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MICROBIOME MEMORY IN PLANTS: INTEGRATING EPIGENETIC REGULATION AND TRANSGENERATIONAL MICROBIAL INHERITANCE

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ABSTRACT
Plants continually encounter fluctuating biotic and abiotic conditions, while their associated microbial communities influence nutrient acquisition, growth, immunity and stress tolerance. The emerging concept of plant microbiome memory describes the capacity of a plant-microbiome system to retain information from previous interactions and use it to shape subsequent microbial recruitment and host responses. This review synthesizes evidence for the integration of plant epigenetic regulation and the transgenerational transmission of seed-associated microorganisms as complementary, but mechanistically distinct, routes through which biological experience may persist. DNA methylation, histone modifications, chromatin remodeling and small RNA pathways can maintain or re-establish stress-responsive gene-expression states without altering the DNA sequence, yet their persistence ranges from a few clonal generations to stable inheritance and is frequently reset during sexual reproduction. A notable example is acquired cold tolerance in rice, where multigenerational cold exposure was associated with hypomethylation of the *ACT1* promoter and stable inheritance of an adaptive phenotype. Microbial interactions can also leave persistent host effects: plant growth-promoting bacteria induce DNA-methylation changes associated with growth promotion that outlast the inoculant, and rhizobacterial priming has been linked to enhanced resistance in wheat descendants. In parallel, tracked and community-level studies in common bean, wheat, rice and other species show that seed-associated bacteria and fungi are transmitted selectively across generations, although ecological legacies such as priority effects and soil conditioning can mimic inheritance. Collectively, these findings support a framework in which host epigenetic states, microbial inheritance and environmental filtering interact to influence plant performance across generations. However, direct experimental demonstration that inherited microbes and inherited epigenetic marks jointly constitute a causal, adaptive memory remains limited. We discuss current evidence, an evidence-strength hierarchy, methodological requirements and opportunities for microbiome-informed crop improvement and climate-resilient agriculture.

KEYWORDS: plant microbiome; microbiome memory; epigenetics; DNA methylation; histone modification; seed endophytes; vertical transmission; transgenerational inheritance

INTRODUCTION

Plants are not autonomous biological units; they develop in association with diverse microbial communities inhabiting the rhizosphere, phyllosphere and internal tissues. These microorganisms influence nutrient acquisition, resource use, plant development, pathogen exclusion and tolerance to environmental stress. The composition and function of plant-associated microbiomes are shaped by host genotype, developmental stage, soil properties, climate, agricultural management and microbial dispersal (Trivedi *et al.,* 2020). The microbiome is therefore dynamic, but some microbial members and host responses persist over time or across plant generations (Lopes *et al.,* 2026). The idea of "microbiome memory" extends the concept of plant stress memory to the plant–microbe partnership. Lopes *et al.* (2026) describe microbiome memory as the capacity of plants to retain, recall and respond to previous microbial interactions, influencing subsequent microbial recruitment and physiological responses. This concept encompasses more than the persistence of an inoculated microorganism. A prior interaction may alter host gene expression, root exudation, immune recognition or the structure of the resident microbial community, thereby changing the outcome of later encounters. Memory may therefore be ecological, biochemical or epigenetic, and it may persist within an individual plant or be transmitted to offspring.

Two processes are especially relevant to a transgenerational framework. First, plants can retain stress- or microbe-associated regulatory states through epigenetic mechanisms, including DNA methylation, histone modifications and small RNA-mediated regulation (Quadrana & Colot, 2016; Lämke & Bäurle, 2017). Second, seeds can carry microorganisms from parental plants to the next generation, providing an early microbial inoculum for offspring (Abdelfattah *et al.,* 2022). Seeds may thus act as dual carriers of biological continuity: they transmit the plant embryo, they may transmit microbial partners and, potentially, they may transmit epigenetic information. Evidence from rice, common bean and wheat provides important examples of these processes, although the extent to which they operate as a single, causally linked memory system remains to be established (Song *et al.,* 2025; Sulesky-Grieb *et al.,* 2024; Vujanovic *et al.,* 2019).

Three conceptual cautions frame this review. First, somatic persistence, intergenerational effects and transgenerational inheritance describe different persistence patterns rather than obligatory successive stages; whether a response is retained, reset or transmitted depends on the organism, reproductive mode, exposure timing and the biology of the carrier (Aswathi *et al.,* 2025; Heard & Martienssen, 2014). Second, stable epigenetic inheritance does occur in plants, but the environmental induction and adaptive consequences of inherited marks remain important unresolved questions (Quadrana & Colot, 2016; Cao & Chen, 2024). Third, microbial inheritance is fragmented and selective rather than a faithful transmission of an entire beneficial consortium (Abdelfattah *et al.,* 2022; Rodríguez *et al.,* 2020). The central question is therefore not simply whether plants "remember", but what carries the memory and whether it causes offspring protection. Maternal provisioning can transmit environmental effects without inherited chromatin states (Herman & Sultan, 2011), and conditioned soil can improve resistance in subsequent generations without any germline inheritance (Yuan *et al.,* 2018; Kong *et al.,* 2019).

This review examines the molecular basis of plant epigenetic memory, the contribution of microbial interactions to persistent host responses, and the role of seed-associated microorganisms in transgenerational continuity. It also considers how these processes may be integrated into strategies for sustainable crop production and identifies the experimental evidence required to distinguish true memory from short-term acclimation, maternal effects, soil legacies and repeated environmental selection. Throughout, we separate findings that have been experimentally demonstrated from the integrated hypothesis that host epigenetic states and inherited microbiomes act together (Lopes *et al.,* 2026; Beltrán-Torres *et al.,* 2026).

LITERATURE SEARCH STRATEGY

A structured literature search was conducted using the Consensus research platform, an academic search engine indexing more than 220 million research publications from sources including Semantic Scholar, PubMed and other scholarly databases. The search aimed to identify and evaluate published studies addressing plant microbiome memory, microbial inheritance, epigenetic regulation and the persistence of plant responses across generations. Ten targeted searches and one citation-graph search were performed to retrieve relevant literature. The search was designed to meet four objectives: (i) to define plant microbiome memory and distinguish it from acclimation, priming, maternal effects and ecological legacies; (ii) to evaluate experimental evidence that microbial exposure leaves persistent host epigenetic or regulatory effects; (iii) to assess evidence for seed-mediated microbial transmission across plant generations; and (iv) to determine whether host epigenetic inheritance and microbial inheritance have been shown to act together causally, and to identify the experimental evidence still required.

The search strategy focused on five major thematic areas: (i) plant–microbiome interactions and microbial memory; (ii) seed-mediated microbial transmission and inheritance; (iii) ecological memory, rhizosphere legacies and microbial community assembly; (iv) epigenetic mechanisms associated with stress responses and transgenerational inheritance; and (v) the application of microbial inoculants in sustainable agriculture. Relevant search concepts and keywords included microbial persistence, microbial memory, vertical transmission, seed endophytes, priority effects, DNA methylation, histone modifications, small RNA-mediated regulation, stress priming, transgenerational inheritance, root exudates, plant–soil feedback, rhizosphere legacies and agricultural inoculation.

