International Journal of Horticultural Science 2026, 32: 85-101.
https://doi.org/10.31421/ijhs/32/2026/16855

Phytobiome management in horticultural systems: beyond the rhizosphere toward whole-plant microbiome optimization

Ahmad, M.

Institute of Horticultural Sciences, University of Agriculture, Faisalabad, Punjab, Pakistan
Author for correspondence: mohammadahmaduaf@gmail.com

Summary: The plant microbiome is not confined to the soil. Across every anatomical compartment, the rhizosphere, phyllosphere, endosphere, anthosphere, spermosphere, and carposphere, structurally distinct and functionally specialized microbial communities orchestrate processes fundamental to plant health, productivity, and resilience. Yet horticultural science has remained disproportionately anchored to the rhizosphere, leaving the vast microbial landscape inhabiting aerial, floral, seed, and fruit tissues largely unexplored and unmanaged. This blind spot carries profound consequences at a time when global horticultural production confronts an unprecedented convergence of pressures: accelerating climate instability, stringent restrictions on synthetic agrochemicals, mounting soil degradation, and escalating consumer demand for sustainably produced, chemical-free, premium-quality produce. The biological potential embedded within the whole-plant phytobiome to address these intersecting crises remains critically underutilized. A fundamental barrier to progress is the absence of a unifying scientific framework. Existing reviews address plant-associated microbiomes in disciplinary silos, focusing narrowly on rhizosphere bacteria, individual crop species, or single microbial kingdoms, without synthesizing the full cross-compartment, cross-kingdom phytobiome in the horticultural context. No comprehensive framework has yet integrated microbial community dynamics spanning bacteria, fungi, archaea, and viruses across fruit, vegetable, and ornamental crops within a single, coherent, and practically applicable model. This review addresses that gap directly. Through critical synthesis of compartment-resolved phytobiome research across major horticultural systems, we characterize the taxonomic composition, ecological assembly drivers, and agronomic functional roles of microbial communities inhabiting each plant compartment. We demonstrate that phyllosphere microbiomes confer photoprotection and pathogen exclusion; endophytic communities directly modulate secondary metabolite profiles and systemic immunity; anthosphere microbiomes influence pollinator attraction and fruit set; spermosphere communities determine seedling establishment success through vertical microbial inheritance; and carposphere microbiomes govern post-harvest storability and food safety outcomes. We further establish how host genotype, crop developmental stage, management-induced dysbiosis, and climate-driven perturbations collectively shape phytobiome assembly and functional integrity across compartments. Building on this synthesis, proposing to introduce the Whole-Plant Phytobiome Optimization (WPPO) framework, the first integrative, three-tier conceptual model designed specifically for horticultural systems. WPPO encompasses whole-plant phytobiome profiling using multi-omics platforms, identification of functional microbial modules linked to target agronomic traits, and precision compartment-targeted intervention through synthetic microbial communities (SynComs), encapsulated biostimulants, and digitally guided delivery systems integrated with IoT sensor networks and machine learning decision-support tools. Applied across the full crop life cycle, from spermosphere conditioning at seed priming to carposphere biopreservation at post-harvest, WPPO offers a scalable, evidence-based, and technologically integrated roadmap toward substantially reduced agrochemical dependence, enhanced crop resilience, superior produce quality, and the deployment of ecologically precise next-generation biocontrol and biostimulant strategies.

Ahmad, M. (2026): Phytobiome management in horticultural systems: beyond the rhizosphere toward whole-plant microbiome optimization. International Journal of Horticultural Science 32: 85-101. https://doi.org/10.31421/ijhs/32/2026/16855

Key words: phytobiome, plant microbiome, rhizosphere, carposphere, horticultural crops, biocontrol, biostimulants, precision horticulture, sustainable agriculture

1. Introduction

Modern horticulture stands at a critical juncture. Global demand for fresh fruits, vegetables, and ornamental plants continues to escalate, driven by population growth, dietary transitions, and urbanization, while the ecological and regulatory foundations underpinning conventional production are simultaneously eroding. The European Union's Farm to Fork Strategy mandates a 50% reduction in the use of synthetic pesticides and a 20% reduction in fertilizer use by 2030, with parallel regulatory trends emerging across North America and Asia (European Commission, 2020). Climate change projections indicate that heat stress, drought, and shifting precipitation patterns will disproportionately affect high-value horticultural crops, many of which possess narrow thermal optima and high water requirements (Bisbis et al., 2018). These converging pressures demand biological solutions of commensurate sophistication, and the plant microbiome represents perhaps the most promising, yet least fully harnessed, biological resource available to horticultural science.

The concept of the plant microbiome has undergone profound conceptual expansion over the past two decades. The foundational insight articulated by Lorenz Hiltner in 1904 that the plant root creates a microbially enriched zone of intense biological activity has been progressively refined into the recognition that plants are, in their entirety, meta-organisms: holobionts whose fitness is inseparable from the collective genetic and metabolic contributions of their associated microbial partners (Vandenkoornhuyse et al., 2015; Berg et al., 2020; Trivedi et al., 2020). This holobiont perspective demands a correspondingly comprehensive research agenda, one that moves beyond the soil surface to encompass the full architectural complexity of the plant phytobiome.

The term 'phytobiome' was formalized by Leach et al. (2017) to describe the system encompassing the plant and all associated organisms, microorganisms, macro-organisms, and viruses living in, on, and around it within its abiotic environment. This definition encompasses not only the rhizosphere but also the phyllosphere (leaf surface microbiome), endosphere (internal tissue microbiome), anthosphere (floral microbiome), spermosphere (seed-associated microbiome), and carposphere (fruit surface and internal microbiome). Each compartment harbors taxonomically and functionally distinct microbial communities shaped by unique physicochemical environments, host-derived chemical gradients, and differential ecological selection pressures. The failure to integrate these compartments into a coherent management framework represents one of the most significant unexploited opportunities in applied horticultural science.

In horticultural systems specifically, this gap is particularly consequential. Horticultural crops are characterized by extraordinary biological and agronomic diversity spanning annual vegetables, perennial fruit trees, soft fruits, ornamentals, and cut flowers, and by production systems ranging from open-field cultivation and traditional orcharding to sophisticated controlled-environment agriculture (CEA) and hydroponic vertical farming. Each system imposes distinct phytobiome dynamics and presents unique microbiome management opportunities. Yet the scientific literature addressing phytobiome management in horticulture remains fragmented, compartment-siloed, and lacking in integrative conceptual frameworks.

Despite growing research investment in plant microbiome science broadly, horticultural applications have lagged agronomic crops. Reviews of rhizosphere microbiomes in vegetable crops (Compant et al., 2019), endophytic fungi in fruit trees (Hardoim et al., 2015), phyllosphere bacteria in model species (Vorholt, 2012), phytobiome modulation for disease control (Panwar et al., 2025), and soil-phytomicrobiome interactions under climate change (Chen et al., 2023) have advanced compartment-specific knowledge considerably. However, these advances have been achieved in disciplinary isolation. No comprehensive review has synthesized microbiome dynamics across all major plant compartments within a horticultural context, nor proposed an integrative management framework applicable to the diversity of horticultural production systems. This review is specifically designed to address that deficit.

We synthesize evidence on the structure, assembly mechanisms, and functional ecology of microbial communities across six primary plant compartments in major horticultural crops (***Table 1***). We examine the biotic and abiotic drivers governing phytobiome assembly, the management practices that disrupt or enhance microbial community function, and the emerging technological platforms enabling precision phytobiome engineering. Building on this synthesis, we propose the Whole-Plant Phytobiome Optimization (WPPO) framework, an integrative, three-tier model providing a practical roadmap for deploying compartment-specific microbiome management across the full horticultural crop life cycle, from seed priming to post-harvest bio-preservation.

2. Compartment-specific phytobiome architecture in horticultural crops

The plant body constitutes a structured series of distinct microbial habitats, each governed by different physicochemical conditions, host-derived chemical signals, and ecological dynamics. Understanding the architecture of these compartments is the essential first step toward integrated phytobiome management. The following sections characterize the microbiome of each major plant compartment, with specific emphasis on horticultural crop systems (***Figure 1***).

2.1. Rhizosphere microbiome: established knowledge and horticultural specificity

The rhizosphere, the zone of soil immediately surrounding and influenced by plant roots, remains the most intensively studied plant-associated microbial habitat. Root-released exudates, including sugars, amino acids, organic acids, and phenolic compounds, create a nutrient-enriched microenvironment supporting microbial biomass 10- to 100-fold greater than bulk soil (Bais et al., 2006). The composition and quantity of root exudates are highly crop-specific, which drives the recruitment of taxonomically distinct rhizobiome communities in different horticultural species (Sasse et al., 2018; Zhalnina et al., 2018).

2.1.1. Core rhizobiome architecture in vegetable and fruit crops

Tomato (*Solanum lycopersicum*) has emerged as a model horticultural species for rhizobiome research. Metagenomic studies reveal a core rhizobiome dominated by Proteobacteria, Actinobacteria, Firmicutes, and Acidobacteria, with consistent enrichment of Pseudomonas, Bacillus, and Streptomyces relative to bulk soil (Xu et al., 2018; Bulgarelli et al., 2013; Berendsen et al., 2012). Strawberry (*Fragaria x ananassa*) rhizobiome studies similarly identify Pseudomonas and Bacillus as dominant taxa, alongside abundant arbuscular mycorrhizal fungi (AMF) of the genera Glomus and Rhizophagus, which form obligate symbioses critical for phosphorus acquisition under field conditions (Mo et al., 2024).

In perennial fruit tree systems, rhizobiome architecture is further complicated by multi-year succession dynamics and the dominant influence of rootstock genotype. Studies in grapevine (*Vitis vinifera*), apple (*Malus domestica*), and citrus have consistently demonstrated that rootstock identity exerts a more powerful influence on rhizobiome composition than either soil type or geographic location, suggesting that the root exudate metabolome itself genetically determined is the primary driver of microbial community recruitment (Vives-Peris et al., 2020; Cadenas, 2024). This finding has immediate practical implications: rootstock selection constitutes a de facto microbiome engineering decision, one that has historically been made without consideration of microbiome consequences.

2.1.2. Mycorrhizal networks as phytobiome infrastructure

Arbuscular mycorrhizal fungi (AMF) deserve particular attention as structural and functional anchors of the horticultural rhizobiome. AMF form obligates mutualistic associations with the majority of horticultural crops, notable exceptions including brassicaceous vegetables, which are non-mycorrhizal, and their hyphal networks extend the effective root volume by several orders of magnitude (Smith & Read, 2008). Beyond direct nutrient acquisition, AMF hyphae functions as microbial highways, facilitating the spatial distribution of bacterial communities across the rhizosphere and creating microsites of elevated microbial activity associated with phosphorus solubilization, nitrogen cycling, and bioprotective activity (Bonfante & Anca, 2009).

Table 1. Overview of the six primary phytobiome compartments in horticultural crops: key microbial communities, functions, and agronomic relevance.

