qian et al. (2014)
Peach (*Prunus Persica*)	Urease, dehydrogenase, and phosphatase	Effect of soil fumigation, SSP, PGPR, and biocontrol along with control (recommended package of practices)	Highest activity in the rhizosphere with combined treatment, and the lowest value obtained in *in-situ* grafted plant with the recommended package of practices.	Thakur and Sharma (2018)
Citrus cultivar Huangguogan (*Citrus reticulata* × *Citrus sinensis*)	Antioxidant enzymes, superoxide dismutase, guaiacol peroxidase, and catalase	The physiological effects of nitrogen supplementation (0 to 2.72 kg/year) on the plant	Both excessive and deficient N decreased the activities of antioxidant enzymes, while the activities of antioxidant enzymes increased under an appropriate amount of N.	Liao et al. (2019)
Grape *(vinifera)* indica	–	Five treatments, namely no fertilization with the typical chemical fertilization years, increased organic fertilizer (cow manure), reduced chemical fertilizer, increased organic fertilizer, and reduced chemical fertilizer in sandy soil.	Application of organic fertilizer with reduced chemical fertilizer for two years showed the greatest effect on the bacterial community and activity of the rhizosphere soil.	Wu et al. (2020)

phytobiomes is strongly advocated. This implies a better description of plant-associated microbiota associated with either one fruit cultivar or different species of the same cultivar, or both at different growth stages of development, with all these issues currently understudied. In addition, most of the physiological experiments aiming at physiological and genotypic screening are performed in the absence of the associated microbiota (Nogales, 2015).

6 Conclusion and futuristic viewpoints

The structure of indigenous microbial communities is reported to exert a multi-fold influence on the composition of plant-preferred microbiota. However, this raises another question: Is large microbial diversity or functional redundancy more important in enabling distinct microbiomes with equivalent or variable functionality? This opens up another counter question: is a rootstock-scion combination that prefers an optimal microbiome in one soil operationally effective in another soil? Do crop breeding techniques need to be highly contextual and individually tailored to specific soil types and management practices? The impacts of rhizosphere microbiomes on nutrient cycling need to be quantified through plant–soil system and relevant methods of evaluation need to be found.

The plant roots release compounds that serve as a source of energy for microorganisms. A high concentration of root exudates deposited into the rhizosphere attracts more metabolically active microorganisms to the roots than to other parts of the rhizosphere. Concerns over the excessive use of chemical/synthetic inputs have meant organic farming has become increasingly popular, promoting bio-preparations developed from rhizosphere microorganisms responsible for stimulatory responses to plant growth and development. Large-scale applications of plant growth-promoting microbes is likely to reduce the use of inorganic fertilizers to put fruit crops elevate functional corridors. A conceptual framework that exploits rhizosphere-endosphere-phyllosphere microbial diversity for bioprospecting soil-plant health to develop a revisited fruit production system has been proposed as a case study (Figure 4). The process of RH also needs to be viewed as a way to develop climate-smart soil with disease -suppressive abilities that can produce microbially engineered fruit crops. These futuristic viewpoints would lay a better foundation for understanding nutrient-microbe synergy for exploiting the productivity potential of growing, much nearer to natural farming. Rhizosphere microorganisms, apart from the activity in promoting plant growth, also offer the possibility of bioremediation of rhizospheres contaminated with pesticide residues and antagonism to different phytopathogens. Despite numerous studies on rhizosphere microorganisms, there still exists a strong need for a more elaborate understanding of the principles of

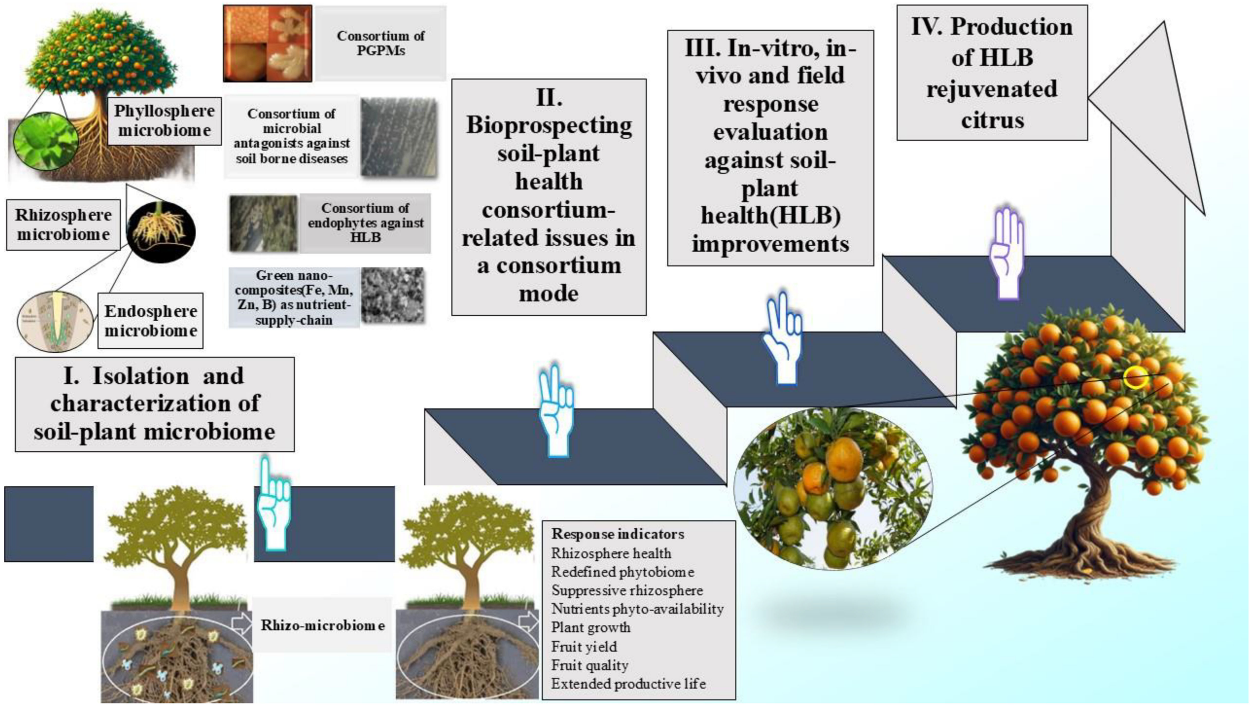


FIGURE 4
Conceptual framework for exploiting citrus phytobiome (citrus infected with Huanglongbing, HLB disease as a case study) by bioprospecting soil-plant health for developing a microbe-mediated citrus production system.

rhizosphere ecology, describing microorganism function and diversity. Such candid understanding of the dynamics and composition of microbial communities developing out of RH as a newly proposed field of research could help decode microbial communication with fruit trees.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding authors.

Author contributions

AS: Conceptualization, Methodology, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing, Formal analysis, Project administration. SM: Conceptualization, Data curation, Formal analysis, Resources, Writing – original draft, Investigation, Methodology, Visualization, Writing – review & editing. PB: Conceptualization, Formal analysis, Investigation, Methodology, Resources, Supervision, Visualization, Writing – original draft, Writing – review & editing. DH: Conceptualization, Formal analysis, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. VP: Conceptualization, Investigation, Methodology, Project administration, Supervision, Validation, Writing – review & editing. SM: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – review & editing. VZ: Conceptualization, Formal analysis, Methodology, Validation, Writing – original draft.

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