Following retrieval, the literature was screened for relevance to the objectives of the review, with duplicate records excluded before selection. Particular emphasis was placed on experimental studies investigating microbial persistence, seed-to-seed transmission, host epigenetic modifications and functional responses in subsequent plant generations. Review articles and conceptual publications were also considered to provide background information and identify emerging research directions. The interpretation of the selected literature distinguished between primary experimental evidence and secondary or conceptual discussions. Studies were evaluated with particular attention to the identification and tracking of microbial strains, persistence of microbial populations, assessment of host molecular responses, examination of stress-free descendant generations and measurement of offspring phenotypic outcomes. Alternative explanations, including maternal provisioning, environmental reacquisition, soil microbial legacies and parental effects, were considered when interpreting evidence for transgenerational inheritance.

Conceptual basis of plant and microbiome memory

From acclimation to ecological and transgenerational memory

Several related terms describe plant responses to previous environmental exposure, but they refer to different biological scales. Acclimation or hardening generally denotes physiological adjustment during or shortly after exposure. Priming refers to a latent state induced by an earlier stimulus that enables a faster or stronger response when the plant is challenged again. Stress memory describes the persistence of such altered responsiveness beyond the initial exposure (Lämke & Bäurle, 2017; Aswathi *et al.,* 2025). Intergenerational effects are detected in the immediate offspring of exposed parents, whereas transgenerational memory refers to the transmission of stress-associated phenotypes or regulatory states to offspring that were not directly exposed to the original stimulus (Heard & Martienssen, 2014; Fitz-James & Cavalli, 2022). These categories describe different persistence patterns, not obligatory successive stages (Aswathi *et al.,* 2025). Ecological memory is broader still: it describes how past disturbances influence the present structure or future functioning of organisms, populations or ecosystems (Ogle *et al.,* 2015; Zhang *et al.,* 2026). Microbiome memory adds a community dimension to these concepts. The relevant record may be retained in the plant, in microbial community composition, in the surrounding soil, or in interactions among these compartments. For example, a plant previously colonized by a beneficial bacterium may subsequently recruit a similar microbial consortium because its root exudate profile or immune state has changed. Alternatively, a microbial population may persist in seed tissues and colonize the next generation during germination. These routes can produce similar outcomes but are mechanistically distinct and should be tested separately (Lopes *et al.,* 2026; Azarbad & Alizadeh, 2026).

Ecological legacies: priority effects and soil conditioning

Some of the strongest evidence for persistence in plant-microbe systems is ecological rather than epigenetic. Arrival history shapes microbiome assembly: in existed experiments with synthetic communities, established leaf and root communities resisted some late-arriving strains, and keystone strains influenced the outcome of community assembly (Carlström *et al.,* 2019; Wippel *et al.,* 2021). Root exposure timing and host age further modify colonization outcomes (Aleklett *et al.,* 2022; Burr *et al.,* 2022). Such priority effects represent historical contingency in microbial assembly, not necessarily host epigenetic memory (Debray *et al.,* 2021). Soil conditioning is a second ecological legacy. Root exudates can drive the soil-borne legacy of aboveground pathogen infection, and plant-soil feedback can contribute to the apparent inheritance of seed and rhizosphere communities (Yuan *et al.,* 2018; Kong *et al.,* 2019). Likewise, in reciprocal designs, light conditions under which parents were grown influenced offspring responses through both parental effects and soil legacy effects (Xue *et al.,* 2022). Consequently, an offspring benefit measured in conditioned soil cannot be attributed to a heritable host state or an inherited microbe without soil-exchange controls.

Table 1 contrasts the carriers, recruitment mechanisms and modifiers of ecological legacies with those of host regulatory persistence.

Table 1. Distinct carriers underlying ecological legacies and host regulatory persistence

Dimension	Ecological legacy	Host regulatory persistence	References
Information carrier	Community composition and arrival history	Persistent host methylation-associated regulation	Carlström *et al.* (2019); Chen *et al.* (2022)
Recruitment mechanism	Exudate chemistry and microbial preferences	Inoculation-associated transcriptional changes	Zhalnina *et al.* (2018); Chen *et al.* (2022)
Descendant exposure	Previously conditioned soil	Inherited or reconstructed regulatory states	Yuan *et al.* (2018); Fitz-James & Cavalli (2022)
Major modifier	Environment and colonization timing	Genotype and reproductive resetting	Debray *et al.* (2021); López *et al.* (2024)

The plant–microbiome system as a memory unit

A useful working model views microbiome memory as the outcome of interactions among three components: the host plant, its microbial partners and the environment. The host provides selective habitats and resources; microbes modify host physiology and local ecological conditions; and environmental factors influence both partners. Memory can emerge when an earlier interaction changes one or more of these components in a way that persists after the initiating stimulus has ended. This model does not assume that every persistent association is adaptive. A transmitted microorganism may be neutral or pathogenic (Hu *et al.,* 2025; Khan *et al.,* 2025), and a stable epigenetic mark may impose a growth cost under conditions different from those in which it was induced (Lämke & Bäurle, 2017).