Compartment	Key microbial phyla / taxa	Primary functions	Horticultural relevance
Rhizosphere	Proteobacteria, Actinobacteria, Firmicutes, Acidobacteria; Pseudomonas, Bacillus, Streptomyces; AMF (Glomus, Rhizophagus)	Nutrient solubilization (P, K, Fe); N-fixation; ISR induction; disease suppression	Rootstock-dependent microbiome recruitment; replant disease management; soil suppressiveness
Phyllosphere	Proteobacteria (Methylobacterium, Sphingomonas, Pseudomonas); Actinobacteria; Cladosporium, Alternaria, Aureobasidium	Biocontrol of foliar pathogens; frost protection; photoprotection	Botrytis suppression in grapevine/strawberry; biological ice-nucleation management in peach/citrus
Endosphere	Bacteroidetes, Proteobacteria, Firmicutes; Trichoderma, Beauveria, non-pathogenic Colletotrichum	Secondary metabolite elicitation; systemic immunity; growth promotion	Polyphenol/aroma enhancement in tomato, strawberry, grape; vascular disease protection
Anthosphere	Acinetobacter, Gluconobacter, Rosenbergiella; Metschnikowia, Starmerella yeasts	Nectar chemistry modification; pollinator attraction; floral microclimate regulation	Pollination efficiency in enclosed systems (polytunnels, greenhouses); fruit set improvement
Spermosphere / Seed	Pseudomonas, Bacillus, Paenibacillus; Trichoderma; vertically transmitted endophytes	Seedling establishment; competitive exclusion of soil-borne pathogens; priming of immune pathways	Seed treatment / priming with SynComs and PGPR; founding microbiome optimization
Carposphere	Candida, Cryptococcus, Aureobasidium; Bacillus subtilis; lactic acid bacteria	Post-harvest pathogen suppression; terroir-linked flavor expression; shelf-life extension	Biopreservation of apple, pear, citrus, stone fruits; premium produce differentiation

AMF = arbuscular mycorrhizal fungi; ISR = induced systemic resistance; PGPR = plant growth-promoting rhizobacteria; SynCom = synthetic microbial community.

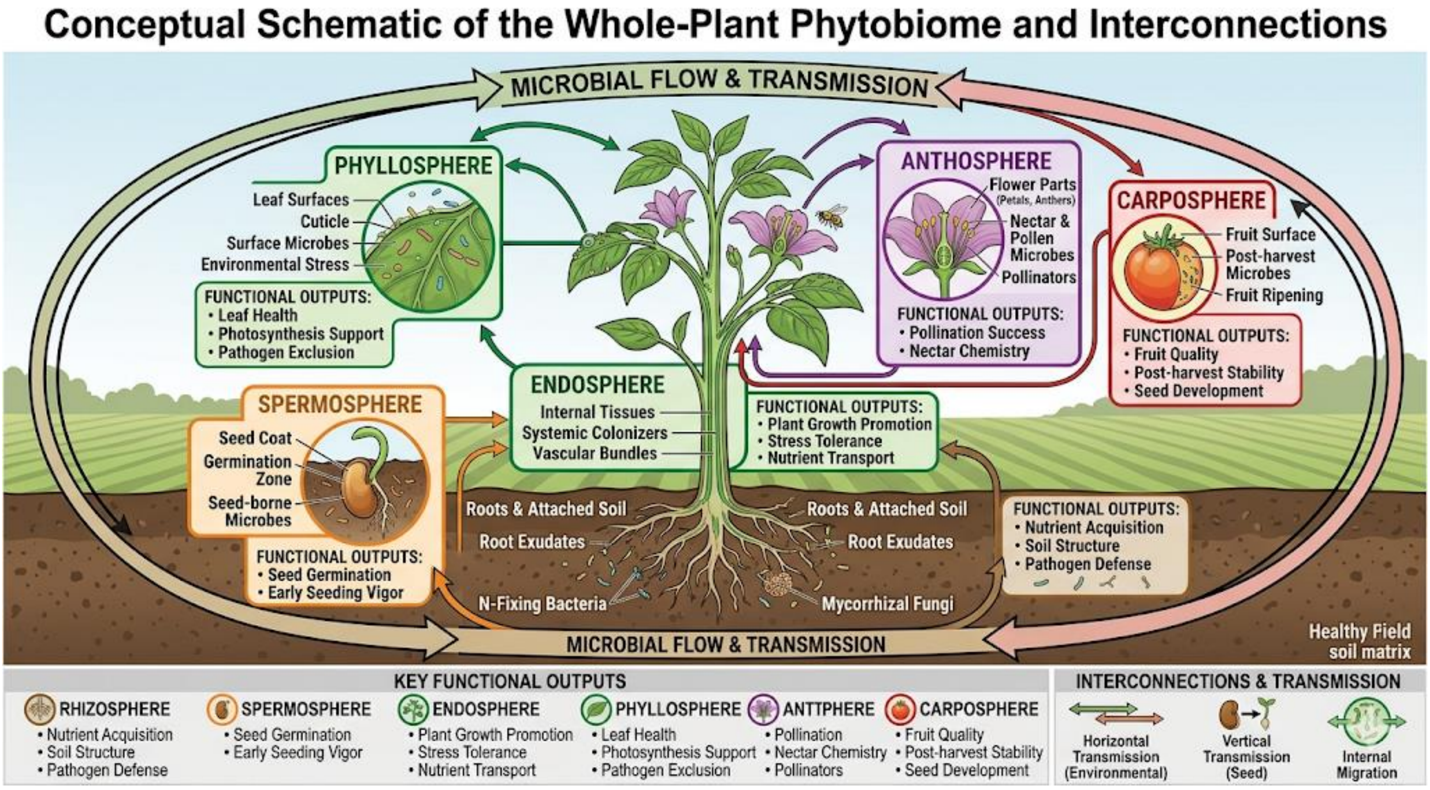

Figure 1. Whole-plant phytobiome diagram illustrates the six anatomically distinct microbial compartments, the primary ecological and chemical gradients governing each, and the functional outputs relevant to horticultural crop performance (this pictorial diagram is originally created by author by using different means of media available).

Common mycorrhizal networks (CMNs) connecting neighboring plants in orchards and intercropping systems further extend phytobiome connectivity beyond the individual plant, enabling microbiome-mediated inter-plant signaling and resource redistribution. The disruption of CMNs by tillage, fumigation, and intensive fertilization represents a form of phytobiome infrastructure damage with cascading consequences for rhizobiome function and plant resilience (Barto et al., 2011).

2.2. Phyllosphere microbiome: the aerial frontier

The phyllosphere, the collective surface of above-ground plant parts, particularly leaves, constitutes one of the largest microbial habitats on Earth, with an estimated total leaf surface area of approximately 6.4 x 10^8 km^2 globally (Vorholt, 2012). This habitat is characterized by extreme physiological challenges for its microbial inhabitants: high UV irradiance, desiccation, osmotic stress, wide temperature fluctuations, and low nutrient availability. Despite these hostile conditions, phyllosphere communities are taxonomically diverse, functionally active, and increasingly recognized as important modulators of plant health and productivity.

2.2.1. Ecological filters shaping leaf surface communities

Phyllosphere microbial communities are shaped by a hierarchy of filters operating across spatial scales. At the macro-scale, climate and geography set broad boundaries on community composition. At the meso-scale, crop species identity and cultivar determine the surface wax composition, stomatal density, and exudate chemistry that govern microbial colonization potential. At the micro-scale, variation across leaf age, surface topography, and proximity to stomatal openings creates microhabitat heterogeneity that drives within-leaf community variation (Lindow & Brandl, 2003).

The core phyllosphere microbiome of horticultural crops is typically dominated by Proteobacteria (particularly Methylobacterium, Sphingomonas, and Pseudomonas) and Actinobacteria, with fungal communities characterized by Cladosporium, Alternaria, and Aureobasidium as consistent members (Rastogi et al., 2013). Methylobacterium deserves particular attention in horticultural contexts: these methylotrophic bacteria metabolize methanol released by pectin demethylation during cell wall maturation. This process intensifies during fruit ripening, creating a metabolic linkage between host developmental physiology and phyllosphere microbial community dynamics.

2.2.2. Phyllosphere functions in horticultural crop protection

Phyllosphere microorganisms perform several functions of direct agronomic relevance. Biocontrol activity is perhaps the most practically significant: epiphytic bacteria and yeasts that colonize leaf and fruit surfaces can suppress foliar and post-harvest pathogens through competitive exclusion, antibiosis, and induced resistance mechanisms. *Aureobasidium pullulans*, a ubiquitous phyllosphere yeast, has been particularly well-studied as a biocontrol agent against *Botrytis cinerea* in grapevine and strawberry, with commercial formulations (e.g., Botector) demonstrating efficacy comparable to conventional fungicides under moderate disease pressure (Galli et al., 2021).

Frost protection represents a second commercially important phyllosphere function. Ice nucleation-active strains of *Pseudomonas syringae* colonizing leaf surfaces can initiate frost damage at temperatures as high as -2 degrees Celsius. The application of competitive ice nucleation-inactive bacterial strains to displace ice-active populations, biological ice nucleation management, has demonstrated potential for frost damage mitigation in sensitive horticultural crops, including peach, strawberry, and citrus, under conditions of moderate frost (Lindow, 1983). This example illustrates a broader principle: phyllosphere microbiome composition directly affects frost tolerance thresholds, representing a tractable target for microbiome-based crop protection.

2.3. Endosphere: the inner microbial sanctum

The endosphere, encompassing the internal tissues of roots, stems, leaves, and reproductive organs, harbors microbial communities that have breached the physical barriers of the plant body and colonize intercellular spaces, vascular tissues, and occasionally even intracellular compartments. Endophytic microorganisms, by definition, cause no symptomatic disease under normal conditions, represent a subset of the broader endobiome, and constitute some of the most agriculturally promising plant-associated microorganisms known.

2.3.1. Tissue-specific endosphere colonization

Root endosphere communities are derived primarily from the adjacent rhizobiome but are subject to a progressive filtering process as microorganisms transit the rhizoplane and endodermis. The resulting endosphere community is typically less diverse but more functionally selected than the rhizobiome, enriched in taxa capable of tolerating the oxidative and antimicrobial defense mechanisms of the plant apoplast (Edwards et al., 2015; Compant et al., 2021). In horticultural crops, root endosphere communities show strong crop-species specificity: the endobiome of solanaceous crops (tomato, pepper, eggplant) differs markedly from that of cucurbits (cucumber, melon, squash) even when cultivated in identical soils, reflecting genotype-specific filtering mechanisms.

Stem and vascular endosphere communities deserve special attention in the context of systemic plant diseases. The xylem vessels, traditionally considered a largely sterile environment, harbor a specialized bacterial community, the xylem microbiome, which plays incompletely understood roles in vascular function and disease resistance. The devastating emergence of *Xylella fastidiosa* as a pathogen of olive (*Olea europaea*) in Mediterranean Europe has renewed interest in the xylem microbiome as both a disease vulnerability target and a potential source of biocontrol agents capable of competing with vascular pathogens for colonization niches (Román-Écija et al., 2026).

2.3.2. Endophytic contributions to crop quality

Beyond their well-established roles in plant growth promotion and disease suppression, endophytic microorganisms exert direct and significant effects on the organoleptic and nutritional quality of horticultural produce. Endophytic fungi of the genera Trichoderma, Beauveria, and Colletotrichum (in non-pathogenic strains) have been shown to enhance the accumulation of secondary metabolites, including polyphenols, carotenoids, and volatile aroma compounds, in tomato, strawberry, and grape (Colla et al., 2015). These quality enhancements occur through mechanisms including elicitation of the phenylpropanoid pathway, modulation of ethylene signaling, and altered sugar-to-acid ratios, all of which are key determinants of consumer quality perception.