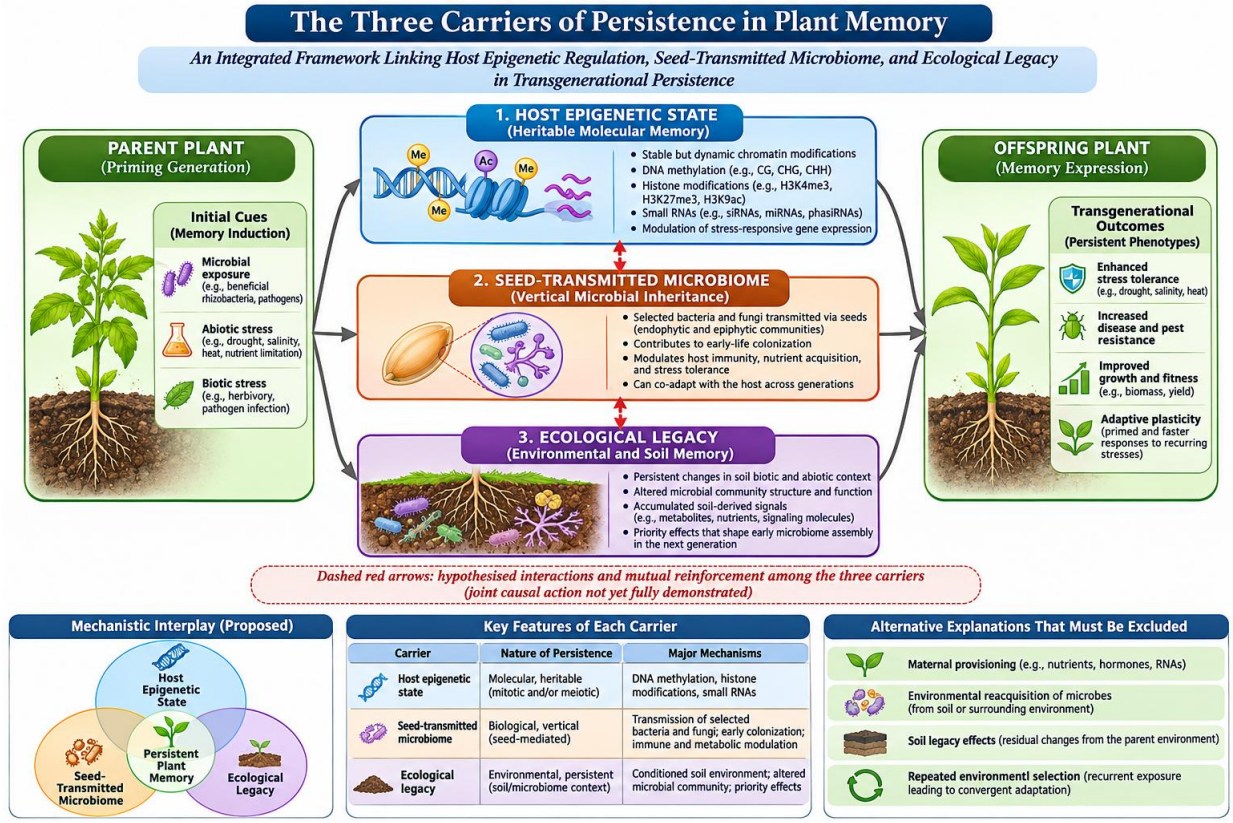

Figure 1. Conceptual framework of plant microbiome memory. Host epigenetic states, seed-transmitted microbes and ecological legacies are three distinct carriers of persistence between parent and offspring plants; their joint causal action (dashed arrows) remains a hypothesis, and maternal provisioning, microbial reacquisition, soil legacies and repeated selection must be excluded.

Epigenetic mechanisms underlying plant memory

DNA methylation and its regulation

DNA methylation is a major epigenetic modification in plants and involves the addition of a methyl group to cytosine. Unlike the DNA sequence itself, methylation patterns can be modified in response to developmental and environmental signals (Chang *et al.,* 2020; Lodhi & Srivastava, 2025). Plant methylation occurs in CG, CHG and CHH sequence contexts, where H represents A, T or C, and distinct maintenance systems act on each context. MET1 primarily maintains CG methylation, whereas the chromomethylases CMT3 and CMT2 and the de novo methyltransferase DRM2 contribute differently to non-CG methylation (Cao *et al.,* 2003; Ou *et al.,* 2012; Chen *et al.,* 2022). De novo methylation is established through the RNA-directed DNA methylation (RdDM) pathway, in which small interfering RNAs guide the methylation machinery to selected genomic regions (Hu & Xu, 2021), while active demethylation can occur through DNA glycosylases such as ROS1 (Zhang *et al.,* 2026). Methylation can influence transcription by altering chromatin structure or the accessibility of regulatory DNA to transcription factors. Its effect is context-dependent: promoter methylation is often associated with reduced transcription, whereas gene-body methylation can have different relationships with gene activity (Fedoroff, 2012; Zhang *et al.,* 2026). Environmental stress may induce local or genome-wide methylation changes, and some of these changes persist after recovery. Such persistence provides a possible molecular basis for stress memory, although a methylation difference alone does not establish that it causes a heritable adaptive phenotype (Lodhi & Srivastava, 2025). Methylation states should not be described as either permanently stable or completely reversible: they can persist, decay or undergo targeted resetting during development and reproduction (Hauser *et al.,* 2011; Wibowo *et al.,* 2016; Martins & Law, 2023).

Histone modifications and chromatin remodeling

Histone proteins package DNA into chromatin, and covalent modifications of histone tails influence chromatin accessibility and transcription. Marks such as H3K4me3, H3K36me3 and histone acetylation are commonly associated with transcriptionally active chromatin, whereas H3K9me2 and H3K27me3 are associated with repressive chromatin states. The addition, removal and recognition of these marks are mediated by "writers", "erasers" and "readers". Their coordinated activity allows plants to regulate stress-responsive genes while retaining the capacity to return to a different transcriptional state during recovery (Zhang *et al.,* 2026). Histone modifications and chromatin remodeling regulate defense-related transcription in plant–pathogen interactions (Ramirez-Prado *et al.,* 2018; Kang *et al.,* 2022), although their involvement in a response does not by itself demonstrate inheritance. Chromatin-remodeling complexes, including SWI/SNF-related machinery, can reposition or restructure nucleosomes and thereby alter access to regulatory sequences. Histone modification, DNA methylation and RdDM interact rather than acting as interchangeable pathways. For example, H3K9me2 can participate in a feedback relationship with CHG methylation, contributing to stable heterochromatin, and loss of RdDM in maize chromomethylase and DDM1-type remodeler mutants illustrates the interdependence of these systems (Fu *et al.,* 2018). In rice, the effect of RNA polymerase V on 24-nt siRNA accumulation depends on DNA methylation context and histone modifications (Zheng *et al.,* 2021). Such interactions provide a mechanistic basis for the persistence of gene-expression states, but their specific contribution to memory of microbial partners remains incompletely characterized.

Small RNAs and epigenetic regulation

Small RNAs provide sequence-guided regulation of gene expression. In the RdDM pathway, 24-nucleotide small interfering RNAs help direct DNA methylation to homologous genomic regions, and mobile small RNAs can move between tissues and regulate genome-wide DNA methylation in recipient cells (Lewsey *et al.,* 2016; Hu & Xu, 2021). Other small RNAs, including microRNAs, regulate target transcripts post-transcriptionally. Long non-coding RNAs (lncRNAs), by contrast, are a distinct class that is not defined by small size and can interact with chromatin-associated complexes; they should not be grouped with small RNAs (Ali & Tang, 2024). These pathways can connect environmental perception to stable or semi-stable gene regulation. Stress-induced small RNAs have also been proposed as potential carriers of regulatory information into reproductive tissues and developing seeds, although the extent and reliability of this transmission vary among biological contexts (Zhang *et al.,* 2026).

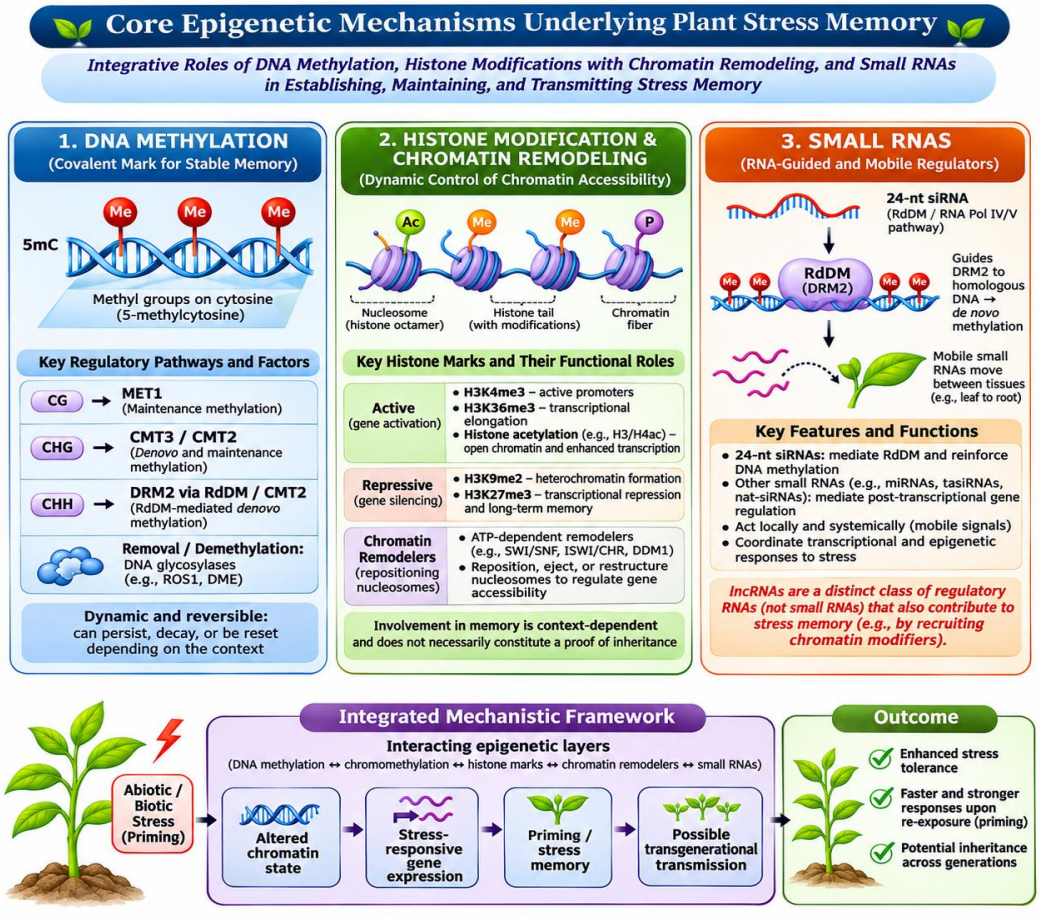

Figure 2. Principal epigenetic mechanisms underlying plant memory: DNA methylation and its maintenance pathways, histone modification and chromatin remodeling, and small RNA-directed regulation. These layers interact, and their involvement in a response does not by itself demonstrate inheritance.

Stress priming and persistence of epigenetic states

Following an initial stress exposure, plants may display altered expression of defense- or stress-associated genes during recovery and respond more rapidly upon re-exposure. Histone marks at stress-responsive loci, DNA methylation changes and small RNA activity can contribute to this primed state (Lämke & Bäurle, 2017). Repeated drought exposure, for example, modifies transcriptional responses in *Arabidopsis*, and different classes of dehydration stress-memory genes have been identified (Ding *et al.,* 2012; Ding *et al.,* 2013), while heat and cold responses can involve chromatin-associated regulation (Zhang *et al.,* 2026). Importantly, memory can be transient, reversible or persistent, and its duration and adaptive value depend on the nature of the stress, plant genotype, developmental stage and the costs of maintaining the primed state. Persistence varies sharply among systems. Stress-induced methylation changes were heritable through asexual generations in dandelions (Verhoeven *et al.,* 2010), duckweed lineages retained some methylation differences for 3–12 clonal generations (Prelovšek *et al.,* 2022), and strawberry retained heat-stress-associated marks for at least three asexual generations (López *et al.,* 2024). In clonal white clover, transgenerational effects and epigenetic memory were likewise detectable (González *et al.,* 2018). Such clonal findings are informative, but they cannot by themselves establish meiotic transmission in sexually reproducing crops (Prelovšek *et al.,* 2022; González *et al.,* 2018). Conversely, mild drought-induced methylation changes were not inherited in *Arabidopsis* (Van Dooren *et al.,* 2020), and hyperosmotic stress memory in *Arabidopsis* can be restricted in the male germline by DNA glycosylase activity and may disappear after one stress-free generation (Wibowo *et al.,* 2016; Lämke & Bäurle, 2017). Positive examples of inheritance include heavy-metal-induced methylation patterns and enhanced tolerance in rice (Ou *et al.,* 2012) and parental salt-stress-induced epigenetic memory affecting transgenerational plasticity in *Phragmites australis* (Chen *et al.,* 2026). Reproductive transmission of epigenetic marks in *Arabidopsis* involves both reprogramming and protection mechanisms (Cheong, 2025), which explains why many induced states are reset while selected states persist (Hauser *et al.,* 2011; Fitz-James & Cavalli, 2022). These contrasting outcomes caution against generalizing from any one species or stress, and the field continues to face methodological challenges in demonstrating transgenerational epigenetic inheritance (Fallet *et al.,* 2023).

Microbial interactions as triggers of host epigenetic memory

Plant growth-promoting bacteria and DNA methylation

Beneficial microorganisms can influence plant physiology through nutrient mobilization, phytohormone modulation, stress alleviation, pathogen antagonism and changes in host signaling. These interactions may also influence the host epigenome. Chen *et al.* (2022) reported that plant growth-promoting bacterial inoculation induced DNA-methylation reprogramming in plant roots and that growth-promoting effects persisted after the inoculated bacteria were no longer detected in the rhizosphere. The study combined methylome and transcriptome profiling with functional inhibition evidence, and the methylation changes were associated with altered expression of plant growth-related genes. This provides a direct example of within-generation microbial effects: microbial exposure can leave a persistent host-associated imprint that does not depend on the continued detectable presence of the inoculant. Such findings are central to the microbiome-memory hypothesis because they suggest that a microbial interaction may modify the host in a way that outlasts the microbial encounter. However, persistent plant performance after inoculant removal should not automatically be interpreted as transgenerational inheritance. It may represent long-lasting within-plant memory, a developmental carry-over effect or an altered soil or host state. Demonstrating inheritance requires controlled propagation and testing of offspring that have not been directly exposed to the original inoculum. The evidence for persistent host regulation after microbial exposure is therefore best rated as moderate, resting on a specific experimental system (Chen *et al.,* 2022).

Rhizobacterial priming of descendants

Evidence that microbial exposure can influence descendants comes from wheat. Devi *et al.* (2025) reported that plant growth-promoting rhizobacteria induced transgenerational immune priming that strengthened wheat defense against *Bipolaris sorokiniana*. This is a positive offspring phenotype, but the molecular carrier of the effect remains unresolved; the result is compatible with an inherited epigenetic state, an inherited microbial component, or maternal provisioning, and it does not by itself distinguish among them. Comparable caution applies to mycorrhizal systems, in which paternal arbuscular mycorrhizal fungal status affected DNA methylation in seeds (Varga & Soulsbury, 2017), and in which the transition from plastic responses to transgenerational legacies has recently been reviewed (Beltrán-Torres *et al.,* 2026). These observations support a connection between symbiont exposure and offspring regulatory states but do not establish durable adaptive inheritance.