2.4. Anthosphere and spermosphere: emerging frontiers

2.4.1. The floral microbiome

The anthosphere, the microbial community associated with floral tissues including petals, sepals, stamens, pistils, and nectar, represents one of the least studied phytobiome compartments despite its direct relevance to two processes of fundamental horticultural importance: pollination and fruit set. Floral microbiomes are taxonomically distinct from other plant compartments, with nectar-specialized bacteria (including Acinetobacter, Gluconobacter, and Rosenbergiella) and yeasts (Metschnikowia and Starmerella) forming predictable core communities across diverse floral systems (Vannette et al., 2013).

Nectar microorganisms modify nectar chemistry in ways that demonstrably influence pollinator behavior and visitation rates. Microbially fermented nectar has been shown to attract bumblebees more strongly than sterile nectar, suggesting that floral microbiome management could serve as a tool for improving pollination efficiency in enclosed cultivation systems such as polytunnels and greenhouses, where pollinator access is often limited (Herrera et al., 2013). This represents a genuinely novel and underexplored intervention point for horticultural microbiome management.

2.4.2. Seed and spermosphere microbiome

The spermosphere, the zone of soil immediately surrounding a germinating seed, analogous to the rhizosphere for roots, and the seed endobiome together constitute the founding microbiome of the plant. Seed-associated microorganisms are transmitted vertically from mother plant to offspring through mechanisms that remain incompletely characterized but include both surface contamination and endophytic colonization of developing seed tissues (Nelson, 2018; Abdelfattah et al., 2021; Mir et al., 2025). The microorganisms present at germination exert disproportionate influence on subsequent phytobiome development: early colonizers pre-condition root surfaces and internal tissues, establish competitive hierarchies that shape later community assembly, and prime innate immunity pathways that influence responsiveness to subsequent microbial encounters throughout the plant life cycle.

The practical implications of spermosphere microbiome management are substantial. Seed priming with selected microorganisms, bacterial biocontrol agents, mycorrhizal inoculants, and plant growth-promoting rhizobacteria (PGPR) is a commercially established practice. Still, its design has historically been based on single-organism efficacy without consideration of the pre-existing seed microbiome or the downstream community consequences of inoculant application. A more sophisticated approach that accounts for the competitive dynamics between inoculants and resident seed microbiome members, and that optimizes the founding microbiome as an integrated community rather than a collection of individual beneficial strains, represents a significant opportunity for improving seed treatment outcomes.

2.5. Carposphere: the post-harvest dimension

The carposphere, the microbial community inhabiting fruit surfaces and internal tissues, constitutes the final phytobiome compartment in the crop life cycle and the one most directly connected to food safety and post-harvest quality. Fruit microbiomes are established during flower development, diversify during fruit growth through insect, wind, and splash dispersal, and continue to evolve during post-harvest storage under the influence of temperature, modified atmosphere conditions, and surface treatments (Zhang et al., 2021).

The concept of microbial terroir, the hypothesis that geographic origin imprints characteristic microbial signatures on produce, contributing to place-specific flavor and quality profiles, has gained empirical support from metagenomic studies of wine grapes, olive oil fruits, and premium vegetables (Minerdi & Sabbatini, 2025). This connection between phytogeographic microbial identity and product quality creates commercial value for carposphere microbiome management: producers of premium horticultural commodities who can demonstrate and protect characteristic microbial terroir signatures may command quality premiums analogous to those associated with geographic appellations in the wine and cheese sectors.

3. Drivers of phytobiome assembly and dysbiosis in horticultural systems

Phytobiome composition is not static but is continuously shaped by the dynamic interplay of abiotic environmental factors, host biological characteristics, management interventions, and, increasingly, climate change-driven perturbations. Understanding these drivers is essential for predicting phytobiome responses to management and for designing interventions that reliably steer microbiome composition toward desired functional states.

3.1. Abiotic drivers

Soil physicochemical properties, pH, texture, organic matter content, cation exchange capacity (CEC), and mineral element availability, exert foundational influences on rhizobiome composition that cascade upward into other plant compartments through colonization of root surfaces and endosphere. Soil pH is arguably the single most powerful predictor of bacterial community composition across agricultural soils, with shifts of one pH unit producing community changes equivalent in magnitude to those observed across entire continents under natural conditions (Lauber et al., 2009). For horticultural soil management, this means that lime applications and acidification treatments intended to optimize plant nutrient uptake simultaneously engineer the soil microbiome. This consequence should be explicitly incorporated into soil management decision-making.

Irrigation management profoundly affects phytobiome dynamics across multiple compartments. Drip irrigation versus flood irrigation creates fundamentally different soil moisture regimes that select for distinct bacterial and fungal communities: drip-irrigated systems tend to support more diverse, aerobic bacterial communities, while flood-irrigated soils favor anaerobic taxa and can promote the proliferation of water-borne pathogens, including Pythium and Phytophthora species (Van der Wal & De Boer, 2017). Temperature and humidity regimes in controlled environment agriculture (CEA) systems create stable but potentially pathogen-permissive microenvironments in the phyllosphere: the warm, humid conditions optimal for crop growth in many greenhouse systems are equally favorable for the proliferation of foliar fungal pathogens, making phyllosphere microbiome management particularly important in CEA contexts.

3.2. Host genotype and developmental stage

The plant itself is arguably the most powerful single driver of phytobiome composition. The genotype-dependent composition of root exudates, leaf surface metabolites, floral volatiles, and fruit chemistry creates crop- and cultivar-specific chemical environments that selectively recruit and sustain particular microbial communities. Quantitative genetic studies in Arabidopsis and in crop species, including maize and sorghum, have identified heritable plant traits that explain significant proportions of microbiome compositional variance, supporting the concept of plant genotype-microbiome co-evolution (Walters et al., 2018; Lundberg et al., 2012; Fitzpatrick et al., 2018).

In horticultural crops, cultivar-dependent microbiome variation has been documented in tomato (Iquebal et al., 2019), grapevine (Marasco et al., 2018), and strawberry (Mo et al., 2024), with differences in exudate chemistry, root morphology, and leaf surface wax composition identified as proximate mechanisms. These findings have practical implications for cultivar development: the microbiome-recruiting capacity of a new cultivar, its ability to enrich beneficial microbial taxa and exclude or suppress harmful ones, could in principle be incorporated as a breeding selection criterion alongside conventional agronomic trait.

Plant developmental stage imposes temporal structure on phytobiome dynamics that are often overlooked in cross-sectional studies. The rhizobiome community present during vegetative growth differs substantially from that associated with flowering, fruiting, and senescence, reflecting stage-specific changes in root exudate composition, root architecture, and plant immune activity (Chaparro et al., 2014). In horticultural crops, where phenological timing directly affects product quality and marketability, understanding and managing these developmental phytobiome transitions represents an important but underexplored opportunity.

3.3. Management-induced phytobiome disruption

Agricultural management practices have profound and often underappreciated effects on phytobiome integrity. Synthetic fungicide applications are perhaps the most consequential in horticultural contexts: while targeting fungal pathogens, broad-spectrum fungicides simultaneously suppress beneficial fungal taxa, including mycorrhizal fungi, antagonistic yeasts, and fungal endophytes, reducing the bioprotective capacity of the phytobiome and creating ecological release for pathogen resurgence (Karlsson et al., 2014).

Soil fumigation with broad-spectrum biocides, historically the foundation of soil-borne disease management in high-value horticultural crops, including strawberry and vegetables, causes near-total sterilization of the soil microbiome followed by uncontrolled recolonization that can result in microbiome states qualitatively different from and often less suppressive than the pre-fumigation community (van Bruggen & Semenov, 2000). The global phase-out of methyl bromide, the most widely used fumigant, has accelerated interest in biological alternatives. Still, these alternatives require functional native microbiomes to provide the disease suppression that fumigation-dependent systems depend upon, creating a management paradox that only integrated phytobiome approaches can resolve.

Monoculture-driven phytobiome degradation, the progressive decline in rhizobiome diversity and suppressive function associated with continuous cultivation of the same crop, is mechanistically expressed as the accumulation of host-specific pathogens, the depletion of beneficial specialists, and the progressive simplification of microbial interaction networks (Mazzola, 2004). Replant disease syndrome in apple, cherry, and peach orchards, characterized by stunted growth and reduced yield in replanted trees, is increasingly understood as a manifestation of microbiome dysbiosis rather than simple pathogen accumulation, suggesting that microbiome restoration rather than fumigation represents the more appropriate therapeutic framework.

3.4. Climate change as phytobiome disruptor

Anthropogenic climate change is emerging as a powerful and poorly predictable driver of phytobiome disruption. Elevated atmospheric CO_2 concentrations alter root exudate chemistry by shifting plant carbon allocation toward root exudation, increasing the relative proportion of simple sugars, and decreasing that of organic acids, with downstream effects on rhizobiome community composition and functional gene expression (Drigo et al., 2010). Drought stress restructures rhizobiome communities toward osmolyte-producing and desiccation-tolerant taxa, changes that can persist as ecological legacies after moisture restoration. It may compromise the recovery of drought-sensitive beneficial microorganisms.

Temperature increases associated with climate change are predicted to shift phyllosphere microbial community composition toward heat-tolerant taxa, potentially displacing thermosensitive biocontrol agents and altering disease pressure dynamics in ways that are difficult to predict from current understanding (Bebber et al., 2013). Phenological mismatch, the climate-driven desynchronization of crop developmental timing and the phenology of microbiome-dependent ecological services such as pollination, represents a further dimension of climate-phytobiome interaction that deserves dedicated research attention in horticultural systems.

4. Functional microbiome modules and horticultural crop performance

The functional outputs of the phytobiome, plant growth promotion, disease suppression, stress tolerance, and quality enhancement, emerge from the collective activities of organized assemblages of microorganisms operating as functional modules: groups of taxa that perform complementary functions within an integrated biological system. Identifying, characterizing, and manipulating these functional modules is the operational core of phytobiome-based horticultural management.

4.1. Plant growth promotion (PGP) modules

Plant growth-promoting microorganisms (PGPMs) enhance crop productivity through mechanisms including biological nitrogen fixation, phosphate solubilization, potassium mobilization, siderophore-mediated iron acquisition, and phytohormone modulation. These mechanisms are distributed across taxonomically diverse bacterial and fungal taxa, suggesting that PGP function emerges as a network property of the phytobiome rather than residing exclusively in individual species (Compant et al., 2005).

Phytohormone modulation by PGP bacteria is particularly well-documented in horticultural systems. Indole-3-acetic acid (IAA) produced by rhizosphere bacteria, including *Azospirillum brasilense* and *Pseudomonas putida*, promotes root elongation and lateral root development, enhancing nutrient and water uptake capacity. 1-aminocyclopropane-1-carboxylate (ACC) deaminase, an enzyme produced by diverse PGPR, including Burkholderia, Enterobacter, and Variovorax, degrades the ethylene precursor ACC, thereby reducing stress-induced ethylene production and maintaining root growth under conditions of drought, flooding, and heavy metal stress (Glick, 2014).