Signaling pathways linking microbes and the host

Plant recognition of microbial signals can activate interconnected hormone and defense pathways. Salicylic acid is commonly associated with defense against biotrophic pathogens, whereas jasmonic acid and ethylene participate in responses to necrotrophic pathogens, herbivores and several beneficial or pathogenic microbial interactions. Abscisic acid is central to abiotic stress responses, particularly drought and salinity, and can interact with other hormonal pathways. Calcium signaling, reactive oxygen species and mitogen-activated protein kinase cascades further connect perception to transcriptional regulation (Ramirez-Prado *et al.,* 2018). These signaling networks can influence root development, exudation patterns and immune status, thereby shaping the microbial

habitat and subsequent recruitment (Lopes *et al.,* 2026; Zhang *et al.,* 2026). Therefore, microbial recognition alters host signaling; signaling modifies gene expression and potentially epigenetic states; these changes influence root exudates, nutrient availability and immune filtering; and the modified host environment selects a different microbial community. The selected community may then reinforce or modify host responses. This reciprocal model is a useful framework, but individual links require direct testing rather than being assumed from co-occurrence patterns.

Root exudates, microbial recruitment and ecological legacies

Root exudates provide a mechanistic link between plant physiological state and rhizosphere community assembly. Exudate chemistry and microbial substrate preferences drive patterns of rhizosphere community assembly (Zhalnina *et al.,* 2018), and exudate-mediated recruitment has experimental support, including protective *Pseudomonas* enrichment against foliar pathogens and taxifolin-mediated *Bacillus* recruitment that structures disease suppressiveness (Wen *et al.,* 2020; Zhou *et al.,* 2023). Root exudates also support colonization by beneficial rhizobacteria (Chen & Liu, 2024). However, exudation varies with development and genotype, as shown for carrot genotypes (Anderson *et al.,* 2024), so altered chemistry alone does not establish memory. It may reflect current plant status rather than a persistent record of prior exposure. Longitudinal measurements and reciprocal transfer designs are required to establish persistence and causality (Zhalnina *et al.,* 2018; Yuan *et al.,* 2018).

Seed-associated microbiomes and transgenerational transmission

Seeds as microbial reservoirs

Seeds are reproductive structures and early microbial habitats. They can contain bacterial and fungal endophytes that become part of the seedling microbiome during germination. Transmission may occur through internal plant tissues and reproductive structures or through seed surfaces, and seed-associated microbes can influence early colonization, priority effects, nutrient acquisition and interactions with pathogens (Abdelfattah *et al.,* 2022; Qi *et al.,* 2026). Because seedlings develop initially in a relatively constrained environment, microorganisms carried by seeds may have an important role in the establishment of the offspring microbiome (Vujanovic *et al.,* 2019; Sulesky-Grieb *et al.,* 2024). Seed transmission is well demonstrated, but neither universal embryo colonization nor guaranteed protection follows from it (Khan *et al.,* 2025; Azarbad & Alizadeh, 2026). Transmission routes are diverse. Flowers can deliver introduced bacteria into progeny seeds, allowing the seed microbiome and associated traits to be modified at flowering (Mitter *et al.,* 2017), and clonal connections provide another route by which microorganisms move between plant generations (Vannier *et al.,* 2018). Seed-derived microbes can dominate subsequent community assembly, but compartment filtering and microbial traits influence which organisms establish (Wen *et al.,* 2025; Wu *et al.,* 2024; Romão *et al.,* 2025).

Multigenerational transmission of the wheat seed mycobiome

Vujanovic *et al.* (2019) examined fungal endophytes associated with wheat seeds across three successive host generations under control and drought conditions. The study used ITS 5.8S rRNA gene sequencing to characterize the seed mycobiome and investigated the influence of external acquisition of an endophytic *Penicillium* strain and reported transgenerational transmission of fungal seed endophytes and found that drought was associated with changes in mycobiome composition. Plants receiving the *Penicillium* treatment maintained comparatively more stable fungal communities across generations, whereas untreated plants showed greater community fluctuation and increased occurrence of potential phytopathogens. The study linked seed mycobiome dynamics with host stress resilience and phenotype, while also illustrating that environmental conditions can influence the composition of transmitted communities. The wheat study supports the idea that seed-associated fungal communities can persist across generations and that microbial acquisition may influence community stability under stress. It does not, by itself, demonstrate that the plant epigenome is the mechanism responsible for fungal transmission or for the observed community patterns. Rather, it provides evidence for the microbial-inheritance component of a broader microbiome-memory framework.

Stable transmission of the common bean seed bacteriome

Sulesky-Grieb *et al.* (2024) investigated bacterial seed endophytes in common bean (*Phaseolus vulgaris* L.) across three plant generations. The experiment compared control, drought and excess-nutrient conditions in a multigenerational factorial design and used 16S rRNA gene profiling to assess bacterial community composition and identified 22 bacterial members that were stably transmitted across generations regardless of the parental plant condition, indicating that parental environmental conditions do not necessarily erase the core transmitted seed microbiome.

Directly tracked transmission and other systems

Taxonomic overlap between parental and offspring seeds is suggestive but can be confounded by environmental reacquisition. Stronger evidence is obtained when a defined strain is tracked from parent to progeny. Labelled *Pantoea* core endophytes were shown to undergo seed-mediated vertical transmission (Sanz-Puente *et al.,* 2025), providing stronger inheritance evidence than taxonomic overlap alone, and bacteria introduced at flowering were recovered from progeny seeds (Mitter *et al.,* 2017). Community-level and isolate-level studies in other species reveal both consistency and variability (Table 2). In rice, longitudinal analysis showed that 29 bacterial and 34 fungal members were transmitted from seed to seed (Kim *et al.,* 2022), and genomic similarity between parent- and offspring-derived isolates identified core vertically transmitted bacterial lineages (Zhang *et al.,* 2022). In oak,

embryo and pericarp communities differed, indicating distinct seedling transmission routes (Abdelfattah *et al.,* 2020). In *Setaria viridis*, inheritance varied among seed batches and environmental replenishment remained important (Rodríguez *et al.,* 2020), and a core microbiome has also been described in cotton seeds (Wu *et al.,* 2024).