Meta-analyses of PGPR inoculation trials in horticultural crops reveal mean yield increases of 10-20% across diverse crop-microorganism combinations, with considerably higher effects under nutrient-limited and water-stressed conditions (Arif et al., 2020; Backer et al., 2018). These effect sizes are agronomically significant but variable, with inoculant performance depending critically on compatibility with the resident phytobiome, environmental conditions, and the formulation technology used for delivery, factors that a WPPO framework explicitly addresses.

4.2. Bioprotective microbiome modules

The capacity of well-structured plant microbiomes to suppress diseases, soil suppressiveness, represents one of the most economically valuable and ecologically complex properties of the phytobiome. Disease-suppressive soils, characterized by reduced incidence and severity of soil-borne diseases despite the presence of pathogens and susceptible hosts, have been documented for Fusarium wilts, Rhizoctonia damping-off, Pythium root rot, and Sclerotinia stem rot in diverse horticultural cropping systems (Weller et al., 2002; Mendes et al., 2013; Raaijmakers & Mazzola, 2016).

The mechanisms underlying soil suppressiveness include antibiosis (the production of antifungal and antibacterial compounds by resident microorganisms), competition for limiting resources (iron via siderophores, carbon, and microsites), and the induction of systemic plant immunity. Induced Systemic Resistance (ISR), triggered by non-pathogenic rhizosphere bacteria and fungi, is mechanistically distinct from pathogen-triggered Systemic Acquired Resistance (SAR) but equally effective in providing broad-spectrum disease protection (Pieterse et al., 2014). ISR has been documented against bacterial, fungal, and viral diseases in horticultural crops, including tomato, cucumber, lettuce, and grapevine, and represents a tractable target for phytobiome engineering.

4.3. Quality enhancement microbiome modules

Perhaps the most commercially compelling functional module of the horticultural phytobiome is its capacity to enhance organoleptic and nutritional quality. The microbiome influences produce quality through multiple mechanisms operating at different compartment levels and different points in the crop life cycle.

In the rhizosphere and endosphere, PGPR and mycorrhizal fungi enhance fruit sugar and organic acid accumulation by improving phosphorus and potassium nutrition, both of which are critical determinants of fruit sweetness and acidity balance in tomato, strawberry, and stone fruits. Endophytic fungi, including non-pathogenic Colletotrichum and Trichoderma strains, have been shown to elicit the phenylpropanoid pathway, increasing the accumulation of anthocyanins, flavonols, and hydroxycinnamic acids that contribute to the color, flavor, and nutritional value of fruits and vegetables (Colla et al., 2015). Volatile aroma compound profiles, critical quality determinants in premium fruits and ornamentals, are modified by both rhizobiome and endobiome members through effects on terpenoid biosynthesis pathways and ethylene signal transduction.

4.4. Stress resilience modules

The capacity of plant-associated microorganisms to buffer crops against abiotic stress represents an increasingly critical functional module as climate extremes intensify (Liu et al., 2020; Bakker et al., 2020). Osmolyte-producing rhizobacteria, including strains of Bacillus, Pseudomonas, and Azospirillum that accumulate proline, glycine betaine, and trehalose in response to water deficit, enhance plant osmotic adjustment capacity, improving water use efficiency and yield stability under drought stress (Yang et al., 2009).

Heat stress tolerance induction by phyllosphere and rhizosphere microorganisms has been demonstrated in multiple horticultural crops. Volatile organic compounds (VOCs) produced by rhizobacteria, including 2,3-butanediol and acetoin, have been shown to induce thermotolerance in Arabidopsis and in tomato seedlings, with protective effects that persist through subsequent stress exposure events, suggesting an epigenetic mechanism of microbiome-mediated stress memory (Ryu et al., 2004). This priming of stress tolerance by microbiome-derived signals represents a potentially transformative strategy for adapting horticultural production to the intensifying heat stress conditions projected under climate change scenarios.

5. Technologies for phytobiome characterization and engineering

The translation of phytobiome science from discovery to practical application depends critically on the availability of technological platforms capable of characterizing complex microbial communities with sufficient resolution, identifying functional modules, and delivering targeted microbiome interventions with precision. Recent years have seen transformative advances across all three capability domains.

5.1. Next-generation sequencing approaches

Amplicon sequencing targeting the 16S rRNA gene (for bacteria and archaea) and the internal transcribed spacer (ITS) region (for fungi) has become the standard tool for phytobiome community profiling. When applied with appropriate experimental design, including matched bulk soil controls, multiple time-point sampling, and cultivation-system replication, amplicon sequencing provides robust information on community diversity, composition, and the relative abundances of key taxa across plant compartments (Caporaso et al., 2012). However, amplicon sequencing has important limitations: it cannot directly measure functional gene content, is subject to primer bias that can systematically underrepresent certain microbial groups and provides taxonomic identification at resolutions that are often insufficient for species-level ecological interpretation.

Shotgun metagenomics overcomes the functional gene limitation of amplicon sequencing by sequencing total community DNA, providing simultaneous information on taxonomic composition and functional gene content. Applied to horticultural phytobiome research, metagenomics has enabled the identification of functional gene clusters associated with biocontrol activity, stress tolerance, and plant growth promotion in rhizosphere and endosphere communities, creating the functional microbiome maps needed to guide targeted engineering interventions (Mendes et al., 2018). Long-read sequencing technologies from Pacific Biosciences (PacBio) and Oxford Nanopore Technologies are further advancing phytobiome characterization by enabling the assembly of complete microbial genomes from complex community samples, resolving the genomic context of functional genes, and enabling strain-level resolution of ecologically important taxa.

5.2. Multi-omics integration for phytobiome function decoding

The most comprehensive insights into phytobiome function emerge from the integration of multiple omics datasets. Metabolomics-metagenomics co-analysis, pairing root exudate or plant tissue metabolite profiles with rhizobiome or endobiome community data, enables the identification of specific plant metabolites that recruit or suppress particular microbial taxa, information essential for rational exudate-mediated microbiome engineering through crop breeding (Zhalnina et al., 2018).

Microbiome network analysis, the construction of co-occurrence networks from community abundance data, and the identification of hub taxa that serve as network connectivity nodes, provide a particularly powerful tool for identifying priority management targets. Hub taxa, which maintains disproportionate numbers of ecological interactions within the microbiome network, often perform keystone functions whose disruption cascades through the entire community (Banerjee et al., 2018; Agler et al., 2016). Identifying and protecting hub taxa or deliberately introducing them as part of microbiome restoration strategies represents a leverage-maximizing approach to phytobiome management that could not be identified through single-species focused approaches.

5.3. Synthetic microbial communities (syncoms)

Synthetic microbial communities, defined as assemblages of multiple characterized microbial strains designed to recapitulate or augment specific phytobiome functions, represent the cutting edge of microbiome engineering technology (Toju et al., 2018; Vorholt et al., 2017). Unlike conventional single-strain inoculants, SynComs are designed from first principles to provide complementary functional coverage, ecological stability through niche complementarity, and robustness against displacement by the resident microbiome through competitive network design (Vorholt et al., 2017).

In horticultural applications, SynCom development is most advanced for soil-borne disease suppression and nutrient acquisition. Studies in tomato and lettuce have demonstrated that SynComs of 4-8 bacterial strains selected for complementary biocontrol mechanisms (antibiosis, competition, and ISR induction) provide superior disease suppression against Fusarium oxysporum and Pythium ultimum compared to any individual component strain, confirming the expected community-level functional enhancement (Hu et al., 2016). [See ***Table 2*** for a comparative overview of SynCom applications across horticultural crops.] The challenge of designing SynComs for foliar application, where phyllosphere-adapted strains with UV tolerance, desiccation resistance, and appropriate surface colonization characteristics are required, is receiving increasing research attention but remains less developed than rhizosphere-targeted SynCom applications.

5.4. Digital agriculture and AI integration

The integration of phytobiome science with digital agriculture technologies creates opportunities for real-time, data-driven microbiome management that were not previously conceivable. IoT-based sensor networks capable of monitoring soil moisture, temperature, electrical conductivity, and gas exchange can serve as proxy indicators of phytobiome activity, monitoring respiration, nutrient cycling, and hydrolytic enzyme activity in the root zone and potentially triggering automated microbiome management interventions when sensor data indicate suboptimal conditions (Yue et al., 2022).

Machine learning approaches, including random forest models and deep learning architectures trained on large phytobiome datasets, are demonstrating increasing capability for predicting crop performance outcomes from microbiome compositional data, in some cases outperforming predictions based on soil chemistry and climate variables alone (Hassani et al., 2018). As training datasets grow in size and geographic diversity, these predictive models will enable the prescription of site-specific microbiome management recommendations analogous to the variable rate prescription maps used in conventional precision agriculture.

6. The Whole-Plant Phytobiome Optimization (WPPO) framework

The synthesis of compartment-specific phytobiome knowledge, functional module characterization, and emerging engineering technologies presented in the preceding sections provides the foundation for a new integrative management paradigm. We propose the Whole-Plant Phytobiome Optimization (WPPO) framework as the conceptual architecture for translating this knowledge into practical horticultural management. WPPO is designed as a three-tier model that can be applied across the full diversity of horticultural crops and production systems, from small-scale organic market gardens to large-scale commercial CEA operations (***Figure 2***).

6.1. Rationale: beyond the compartment silo

The fundamental premise of WPPO is that optimal phytobiome management cannot be achieved through compartment-specific interventions designed and implemented in isolation. Plant compartments are not independent microbiome habitats: they are interconnected nodes in an integrated microbial network through which community members move, interact, and collectively determine the emergent functional outputs that plant health and productivity depend upon. Root endophytes colonize stems and leaves; phyllosphere microorganisms are washed to root zones by irrigation and rain; seed-derived founding populations influence rhizobiome assembly for weeks after germination; and floral microbiomes affect the carposphere community that ultimately governs post-harvest quality.

This interconnectedness means that management interventions targeted at one compartment will inevitably have positive or negative effects on others. A fungicide application designed to protect the phyllosphere from Botrytis cinerea will simultaneously reduce the diversity of the endospheric fungal community, potentially compromising the quality-enhancing endophytic modules described in Section 4.3. A rhizosphere SynCom application of nitrogen-fixing bacteria may alter root exudate chemistry in ways that shift the founding community of the endosphere. WPPO makes these cross-compartment interactions explicit and designs management strategies that optimize the whole-plant microbiome as an integrated system.

6.2. Whole-plant phytobiome profiling

The first tier of WPPO establishes a comprehensive microbiome baseline for the target crop in its production environment. This involves simultaneous multi-compartment sampling of the rhizosphere, root endosphere, stem endosphere, leaf phyllosphere, leaf endosphere, and (at appropriate developmental stages) flowers and fruit, combined with multi-omics characterization using amplicon sequencing for community composition, metagenomics for functional gene content, and metabolomics for host-microbiome metabolic interface characterization.

The output of Tier 1 profiling is a phytobiome map: a quantitative characterization of the microbial community inhabiting each compartment, including taxonomic composition, functional gene content, predicted metabolic activities, network structure, and identification of hub taxa. This baseline map serves as the reference against which management-induced phytobiome changes can be evaluated and toward which restoration interventions can be targeted when dysbiosis is detected. For high-value perennial crops, including grapevine, apple, and citrus, phytobiome profiling at multiple time points across the growing season provides additional temporal resolution that captures developmental phytobiome dynamics and identifies stage-specific intervention windows.

6.3. Functional module identification and targeting

The second tier of WPPO translates the phytobiome map generated in Tier 1 into a functional diagnosis: an assessment of which functional modules are present, abundant, and active, which are depleted or functionally compromised relative to a reference suppressive or high-performance microbiome, and which key taxa or functional genes represent priority targets for management intervention.

This functional diagnosis is guided by a library of characterized functional modules, compilations of the taxa, functional genes, and community network structures associated with specific agronomic outcomes assembled from the primary research literature and updated as new findings emerge. For example, a functional module associated with Fusarium wilt suppression in tomato might include specific Pseudomonas and Bacillus strains producing 2,4-diacetylphloroglucinol (DAPG), network hub taxa providing ecological stability to the suppressive community, and mycorrhizal partners enhancing the systemic resistance baseline of the host. A Tier 2 diagnosis comparing the target crop's phytobiome against this module template can identify which components are present, which are absent, and which are present but functionally inactive, distinctions that determine whether the appropriate intervention is microbiome supplementation, stimulation, or ecological restructuring.

6.4. Precision compartment-targeted intervention

The third tier of WPPO translates functional diagnoses into targeted management interventions. The key principle of Tier 3 is compartment specificity: different interventions are designed to reach and modify the microbiome of specific plant compartments, rather than broadcasting microbiome-affecting inputs non-specifically across the entire plant-soil system. This compartment targeting both increases intervention efficiency and reduces the risk of off-target effects on compartment microbiomes not requiring modification.

Seed treatment interventions coating seeds with SynComs, encapsulated individual strains, or microbiome-stimulating biological matrices target the spermosphere and early colonizing root endosphere and rhizobiome. Root zone drenching with SynCom formulations targets the rhizobiome and root endosphere. Trunk or stem injection in perennial fruit crops targets the vascular endosphere. Foliar spray applications with phyllosphere-adapted microbial formulations target the phyllosphere and leaf endosphere. Floral spray applications at specific developmental stages target the anthosphere. Post-harvest treatment with carposphere biocontrol agents targets carposphere composition and post-harvest disease suppression.

The selection and timing of Tier 3 interventions is guided by sensor network data and machine learning prediction models integrated into a digital decision-support platform, the WPPO management system. This system continuously integrates environmental sensor data (temperature, humidity, soil moisture, nutrient levels), satellite or drone-based crop health indices, and periodic phytobiome monitoring data (using rapid field-deployable qPCR or targeted amplicon sequencing for key indicator taxa) to generate dynamic recommendations for phytobiome management interventions throughout the crop cycle.

6.5. WPPO integration with precision horticulture

The full realization of WPPO as a practical management system requires integration with the broader precision horticulture technology ecosystem. Variable rate application (VRA) systems capable of delivering liquid biological formulations at spatially variable rates within a field or greenhouse, driven by microbiome prediction maps generated from high-resolution sampling data, are technically feasible with current agricultural machinery and are beginning to be demonstrated in research settings. The development of rapid, low-cost field-deployable microbiome monitoring technologies, including lateral flow assays for indicator microbial taxa and portable qPCR devices, is enabling the near-real-time phytobiome monitoring that Tier 3 intervention optimization requires.

Table 2. Representative studies of synthetic microbial communities (SynComs) and multi-strain bioinoculants in horticultural crops, showing target compartments, consortium composition, and key agronomic outcomes.

Crop	Target Compartment	SynCom / Bioinoculant Composition	Key Outcome	Reference
Tomato	Rhizosphere / Root endosphere	4-strain Pseudomonas + Bacillus SynCom (DAPG-producing)	Fusarium wilt suppression >60%; ISR activation	Hu et al. (2016)
Lettuce	Rhizosphere	6-strain consortium incl. *Pseudomonas fluorescens* + *Serratia plymuthica*	Pythium damping-off reduced by 72%; improved seedling vigour	Hu et al. (2016)
Strawberry	Root endosphere + phyllosphere	*Trichoderma harzianum* + *Bacillus subtilis* + AMF (Rhizophagus)	Botrytis incidence reduced; fruit anthocyanin content +18%	Colla et al. (2015)
Grapevine	Phyllosphere	*Aureobasidium pullulans* (commercial: Botector)	Botrytis cinerea control comparable to conventional fungicide under moderate pressure	Galli et al. (2021)
Apple / Pear	Carposphere (post-harvest)	*Candida oleophila* + *Bacillus subtilis* biopreservation blend	Blue mould and grey mould suppressed; 3-week shelf-life extension	Spadaro & Droby (2016)
Cucumber	Rhizosphere	*Pseudomonas putida* + *Azospirillum brasilense* + *Trichoderma asperellum*	Yield +22%; Fusarium crown rot significantly reduced	Backer et al. (2018)

DAPG = 2,4-diacetylphloroglucinol; AMF = arbuscular mycorrhizal fungi; ISR = induced systemic resistance.

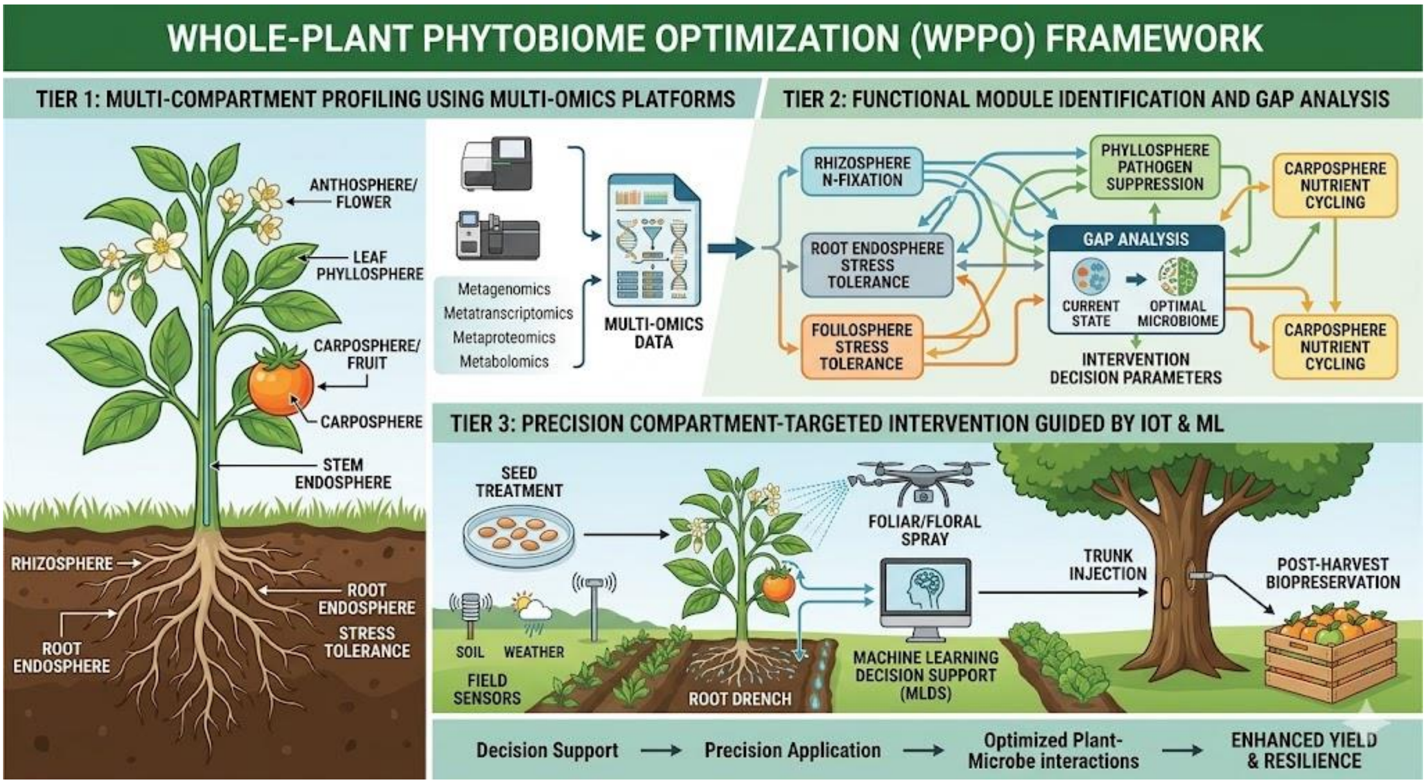

Figure 2. The Whole-Plant Phytobiome Optimization (WPPO) framework. The three-tier model integrates whole-plant microbiome profiling, functional module diagnosis, and precision compartment-targeted intervention, applied across the full horticultural crop life cycle from seed to post-harvest (this figure is created by author himself by using different means of media available).

7. Phytobiome management in specific horticultural systems

7.1. Protected cultivation and controlled environment agriculture

Controlled environment agriculture encompassing heated greenhouses, polytunnels, hydroponic systems, and enclosed vertical farms creates uniquely managed phytobiome environments distinguished from field production by the relative exclusion of external microbial inputs, the persistence of microbiome populations across production cycles in re-used growing media or recirculated nutrient solutions, and the precise controllability of temperature, humidity, and light regimes that govern microbial growth conditions.

Hydroponic and aeroponic systems, in which roots grow directly in nutrient solutions without soil substrate, create rhizobiome conditions radically different from soil-based production. The rhizobiome of hydroponic tomato and lettuce is dominated by Proteobacteria and Bacteroidetes adapted to aquatic nutrient-rich environments, with substantially lower diversity than soil-based rhizobiomes (Lee & Lee, 2015). This reduced diversity creates both vulnerability, the absence of diverse suppressive microbiomes makes hydroponic systems particularly susceptible to root rot pathogens, including Pythium and Fusarium, and opportunity: the simplified community structure of hydroponic root zones may be more tractable for SynCom engineering than the complex communities of agricultural soils.

7.2. Organic horticultural systems

Organic horticultural production systems, by definition excluding synthetic pesticide and fertilizer inputs, are more dependent on phytobiome-mediated ecosystem services for crop nutrition and disease suppression than conventional counterparts. Comparative microbiome studies consistently demonstrate higher rhizobiome diversity, greater functional gene richness, and stronger disease-suppressive potential in organically managed soils compared to conventional equivalents, supporting the biological plausibility of organic management claims (Lupatini et al., 2017).

Compost application, the foundational soil amendment practice of organic horticulture, enriches the rhizobiome with diverse saprophytic fungi and bacteria that decompose organic matter, cycle nutrients, and in many cases provide direct biocontrol activity against soil-borne pathogens. Compost from diverse organic feedstocks consistently produces more disease-suppressive soil amendments than single-feedstock composts, suggesting that microbiome diversity is itself a functional outcome to be optimized in compost production (Bonanomi et al., 2010).

7.3. Orchard ecosystem phytobiome management

Perennial fruit tree orchards present a phytobiome management context fundamentally different from annual crop systems. The multi-year to multi-decade production lifespan of orchard trees means that phytobiome interventions at establishment can exert lasting effects on microbiome composition and function throughout the productive life of the orchard. Conversely, phytobiome dysbiosis, as expressed in replant disease syndrome, can persist for years after the initial disturbance, resisting recovery through conventional management.