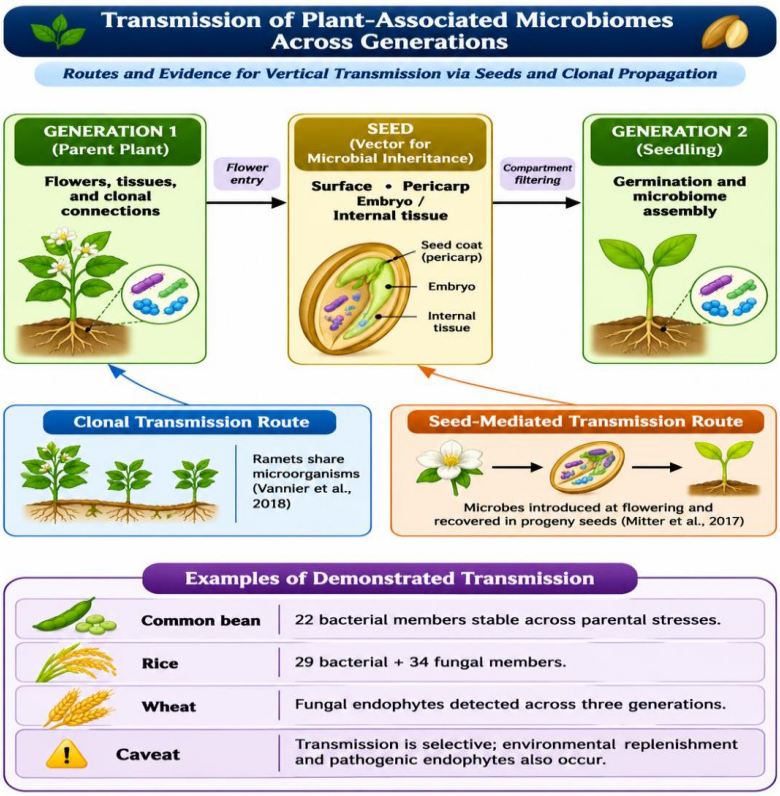

Figure 3. Routes of microbial transmission between plant generations through seeds, with examples of demonstrated transmission (Vannier *et al.,* 2018; Mitter *et al.,* 2017; Sulesky-Grieb *et al.,* 2024; Kim *et al.,* 2022; Vujanovic *et al.,* 2019; Sanz-Puente *et al.,* 2025).

Table 2. Seed transmission findings across plant systems and their biological boundaries

System	Observed finding	Important boundary	Reference
Common bean	22 bacterial members persisted	Stable across tested parental stresses	Sulesky-Grieb *et al.* (2024)
Wheat	Seed fungal endophytes transmitted across three generations	Drought altered mycobiome composition	Vujanovic *et al.* (2019)
Rice	29 bacterial and 34 fungal members transmitted	Community-level longitudinal evidence	Kim *et al.* (2022)
Rice endophytes	Parent–offspring isolates showed genomic similarity	Particular core bacterial lineages	Zhang *et al.* (2022)
***Pantoea* endophytes**	Labelled bacteria transmitted through seeds	Persistence and function of each strain need separate testing	Sanz-Puente *et al.* (2025)
Oak	Embryo and pericarp communities differed	Distinct seedling transmission routes	Abdelfattah *et al.* (2020)
Setaria viridis	Inheritance varied among seed batches	Environmental replenishment remained important	Rodríguez *et al.* (2020)

Comparing bacterial and fungal inheritance

Together, the wheat and common bean studies show that both fungal and bacterial components of seed-associated microbiomes can be transmitted across generations. However, the patterns are not identical. The wheat study highlighted shifts in fungal community composition under drought and the influence of *Penicillium* acquisition, whereas the common bean study identified a stable set of bacterial members despite parental environmental treatments. These differences underline the importance of host species, microbial kingdom, experimental design, stress regime and inoculation history when interpreting microbial inheritance. Transmission is selective rather than a faithful transfer of the complete parental consortium (Abdelfattah *et al.,* 2022; Rodríguez *et al.,* 2020), and seed-borne endophytes also include organisms with pathogenic or toxin-producing effects, contradicting the notion of uniformly beneficial inheritance (Hu *et al.,* 2025; Khan *et al.,* 2025).

Direct evidence for transgenerational epigenetic adaptation

A particularly strong example of environmentally induced epigenetic inheritance is provided by Song *et al.* (2025), who investigated acquired cold tolerance in cultivated rice (*Oryza sativa* L.). Cold-sensitive rice plants were exposed to recurrent cold stress during reproductive development, and progeny with improved seed-setting under cold conditions were selected across generations. The acquired cold-tolerance phenotype persisted in inbred progeny for at least five generations without continued cold exposure. The study identified DNA hypomethylation in a promoter region of the *acquired cold tolerance 1* (*ACT1*) gene, which was associated with altered *ACT1* expression under cold stress and with improved seed setting. They used targeted DNA-methylation editing to support a functional role for the methylation state, rather than relying solely on correlation, and reported an association between natural variation in *ACT1* methylation, rice cold tolerance and geographic distribution. The work therefore provides direct evidence that an environmentally induced epiallele can contribute to the stable inheritance of an adaptive plant trait. The rice study is highly relevant to microbiome memory because it demonstrates that environmental experience can be encoded in a plant epigenetic state and persist across generations, consistent with broader evidence that transgenerational epigenetic inheritance contributes to plant adaptation, domestication and breeding (Quadrana & Colot, 2016; Cao & Chen, 2024). Nevertheless, it is not a direct demonstration of microbiome-mediated inheritance: the inducing factor was cold stress, not microbial inoculation. It should therefore be used as mechanistic support for the feasibility of transgenerational epigenetic memory, while microbial studies are used to support the persistence and transmission of microbial partners. Connecting these two evidence streams is a central research opportunity.

Integrating epigenetic inheritance and microbial transmission

The available evidence suggests two potentially complementary routes of biological continuity. The first is host-mediated: environmental or microbial exposure alters DNA methylation, histone marks, chromatin accessibility or small RNA profiles, potentially changing gene expression in later developmental stages or offspring. The second is microbiome-mediated: microorganisms associated with parental plants are carried in or on seeds and contribute to microbial assembly in the next generation. These processes may operate independently, but they may also interact. For example, an inherited microbial consortium could stimulate hormone signaling and epigenetic reprogramming in the offspring. Conversely, parental epigenetic changes could alter seed traits, root exudation or immune filtering, influencing which microorganisms are recruited after germination. Microbial metabolites and signaling molecules may also influence chromatin-associated pathways. Such reciprocal interactions could create a feedback system in which host regulatory states and microbial communities jointly shape offspring responses to stress. The conceptual model proposed in recent discussions of microbiome memory therefore treats seeds as potential carriers of both microbial and epigenetic legacies (Lopes *et al.,* 2026; Beltrán-Torres *et al.,* 2026). At present, however, the evidence is stronger for the individual components than for their integrated causal operation (Table 3). Representative studies for each component are summarized in Table 4. Selected microbes passing through seeds and the influence of ecological history on assembly are supported by tracking, multigenerational and manipulated arrival-order experiments (Sanz-Puente *et al.,* 2025; Sulesky-Grieb *et al.,* 2024; Carlström *et al.,* 2019; Wippel *et al.,* 2021). Persistent host regulation after microbial exposure and descendant protection after microbial priming are each supported in specific systems (Chen *et al.,* 2022; Devi *et al.,* 2025). By contrast, the claim that inherited microbes and inherited host epigenetic states universally act together to improve offspring fitness remains unestablished (Azarbad & Alizadeh, 2026; Beltrán-Torres *et al.,* 2026). These studies collectively make the integrated model plausible, but they do not yet establish that a specific inherited microbial taxon causes a defined epigenetic mark that is then transmitted and produces an adaptive phenotype in the next generation.