Cover crop management in orchard alleys has emerged as one of the most effective and ecologically sound tools for orchard phytobiome management. Diverse cover crop mixtures, including legumes, grasses, and forbs, enhance rhizobiome diversity through the complementary root exudate contributions of different plant species, promote AMF hyphal network development, and create aboveground habitat complexity that reduces foliar pathogen pressure through microclimate modification and antagonist habitat provision (Montanaro et al., 2010).

7.4. Post-harvest phytobiome management

The carposphere microbiome established during crop growth continues to evolve during post-harvest handling, storage, and distribution, with composition and succession dynamics that determine the rate and nature of quality deterioration and pathogen-driven decay. The application of biocontrol yeast and bacterial formulations to fruit surfaces at harvest biopreservation constitutes the most commercially developed application of phytobiome management in post-harvest horticulture, with products based on *Candida oleophila*, *Cryptococcus albidus*, and *Bacillus subtilis* registered in multiple countries for post-harvest disease control in apple, pear, citrus, and stone fruits (Spadaro & Droby, 2016).

8. Challenges, limitations, and key research gaps

8.1. Methodological challenges

The technical challenges of phytobiome research are substantial and have not yet been fully resolved. Sampling standardization across plant compartments remains a significant obstacle to inter-study comparability: different research groups use different protocols for rhizosphere soil collection, endosphere surface sterilization, phyllosphere washing, and tissue homogenization, generating data that cannot be straightforwardly compared or meta-analyzed. The low microbial biomass of certain compartments, particularly the spermosphere, nectar, and internal fruit tissues, creates DNA extraction and amplification challenges that can introduce contamination and bias, potentially distorting community profiles toward laboratory reagent contaminants rather than genuine plant-associated taxa.

The translation of microbial community profiling data into functional predictions remains technically unreliable. Tools for functional gene prediction from 16S rRNA amplicon data (such as PICRUSt2) make assumptions about genomic content that are violated by the ecologically novel and taxonomically uncharacterized taxa that frequently dominate phytobiome communities in underexplored compartments. Direct functional assessment through metatranscriptomics and metaproteomics provides more reliable functional data. Still, it requires substantially greater analytical investment and is subject to its own technical challenges, including RNA stability and protein extraction efficiency.

Table 3. Key knowledge gaps.

Compartment / Topic	Specific Research Gap and Priority
Anthosphere	No controlled field studies have demonstrated that targeted manipulation of the floral microbiome improves fruit set or quality in commercial horticultural crops. Mechanistic links between nectar microbiome composition and pollinator behavior require quantification.
Spermosphere	Vertical microbiome transmission efficiency from mother plant to offspring seed and its consequences for seedling phytobiome development have not been characterized in commercial horticultural cultivars. The competitive dynamics between seed-transmitted and inoculant strains are poorly understood.
Carposphere	The quantitative relationships between pre-harvest phytobiome management interventions and specific post-harvest pathogen suppression outcomes lack robust experimental support across diverse storage conditions and commodity types.
CEA Phytobiome	Phytobiome dynamics in fully enclosed vertical farm systems with artificial lighting are essentially uncharacterized. The potential for microbiome succession and pathogen community accumulation in recirculating hydroponic systems over multiple production cycles requires urgent investigation.
SynComs in Orchards	Multi-year field trials of synthetic microbial consortia in perennial fruit tree production systems are almost absent from the published literature. Long-term SynCom persistence and community evolution require characterization.
Archaeal Phytobiome	The functional roles of archaea in plant-associated habitats beyond methane metabolism in flooded systems remain virtually unexplored. Archaeal contributions to nitrogen cycling, stress responses, and plant immunity warrant systematic investigation.
Phytobiome x Breeding	Marker-assisted selection and genomic selection approaches for improving the microbiome-recruiting capacity of horticultural cultivars have not been developed or validated. The heritability of microbiome-relevant host traits require quantification in horticultural crops.
Climate Change	Empirical studies characterizing phytobiome responses to combined climate change stressors (elevated CO_2 + drought + heat) are lacking for all horticultural crops. Interactive effects are likely to be non-additive but cannot currently be predicted.

8.2. Translational challenges

The translation of laboratory and greenhouse phytobiome research findings into reliable field-applicable management practices faces a recurring challenge: the ecological context dependency of microbiome function. Microbial inoculants, SynComs, and phytobiome management practices that demonstrate impressive efficacy in controlled experiments frequently fail to reproduce their effects when applied in field conditions characterized by greater environmental variability, higher background microbiome diversity, and the complex interaction networks of real agricultural ecosystems.

Shelf life and formulation stability of microbiome-based products present additional translational barriers. Many of the most functionally effective phytobiome members, including obligate anaerobes, slow-growing oligotrophs, and obligately symbiotic mycorrhizal fungi, are difficult or impossible to formulate into stable commercial products using conventional fermentation and encapsulation technologies. The development of advanced encapsulation systems, including alginate beads, biochar carriers, and hydrogel matrices, is expanding the repertoire of formulatable strains. Still, significant gaps remain between the most functionally desirable phytobiome members and the subset that can currently be delivered reliably ***(Table 3).***

9. Future perspectives and innovation roadmap

9.1. Phytobiome-assisted plant breeding

The integration of phytobiome science with horticultural plant breeding represents a transformative convergence with the potential to create crops simultaneously optimized for agronomic performance and microbiome management capacity. The concept of breeding for microbiome-recruiting traits, selecting cultivars that more effectively recruit beneficial taxa and suppress pathogenic ones through root exudate profiles, surface chemistry, and immune signaling characteristics, is supported by evidence that substantial genetic variation in microbiome-relevant host traits exists within major horticultural crop species (Walters et al., 2018).

Genomic selection approaches that incorporate microbiome composition data as a heritable phenotype, effectively treating the core microbiome as a quantitative trait to be selected for alongside yield, quality, and disease resistance, could systematically improve the phytobiome management capacity of elite horticultural cultivars over breeding cycles. This approach is facilitated by the declining cost of microbiome profiling, which is making the phenotyping of large breeding populations for microbiome composition increasingly feasible.

9.2. Microbiome-based precision nutrition

The development of microbiome-informed fertilization recommendations prescribing nutrient inputs based on the functional status of the soil and plant microbiome, rather than solely on soil chemical analysis, represents an important evolution in precision horticultural nutrition management. Phosphorus-solubilizing microorganisms in the rhizobiome, for example, can mobilize substantial quantities of plant-unavailable soil phosphorus; the abundance and activity of these functional guild members should inform the degree to which supplemental phosphorus fertilization is necessary, potentially enabling significant reductions in phosphorus inputs without compromising crop nutrition.

9.3. Phytobiome commerce and market development

The commercial market for microbiome-based agricultural products is expanding rapidly, with the global biostimulant market projected to reach USD 5.6 billion by 2025, driven largely by microbial product categories (MarketsandMarkets, 2021). Horticultural applications represent a disproportionate share of this market, reflecting the high value of horticultural crops, the intensity of their management, and the particular vulnerability of horticultural production to the disease and quality challenges that microbiome-based products address.

Phytobiome diagnostics-as-a-service, the commercial provision of microbiome profiling and functional diagnosis services to horticultural producers, is an emerging business model with the potential to mainstream Tier 1 and Tier 2 WPPO capabilities without requiring individual producers to develop in-house expertise. Agri-biotech startups offering microbiome testing and interpretation services for high-value horticultural crops, including wine grapes, premium vegetables, and specialty herbs, are already commercializing in North America, Europe, and Australia, with service offerings that are rapidly becoming more accessible and interpretable as data infrastructure matures.

9.4. Cross-disciplinary horizons

The most transformative future developments in phytobiome science for horticulture may emerge from disciplines that are currently only tangentially connected to plant microbiome research. Synthetic biology approaches enabling the design of chassis microorganisms, standardized microbial platforms engineered to express specific combinations of plant-beneficial functions, could radically expand the functional space accessible to phytobiome engineering beyond what is achievable through the selection and combination of naturally occurring strains. The ability to precisely engineer the functional gene content of phytobiome members while retaining their natural ecological competence would fundamentally alter the design possibilities for SynCom and microbial biostimulant development.

The gut-phytobiome axis, the emerging recognition that the microbiome composition of consumed horticultural produce influences the human gut microbiome through the introduction of viable microorganisms and microbiome-modulating plant metabolites, creates a direct link between phytobiome management decisions and human health outcomes that is only beginning to be explored (Blaser, 2017). As evidence accumulates that microbiome quality affects consumer gut microbiome health, the definition of produce quality will expand to include microbiome dimensions, creating new market incentives for phytobiome-conscious horticultural management practices.

Conclusions

The plant microbiome constitutes a biological resource of immense and largely unrealized potential for horticultural production. As this review has demonstrated, the phytobiome extends far beyond the rhizosphere to encompass taxonomically and functionally distinct microbial communities in the phyllosphere, endosphere, anthosphere, spermosphere, and carposphere, each performing specific agronomic functions and each representing a distinct target for management intervention. The characterization of these compartments, the drivers governing their assembly, and the functional modules they support collectively define the scientific foundation for a new paradigm in horticultural crop management.

The Whole-Plant Phytobiome Optimization (WPPO) framework proposed in this review provides the first integrative conceptual architecture for translating this scientific foundation into practical management systems. By organizing phytobiome management across three tiers: profiling, functional module identification, and precision compartment-targeted intervention, and explicitly addressing the temporal dimension of phytobiome dynamics across the crop life cycle, WPPO enables the systematic application of microbiome science to the full diversity of horticultural production contexts.

The path from the WPPO framework to widespread practical implementation requires resolution of significant scientific and technological challenges, the most important of which include the development of standardized multi-compartment sampling protocols, improved tools for translating microbiome compositional data into functional predictions, reliable encapsulation technologies for ecologically effective but currently unformalizable microbial taxa, and multi-year field validation of SynCom and whole-plant microbiome management strategies across diverse horticultural crop systems. The research gaps identified in Section 8 define a prioritized agenda for the scientific work needed to bridge these gaps.

The strategic importance of this work cannot be overstated. As regulatory pressure on synthetic agrochemicals intensifies, as climate change undermines the stability of production systems designed for historical climate envelopes, and as consumers increasingly demand produce grown without chemical interventions, the capacity of horticulture to maintain productivity, quality, and profitability will depend to an ever-greater degree on the sophistication with which biological systems and above all, the plant microbiome are understood and managed. The WPPO framework, and the science of whole-plant phytobiome optimization more broadly represent the essential scientific infrastructure for this transition. The field is ready; the tools are emerging; and the necessity is urgent.

References

Abdelfattah, A., Wisniewski, M., Schena, L., Tack, A.J.M. (2021): Experimental evidence of microbial inheritance in plants and transmission routes from seed to phyllosphere and root. Environmental Microbiology. 23(4): 2199-2214. https://doi.org/10.1111/1462-2920.15392

Agler, M.T., Ruhe, J., Kroll, S., Morhenn, C., Kim, S.T., Weigel, D., Kemen, E.M. (2016): Microbial hub taxa link host and abiotic factors to plant microbiome variation. PLOS Biology. 14(1): e1002352. https://doi.org/10.1371/journal.pbio.1002352

Arif, I., Batool, M., Schenk, P.M. (2020): Plant microbiome engineering: expected benefits for improved crop growth and resilience. Trends in Biotechnology. 38(12): 1385-1396. https://doi.org/10.1016/j.tibtech.2020.04.015

Backer, R., Rokem, J.S., Ilangumaran, G., Lamont, J., Praslickova, D., Ricci, E., Subramanian, S., Smith, D.L. (2018): Plant growth-promoting rhizobacteria: context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. Frontiers in Plant Science. 9: 1473. https://doi.org/10.3389/fpls.2018.01473

Bais, H.P., Weir, T.L., Perry, L.G., Gilroy, S., Vivanco, J.M. (2006): The role of root exudates in rhizosphere interactions with plants and other organisms. Annual Review of Plant Biology. 57: 233-266. https://doi.org/10.1146/annurev.arplant.57.032905.105159

Bakker, P.A., Berendsen, R.L., Van Pelt, J.A., Vismans, G., Yu, K., Li, E., Bentum, S.V., Poppeliers, S.W.M., Gil, J.J.S., Zhang, H., Goossens, P., Stringlis, I.A., Song, Y., de-Jonge, R., Pieterse, C.M.J. (2020): The soil-borne identity and microbiome-assisted agriculture: looking back to the future. Molecular Plant. 13(10): 1394-1401. https://doi.org/10.1016/j.molp.2020.09.017

Banerjee, S., Schlaeppi, K., van der Heijden, M.G.A. (2018): Keystone taxa as drivers of microbiome structure and functioning. Nature Reviews Microbiology. 16(9): 567-576. https://doi.org/10.1038/s41579-018-0024-1

Barto, E.K., Hilker, M., Muller, F., Mohney, B.K., Weidenhamer, J.D., Rillig, M.C. (2011): The fungal fast lane: common mycorrhizal networks extend bioactive zones of allelochemicals in soil. PLoS ONE. 6(11): e27195. https://doi.org/10.1371/journal.pone.0027195

Bebber, D.P., Ramotowski, M.A.T., Gurr, S.J. (2013): Crop pests and pathogens move polewards in a warming world. Nature Climate Change. 3(11): 985-988. https://doi.org/10.1038/nclimate1990

Berendsen, R.L., Pieterse, C.M.J., Bakker, P.A.H.M. (2012): The rhizosphere microbiome and plant health. Trends in Plant Science. 17(8): 478-486. https://doi.org/10.1016/j.tplants.2012.04.001

Berg, G., Smalla, K. (2009): Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. FEMS Microbiology Ecology. 68(1): 1-13. https://doi.org/10.1111/j.1574-6941.2009.00654.x

Berg, G., Rybakova, D., Fischer, D., Cernava, T., Verges, M.C.C., Charles, T., … Schloter, M. (2020): Microbiome definition re-visited: old concepts and new challenges. Microbiome. 8(1): 1-22. https://doi.org/10.1186/s40168-020-00875-0

Bisbis, M.B., Gruda, N., Blanke, M. (2018): Potential impacts of climate change on vegetable production and product quality – a review. Journal of Cleaner Production. 170: 1602-1620. https://doi.org/10.1016/j.jclepro.2017.09.224

Blaser, M.J. (2017): The theory of disappearing microbiota and the epidemics of chronic disease. Nature Reviews Immunology. 17(8): 461-463. https://doi.org/10.1038/nri.2017.77

Bonanomi, G., Antignani, V., Capodilupo, M., Scala, F. (2010): Identifying the characteristics of organic soil amendments that suppress soilborne plant diseases. Soil Biology and Biochemistry. 42(2): 136-144. https://doi.org/10.1016/j.soilbio.2009.10.012

Bonfante, P., Anca, I.A. (2009): Plants, mycorrhizal fungi, and bacteria: a network of interactions. Annual Review of Microbiology. 63: 363-383. https://doi.org/10.1146/annurev.micro.091208.073504

Bulgarelli, D., Schlaeppi, K., Spaepen, S., Ver Loren van Themaat, E., Schulze-Lefert, P. (2013): Structure and functions of the bacterial microbiota of plants. Annual Review of Plant Biology. 64: 807-838. https://doi.org/10.1146/annurev-arplant-050312-120106

Cadenas, A.G. (2024): Root exudates: from plant to rhizosphere and beyond. Plant Cell Reports. https://doi.org/10.1007/s00299-019-02447-5

Caporaso, J.G., Lauber, C.L., Walters, W.A., Berg-Lyons, D., Huntley, J., Fierer, N., ... Knight, R. (2012): Ultra-high-throughput microbial community analysis on the Illumina HiSeq and MiSeq platforms. ISME Journal. 6(8): 1621-1624. https://doi.org/10.1038/ismej.2012.8

Chaparro, J.M., Badri, D.V., Vivanco, J.M. (2014): Rhizosphere microbiome assemblage is affected by plant development. ISME Journal. 8(4): 790-803. https://doi.org/10.1038/ismej.2013.196

Chen, W., Modi, D., Picot, A. (2023): Soil and phytomicrobiome for plant disease suppression and management under climate change: a review. Plants. 12(14): 2736. https://doi.org/10.3390/plants12142736

Colla, G., Nardi, S., Cardarelli, M., Ertani, A., Lucini, L., Canaguier, R., Rouphael, Y. (2015): Protein hydrolysates as biostimulants in horticulture. Scientia Horticulturae. 196: 28-38. https://doi.org/10.1016/j.scienta.2015.08.037

Compant, S., Cambon, M.C., Vacher, C., Mitter, B., Samad, A., Sessitsch, A. (2021): The plant endosphere world - bacterial life within plants. Environmental Microbiology. 23(4): 1812-1829. https://doi.org/10.1111/1462-2920.15240

Compant, S., Duffy, B., Nowak, J., Clement, C., Barka, E.A. (2005): Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. Applied and Environmental Microbiology. 71(9): 4951-4959. https://doi.org/10.1128/AEM.71.9.4951-4959.2005

Compant, S., Samad, A., Faist, H., Sessitsch, A. (2019): A review on the plant microbiome: ecology, functions, and emerging trends in microbial application. Journal of Advanced Research. 19: 29-37. https://doi.org/10.1016/j.jare.2019.03.004

Drigo, B., Pijl, A.S., Duyts, H., Kielak, A.M., Gamper, H.A., Houtekamer, M.J., ... Kowalchuk, G.A. (2010): Shifting carbon flow from roots into associated microbial communities in response to elevated atmospheric CO_2. Proceedings of the National Academy of Sciences. 107(24): 10938-10942. https://doi.org/10.1073/pnas.0912421107

Durán, P., Thiergart, T., Garrido-Oter, R., Agler, M., Kemen, E., Schulze-Lefert, P., Hacquard, S. (2018): Microbial interkingdom interactions in roots promote

Arabidopsis survival. Cell. 175(4): 973-983. https://doi.org/10.1016/j.cell.2018.10.020

Edwards, J., Johnson, C., Santos-Medellin, C., Lurie, E., Podishetty, N.K., Bhatnagar, S., ... Sundaresan, V. (2015): Structure, variation, and assembly of the root-associated microbiomes of rice. Proceedings of the National Academy of Sciences. 112(8): E911-E920. https://doi.org/10.1073/pnas.1414592112

European Commission. (2020): Farm to fork strategy: for a fair, healthy, and environmentally-friendly food system. Publications Office of the European Union. EUR-Lex - 52020DC0381 - EN - EUR-Lex

Fitzpatrick, C.R., Copeland, J., Wang, P.W., Guttman, D.S., Kotanen, P.M., Johnson, M.T.J. (2018): Assembly and ecological function of the root microbiome across angiosperm plant species. Proceedings of the National Academy of Sciences. 115(6): E1157-E1165. https://doi.org/10.1073/pnas.1717617115

Galli, V., Romboli, Y., Barbato, D., Mari, E., Venturi, M., Guerrini, S., Granchi, L. (2021): Indigenous Aureobasidium pullulans strains as biocontrol agents of *Botrytis cinerea* on grape berries. Sustainability. 13(16): 9389. https://doi.org/10.3390/su13169389

Getzke, F., Thiergart, T., Hacquard, S. (2019): Contribution of bacterial-fungal balance to plant and animal health. Current Opinion in Microbiology. 49: 66-72. https://doi.org/10.1016/j.mib.2019.10.009

Glick, B.R. (2014): Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiological Research. 169(1): 30-39. https://doi.org/10.1016/j.micres.2013.09.009

Hardoim, P.R., van Overbeek, L.S., Berg, G., Pirttila, A.M., Compant, S., Campisano, A., ... Sessitsch, A. (2015): The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. Microbiology and Molecular Biology Reviews. 79(3): 293-320. https://doi.org/10.1128/mmbr.00050-14

Hassani, M.A., Duran, P., Hacquard, S. (2018): Microbial interactions within the plant holobiont. Microbiome. 6(1): 58. https://doi.org/10.1186/s40168-018-0445-0

Herrera, C.M., Pozo, M.I., Medrano, M. (2013): Yeasts in nectar of an early-blooming herb: sought by bumble bees, detrimental to plant fecundity. Ecology. 94(4): 906-914. https://doi.org/10.1890/12-0595.1

Hu, J., Wei, Z., Friman, V.P., Gu, S.H., Wang, X.F., Eisenhauer, N., ... Jousset, A. (2016): Probiotic diversity enhances rhizosphere microbiome function and plant disease suppression. mBio. 7(6): e01790-16. https://doi.org/10.1128/mbio.01790-16

Iquebal, M.A., Sharma, P., Jasrotia, R.S., Jaiswal, S., Kaur, A., Saini, M., ... Rai, A. (2019): RNAseq analysis reveals drought-responsive molecular pathways with candidate genes and putative molecular markers in root tissue of wheat. Scientific Reports. 9: 13917. https://doi.org/10.1038/s41598-019-49915-2

Karlsson, I., Friberg, H., Steinberg, C., Persson, P. (2014): Fungicide effects on fungal community composition in the wheat phyllosphere. PLoS ONE. 9(11): e111786. https://doi.org/10.1371/journal.pone.0111786

Lauber, C.L., Hamady, M., Knight, R., Fierer, N. (2009): Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. Applied and Environmental Microbiology. 75(15): 5111-5120. https://doi.org/10.1128/AEM.00335-09

Leach, J.E., Triplett, L.R., Argueso, C.T., Trivedi, P. (2017): Communication in the phytobiome. Cell. 169(4): 587-596. https://doi.org/10.1016/j.cell.2017.04.025

Lee, S., Lee, J. (2015): Beneficial bacteria and fungi in hydroponic systems: types and characteristics of microorganisms and control methods. Scientia Horticulturae. 195: 206-215. https://doi.org/10.1016/j.scienta.2015.09.011

Lemanceau, P., Blouin, M., Muller, D., Moenne-Loccoz, Y. (2017): Let the core microbiota be functional. Trends in Plant Science. 22(7): 583-595. https://doi.org/10.1016/j.tplants.2017.04.008

Lindow, S.E. (1983): Methods of preventing frost injury caused by epiphytic ice-nucleation-active bacteria. Plant Disease. 67(3): 327-333. https://doi.org/10.1094/PD-67-327

Lindow, S.E., Brandl, M.T. (2003): Microbiology of the phyllosphere. Applied and Environmental Microbiology. 69(4): 1875-1883. https://doi.org/10.1128/AEM.69.4.1875-1883.2003