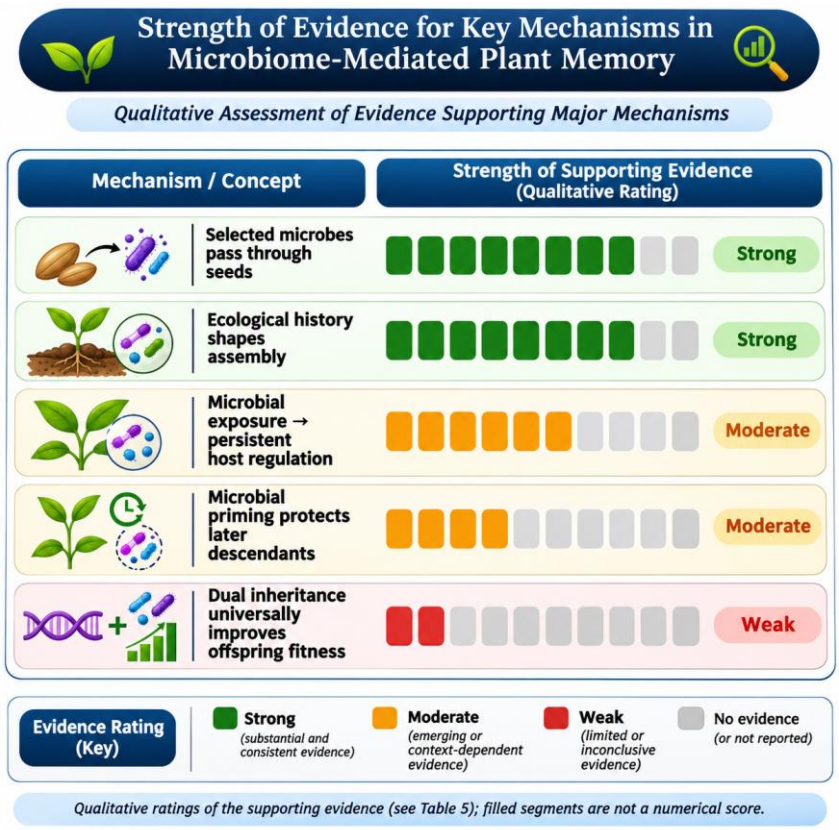

Figure 4. Qualitative strength of evidence for key claims about plant microbiome memory (see Table 4 for supporting references). Filled segments indicate relative evidence strength rather than a numerical score.

The clearest gap is the causal separation of inherited microbes from inherited host regulation, because parental environments can influence both simultaneously, altering microbial communities as well as host-internal seed characteristics (Azarbad & Alizadeh, 2026; Xue *et al.,* 2022). Evidence linking microbial exposure to host DNA methylation is concentrated in bacterial inoculation and mycorrhizal systems, whereas links between seed endophytes and host methylation or histone regulation appear sparse in the literature surveyed for this review (Chen *et al.,* 2022; Varga & Soulsbury, 2017). Genotype-specific responses and uncertain functional consequences further limit extrapolation from methylation persistence alone (González *et al.,* 2018; López *et al.,* 2024)

Table 3. Strength of evidence for key claims about plant microbiome memory

Claim	Evidence strength	Reasoning	References
Selected microbes pass through seeds	Strong	Tracking and multigenerational observations converge	Sanz-Puente *et al.* (2025); Sulesky-Grieb *et al.* (2024)
Ecological history shapes microbiome assembly	Strong	Manipulated arrival-order experiments	Carlström *et al.* (2019); Wippel *et al.* (2021)
Microbial exposure produces persistent host regulation	Moderate	Functional inhibition supports a specific system	Chen *et al.* (2022)
Microbial priming protects later descendants	Moderate	Positive phenotype, unresolved molecular carrier	Devi *et al.* (2025)
Dual (microbial + epigenetic) inheritance universally improves offspring fitness	Weak	Joint causality and generality remain unestablished	Azarbad & Alizadeh (2026); Beltrán-Torres *et al.* (2026)

Table 4. Representative studies supporting components of plant microbiome memory and transgenerational inheritance

Study system	Main approach	Key finding reported	Relevance to memory
Rice (*Oryza sativa*); Song *et al.* (2025)	Multigenerational cold exposure; methylome, transcriptome and methylation editing	ACT1 promoter hypomethylation associated with acquired cold tolerance; phenotype persisted for at least five generations	Direct evidence for a heritable epigenetic contribution to stress adaptation
Wheat (*Triticum*); Vujanovic *et al.* (2019)	ITS 5.8S sequencing across three generations under control/drought conditions, with Penicillium reintroduction	Seed fungal endophytes were transmitted across generations; drought and fungal reintroduction influenced community patterns	Evidence for transgenerational fungal seed microbiome transmission
Common bean (*Phaseolus vulgaris*); Sulesky-Grieb *et al.* (2024)	Three-generation factorial experiment; 16S rRNA profiling	Twenty-two bacterial members were stably transmitted regardless of parental environmental condition	Evidence for stable bacterial seed microbiome inheritance under abiotic stress
Plant–PGPB interaction; Chen *et al.* (2022)	Bacterial inoculation and analysis of root DNA methylation and growth effects	PGPB-associated methylation reprogramming and growth effects persisted after inoculant removal from rhizosphere	Evidence for persistent host epigenetic effects following microbial exposure
Plant epigenetic memory; Zhang *et al.* (2026)	Review of DNA methylation, histone marks, chromatin and small RNA pathways	Synthesizes mechanisms linking environmental stress, epigenetic memory and potential inheritance	Mechanistic framework for stress memory and epigenetic inheritance

Methodological approaches for investigating microbiome memory

Multigenerational experimental designs

Robust evaluation requires experiments that follow defined parental lineages through multiple generations. Parent plants should be exposed to controlled microbial and/or abiotic treatments, while offspring are grown in standardized environments. Reciprocal parental designs and soil exchanges address different inheritance routes and help separate inherited host effects from microbial carry-over and soil legacies (Xue *et al.,* 2022; Kong *et al.,* 2019). Seed resources remain an important alternative explanation and must be controlled (Lämke & Bäurle, 2017). For true transgenerational inheritance, the generation assessed should not have been directly exposed to the original stressor; the appropriate generation depends on the timing of exposure and reproductive biology (Heard & Martienssen, 2014). Parallel lineages maintained without repeated exposure are needed to test persistence and decay, since some states are lost after a single stress-free generation (Lämke & Bäurle, 2017; Wibowo *et al.,* 2016).

Microbiome profiling and transmission tracking

Amplicon sequencing of bacterial 16S rRNA genes and fungal ITS regions can characterize seed-associated communities, as illustrated by the common bean and wheat studies, whereas shotgun metagenomics assesses functional potential (Chen *et al.,* 2022). However, sequence-based detection does not necessarily demonstrate viability, activity or transmission of the same strain. Culture-based isolation, strain-specific markers, fluorescent or genetic labelling, whole-genome comparisons and microscopy strengthen evidence for viable vertical transmission (Sanz-Puente *et al.,* 2025; Zhang *et al.,* 2022). Sampling should include seed surface and internal fractions, with rigorous surface-sterilization controls and negative controls. Low seed microbial biomass, host DNA contamination and spatial sampling heterogeneity complicate inference, and even replicate samples of defined root compartments can differ unexpectedly in diversity (Qi *et al.,* 2026; Attia *et al.,* 2021).