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

Lundberg, D.S., Lebeis, S.L., Paredes, S.H., Yourstone, S., Gehring, J., Maulfair, S., Bouffard, P., Tremblay, J., Engelbrektson, A., Kunin, V., Del Rio, T.G., Edgar, R.C., Eickhorst, T., Ley, R.E., Hugenholtz, P., Tringe, S.G., Dangl, J.L. (2012): Defining the core Arabidopsis thaliana root microbiome. Nature. 488(7409): 86-90. https://doi.org/10.1038/nature11237

Lupatini, M., Keidel, A.L., Jacques, R.J., Toth, T., Perestrelo Oliveira, E., Xu, Z., ... Roesch, L.F.W. (2017): Network topology reveals high connectance levels and few key microbial genera within soil bacterial communities in two organic farming systems. Frontiers in Environmental Science. 4: 84. https://doi.org/10.3389/fenvs.2014.00010

Marasco, R., Rolli, E., Fusi, M., Michoud, G., Daffonchio, D. (2018): Grapevine rootstocks shape underground bacterial microbiome and networking but not potential functionality. Microbiome. 6(1): 3. https://doi.org/10.1186/s40168-017-0391-2

Mazzola, M. (2004): Assessment and management of soil microbial community structure for disease suppression. Annual Review of Phytopathology. 42: 35-59. https://doi.org/10.1146/annurev.phyto.42.040803.140408

Mendes, L.W., Raaijmakers, J.M., de Hollander, M., Mendes, R., Tsai, S.M. (2018): Influence of resistance breeding in common bean on rhizosphere microbiome composition and function. ISME Journal. 12(1): 212-224. https://doi.org/10.1038/ismej.2017.158

Mendes, R., Garbeva, P., Raaijmakers, J.M. (2013): The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. FEMS Microbiology Reviews. 37(5): 634-663. https://doi.org/10.1111/1574-6976.12028

Minerdi, D., Sabbatini, P. (2025): Exploring the grapevine microbiome: insights into the microbial ecosystem of grape berries. Microorganisms. 13(2): 438. https://doi.org/10.3390/microorganisms13020438

Mir, M.Y., Parray, J.A., Hamid, S., Reddy, M.S. (2025): Patterns, function and application of seed microbiome: bacteria, fungi and viruses. Elsevier. eBook ISBN: 9780443247774 https://doi.org/10.1016/C2023-0-51036-5

Mo, Y., Bier, R., Li, X., Daniels, M., Smith, A., Yu, L., Kan, J. (2024): Agricultural practices influence soil microbiome assembly and interactions at different depths identified by machine learning. Communications Biology. 7(1): 1349. https://doi.org/10.1038/s42003-024-07059-8

Montanaro, G., Celano, G., Dichio, B., Xiloyannis, C. (2010): Effects of soil-protecting agricultural practices on soil organic carbon and productivity in fruit tree orchards. Land Degradation and Development. 21(2): 132-138. https://doi.org/10.1002/ldr.917

Nelson, E.B. (2018): The seed microbiome: origins, interactions, and impacts. Plant and Soil. 422(1): 7-34. https://doi.org/10.1007/s11104-017-3289-7

Panwar, M., Tewari, R., Sharma, A. (2025): Phytobiome modulation to control plant diseases. In: Microbial Strategies for Plant Disease Management. Elsevier. https://doi.org/10.1016/B978-0-443-33594-5.00006-8

Pieterse, C.M., Zamioudis, C., Berendsen, R.L., Weller, D.M., Van Wees, S.C., Bakker, P.A. (2014): Induced systemic resistance by beneficial microbes. Annual Review of Phytopathology. 52: 347-375. https://doi.org/10.1146/annurev-phyto-082712-102340

Raaijmakers, J.M., Mazzola, M. (2016): Soil immune responses. Science. 352(6292): 1392-1393. https://doi.org/10.1126/science.aaf3252

Rastogi, G., Sbodio, A., Tech, J.J., Suslow, T.V., Coaker, G.L., Leveau, J.H. (2012): Leaf microbiota in an agroecosystem: spatiotemporal variation in bacterial community composition on field-grown lettuce. ISME Journal. 6(10): 1812-1822. https://doi.org/10.1038/ismej.2012.32

Román-Écija, M., Olivares-García, C., Landa, B.B., Navas-Cortés, J.A. (2026): Extent of stem colonization of Spanish Xylella fastidiosa strains in olive: a proximal sensing approach for early detection of infection. Plant Disease. 110(3): 741-753. https://doi.org/10.1094/PDIS-11-24-2327-RE

Ryu, C.M., Farag, M.A., Hu, C.H., Reddy, M.S., Kloepper, J.W., Pare, P.W. (2004): Bacterial volatiles induce systemic resistance in Arabidopsis. Plant Physiology. 134(3): 1017-1026. https://doi.org/10.1104/pp.103.026583

Santhanam, R., Luu, V.T., Weinhold, A., Goldberg, J., Oh, Y., Baldwin, I.T. (2015): Native root-associated bacteria rescue a plant from a sudden-wilt disease that emerged during continuous cropping. Proceedings of the National Academy of Sciences. 112(36): E5013-E5020. https://doi.org/10.1073/pnas.1505765112

Sasse, J., Martinoia, E., Northen, T. (2018): Feed your friends: do plant exudates shape the root microbiome? Trends in Plant Science. 23(1): 25-41. https://doi.org/10.1016/j.tplants.2017.09.003

Sessitsch, A., Hardoim, P., Doring, J., Weilharter, A., Krause, A., Woyke, T., Mitter, B., Hauberg-Lotte, L., Friedrich, F., Rahalkar, M., Hurek, T., Sarkar, A., Bodrossy, L., van Overbeek, L., Brar, D., van Elsas, J.D., Reinhold-Hurek, B. (2012): Functional characteristics of an endophyte community colonizing rice roots as revealed by metagenomic analysis. Molecular Plant-Microbe Interactions. 25(1): 28-36. https://doi.org/10.1094/MPMI-08-11-0204

Smith, S.E., Read, D.J. (2010): Mycorrhizal symbiosis. Academic Press. https://doi.org/10.1016/B978-0-12-370526-6.X5001-6

Spadaro, D., Droby, S. (2016): Development of biocontrol products for postharvest diseases of fruit: the importance of elucidating the mechanisms of action of yeast antagonists. Trends in Food Science and Technology. 47: 39-49. https://doi.org/10.1016/j.tifs.2015.11.003

Stringlis, I.A., Yu, K., Feussner, K., de Jonge, R., Van Bentum, S., Van Verk, M.C., Berendsen, R.L., Bakker, P.A.H.M., Feussner, I., Pieterse, C.M.J. (2018): MYB72-dependent coumarin exudation shapes root microbiome assembly to promote plant health. Proceedings of the National Academy of Sciences. 115(22): E5213-E5222. https://doi.org/10.1073/pnas.1722335115

Toju, H., Peay, K.G., Yamamichi, M., Narisawa, K., Hiruma, K., Naito, K., Fukuda, S., Ushio, M., Nakaoka, S., Onoda, Y., Yoshida, K., Schlaeppi, K., Bai, Y., Sugiura, R., Ichihashi, Y., Minamisawa, K., Kiers, E.T. (2018): Core microbiomes for sustainable agroecosystems. Nature Plants. 4(5): 247-257. https://doi.org/10.1038/s41477-018-0139-4

Trivedi, P., Leach, J.E., Tringe, S.G., Sa, T., Singh, B.K. (2020): Plant-microbiome interactions: from community assembly to plant health. Nature Reviews Microbiology. 18(11): 607-621. https://doi.org/10.1038/s41579-020-0412-1

Van Bruggen, A.H.C., Semenov, A.M. (2000): In search of biological indicators for soil health and disease suppression. Applied Soil Ecology. 15(1): 13-24. https://doi.org/10.1016/S0929-1393(00)00068-8

Van der Wal, A., De Boer, W. (2017): Dinner in the dark: illuminating drivers of soil organic matter decomposition. Soil Biology and Biochemistry. 105: 45-48. https://doi.org/10.1016/j.soilbio.2016.11.006

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

Vannette, R.L., Gauthier, M.P.L., Fukami, T. (2013): Nectar bacteria, but not yeast, weaken a plant-pollinator mutualism. Proceedings of the Royal Society B: Biological Sciences. 280(1752): 20122601. https://doi.org/10.1098/rspb.2012.2601

Vives-Peris, V., de Ollas, C., Gomez-Cadenas, A., Perez-Clemente, R.M. (2020): Root exudates: from plant to rhizosphere and beyond. Plant Cell Reports. 39(1): 3-17. https://doi.org/10.1007/s00299-019-02447-5

Vorholt, J.A. (2012): Microbial life in the phyllosphere. Nature Reviews Microbiology. 10(12): 828-840. https://doi.org/10.1038/nrmicro2910

Vorholt, J.A., Vogel, C., Carlstrom, C.I., Muller, D.B. (2017): Establishing causality: opportunities of synthetic communities for plant microbiome research. Cell Host and Microbe. 22(2): 142-155. https://doi.org/10.1016/j.chom.2017.07.004

Walters, W.A., Jin, Z., Youngblut, N., Wallace, J.G., Sutter, J., Zhang, W., ... Ley, R.E. (2018): Large-scale replicated field study of maize rhizosphere identifies heritable microbiota. Proceedings of the National Academy of Sciences. 115(28): 7368-7373. https://doi.org/10.1073/pnas.1800918115

Weller, D.M., Raaijmakers, J.M., McSpadden Gardener, B.B., Thomashow, L.S. (2002): Microbial populations responsible for specific soil suppressiveness to plant pathogens. Annual Review of Phytopathology. 40: 309-348. https://doi.org/10.1146/annurev.phyto.40.030402.110010

Xu, J., Zhang, Y., Zhang, P., Trivedi, P., Riera, N., Wang, Y., Liu, X., Fan, G., Tang, J., Coletta-Filho, H.D., Cubero, J. (2018): The structure and function of the global citrus rhizosphere microbiome. Nature Communications. 9(1): 4894. https://doi.org/10.1038/s41467-018-07343-2

Yang, J., Kloepper, J.W., Ryu, C.M. (2009): Rhizosphere bacteria help plants tolerate abiotic stress. Trends in Plant Science. 14(1): 1-4. https://doi.org/10.1016/j.tplants.2008.10.004

Yue, R., Dutta, A. (2022): Computational systems biology in disease modeling and control, review and perspectives. npj Systems Biology and Applications. 8(1): 37. https://doi.org/10.1038/s41540-022-00247-4

Zhang, H., Serwah Boateng, N.A., Ngolong Ngea, G.L., Shi, Y., Lin, H., Yang, Q., Wang, K., Zhang, X., Zhao, L., Droby, S. (2021): Unravelling the fruit microbiome: the key for developing effective biological control strategies for postharvest diseases. Comprehensive Reviews in Food Science and Food Safety. 20(5): 4906-4930. https://doi.org/10.1111/1541-4337.12783

Zhalnina, K., Louie, K.B., Hao, Z., Mansoori, N., da Rocha, U.N., Shi, S., ... Brodie, E.L. (2018): Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. Nature Microbiology. 3(4): 470-480. https://doi.org/10.1038/s41564-018-0129-3 .