Epigenomic and functional validation

Whole-genome bisulfite sequencing or targeted bisulfite sequencing can identify methylation differences, while RNA sequencing can link epigenetic variation to gene-expression changes. Joint transcriptome–methylome measurements connect regulatory layers but require functional perturbation to strengthen causal interpretation (Chen *et al.,* 2022). Chromatin immunoprecipitation sequencing or related assays can characterize histone modifications, and small RNA sequencing can identify candidate regulatory RNAs. Functional tests are essential: targeted methylation editing, as used for *ACT1* in rice (Song *et al.,* 2025), gene perturbation, microbial removal and re-inoculation, or synthetic community reconstruction can help establish causality. Physiological measurements should include stress survival, growth, reproduction and yield rather than relying exclusively on molecular markers.

Applications in sustainable agriculture and crop improvement

Understanding microbiome memory may create opportunities to improve crop resilience through seed microbiome management, beneficial microbial consortia and epigenetic-informed breeding. Seed-based delivery of beneficial microorganisms could help establish early microbial communities and reduce dependence on repeated soil inoculation (Mitter *et al.,* 2017; Romão *et al.,* 2025). Seed biopriming and seed treatments with microorganisms are established approaches that can influence germination and seedling growth (Singh *et al.,* 2023; Cardarelli *et al.,* 2022), and synthetic bacterial communities applied to seeds contributed approximately 80% of seedling microbiota in one experiment (Arnault *et al.,* 2023). That result demonstrates efficient early colonization, not multigenerational agronomic reliability. The stable transmission of selected bacterial or fungal endophytes suggests that some microbial traits could be maintained through seed systems, although stability must be validated across locations, cultivars and production cycles (Sulesky-Grieb *et al.,* 2024; Vujanovic *et al.,* 2019). Microbial inoculation may also be explored as a means of inducing beneficial host states, provided that the effects are reproducible and do not compromise yield or other traits. Field inoculation can improve maize growth through nutrient acquisition and physiological changes without demonstrating inherited memory (Francioli *et al.,* 2025), and formulation, storage viability, competition with resident microbiota, environmental context and inconsistent field performance remain major constraints (O'Callaghan, 2016; O'Callaghan *et al.,* 2022). Epigenetic variation may provide an additional resource for crop improvement. The rice *ACT1* study illustrates how a stress-associated epiallele can contribute to an adaptive trait and remain stable across generations (Song *et al.,* 2025), and epigenetic inheritance is increasingly considered in the context of domestication and breeding (Cao & Chen, 2024). In principle, epigenetic markers associated with desirable stress responses could complement conventional genetic selection. Microbiome-assisted breeding may also consider host genotypes that consistently recruit beneficial microbial partners. Claims of "maximizing adaptation" through these approaches are, however, unsupported at present, and all strategies should be evaluated under field conditions, where soil heterogeneity, climate variation, management practices and resident microbial communities may alter outcomes (Lopes *et al.,* 2026; Zhang *et al.,* 2026).

Limitations and research gaps

Several challenges currently limit the translation of microbiome memory into practical agricultural applications. The persistence of microbial communities or epigenetic marks does not necessarily indicate successful adaptation or improved plant fitness (Heard & Martienssen, 2014; Ogle *et al.,* 2015). Furthermore, maternal effects, seed provisioning, persistent soil legacies and repeated environmental exposure may mimic genuine transgenerational inheritance, complicating the identification of underlying inheritance mechanisms (Herman & Sultan, 2011; Yuan *et al.,* 2018; Xue *et al.,* 2022). The context-dependent nature of microbial communities also presents a major challenge, as microorganisms beneficial to one host or environmental condition may become ineffective or detrimental under different circumstances (Hu *et al.,* 2025). In addition, epigenetic modifications may be reversible or gradually diminish across generations, while the maintenance of a primed physiological state may impose additional metabolic costs on plants (Lämke & Bäurle, 2017; Van Dooren *et al.,* 2020). Similarly, the increased abundance of particular microbial taxa in successive generations does not necessarily indicate vertical transmission, as it may result from repeated environmental selection.

Despite these limitations, several fundamental questions remain to be addressed to establish the mechanisms and agricultural significance of microbiome-mediated memory. One major question concerns whether inherited microorganisms and host epigenetic modifications independently or synergistically contribute to offspring protection, particularly because parental environmental conditions can simultaneously influence microbial communities and seed-associated physiological characteristics (Azarbad & Alizadeh, 2026). Another important consideration is the identification of microbial signals that consistently induce host epigenetic modifications and the extent to which these regulatory states persist through subsequent stress-free sexual generations. Although mechanisms of reproductive transmission have been reported, environmental memory may undergo resetting, necessitating generation-specific validation of its persistence (Cheong, 2025; Wibowo *et al.,* 2016).

Furthermore, establishing whether inherited microbial strains remain viable and metabolically active in subsequent generations is essential, as molecular detection alone cannot confirm their functional contribution. Strain-level tracking combined with functional validation is therefore necessary to distinguish viable inheritance from the persistence of microbial genetic signatures (Sanz-Puente *et al.,* 2025; Qi *et al.,* 2026). The influence of host genetic background and environmental conditions on the stability of microbiome–epigenome interactions also requires further investigation, since these responses may vary considerably among plant genotypes and growing environments (González *et al.,* 2018; López *et al.,* 2024). Moreover, the long-term reliability of inherited benefits under field conditions and during seed storage remains uncertain. Although seed-based microbial delivery offers considerable potential, challenges associated with inoculant viability, ecological competition and the limited availability of multi-environment field validation must be addressed before large-scale agricultural implementation (O'Callaghan, 2016; O'Callaghan *et al.,* 2022).

Addressing these knowledge gaps will require longitudinal and multidisciplinary investigations integrating strain-resolved microbiome profiling, epigenomic analysis, transcriptomics and plant performance assessments across successive generations. Particular emphasis should be placed on distinguishing the mechanisms of inheritance, duration of persistence and actual functional benefits, rather than considering these processes as interchangeable indicators of biological memory (Lämke & Bäurle, 2017; Fallet *et al.,* 2023). Such integrated approaches will

provide a stronger mechanistic foundation for understanding microbiome-mediated inheritance and facilitate the development of reliable microbial strategies for sustainable crop production.

CONCLUSION

Plant microbiome memory is best presented as an umbrella framework for several potentially interacting inheritance and persistence processes, not as an obligatory developmental sequence. Epigenetic mechanisms provide routes for retaining altered gene-regulatory states, while seed-associated microorganisms provide a means of microbial continuity between plant generations, and ecological legacies such as priority effects and soil conditioning add a further layer of persistence that must be separated from both. Evidence from bacterial inoculation studies, rhizobacterial priming in wheat, multigenerational wheat and common bean experiments, tracked *Pantoea* transmission and the rice *ACT1* epiallele demonstrates that persistent host effects, microbial transmission and heritable epigenetic adaptation are biologically plausible and experimentally supported as distinct phenomena. Their integration into a single transgenerational feedback system remains an important but incompletely resolved hypothesis. The defensible message is conditional: plants retain microbial legacies, but their carriers, inheritance stability and benefits require separate demonstration. Clarifying the mechanisms, stability and ecological limits of this process could support the development of microbiome-informed and epigenetically informed strategies for climate-resilient crop production.

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