



REVIEW ARTICLE

Crop microbiome: A way for climate-resilience agriculture

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Abstract

Climate change has a major impact on the global agricultural production as it influences crop productivity, soil stability and dynamics of the ecosystem. In this context, the crop microbiome has emerged as an important biological factor for enhancing agricultural sustainability and climate resilience. This review examines recent field and experimental studies on sustainable farming practices that utilise microbiome dynamics to develop climate-smart farming systems. It outlines the importance of essential processes such as nutrient cycling, disease resistance, stress tolerance and soil carbon stabilisation are impacted by plant-associated microbiomes in the rhizosphere, endosphere and phyllosphere. Farming practices such as conservation tillage, intercropping, cover cropping, irrigation management, organic amendments and integrated nutrient management (INM) have considerable impacts on microbial diversity, structure and function. These practices promote the healthy populations of microbes, with changes in the pattern of root exudation and soil condition, which enhance the health of the soil. Biological nitrogen fixation, phosphorus solubilisation, hormone regulation, induced systemic resistance (ISR) and osmotic regulation processes are microbiome mediated, leading to increased crop productivity and adaptation to environmental changes. Moreover, microbiome-driven function enhances plant defence, increase fertiliser and water use efficiency (WUE) and contribute to greenhouse gas (GHG) mitigation and carbon sequestration. Sustainable farming practices can enhance the resilience of agroecosystems and decrease dependence on synthetic inputs through beneficial crop microbiome interactions. Understanding and managing crop microbiome dynamics offers a promising approach for achieving climate-smart and sustainably intensified agricultural systems.

Keywords: climate-smart agriculture; crop microbiome; plant-microbe interactions; soil microbial communities; sustainable agriculture practices

Introduction

The frequency and severity of extreme weather occurrences have increased due to 1.1 °C increase in the global temperature. Human society faces major challenges related to food security, climate change and the environmental impacts of agricultural activities (1). Global climate change alters the quantity and structure of soil nutrients and has a significant impact on the soil microbial populations, particularly in agricultural ecosystems. Over the years, agriculture has been more reliant on fertilisers, agrochemicals and technology besides supplying the food demands of the globe. The gradual change in methods has transformed the nutrient cycling in farming ecosystems and broken-down food webs that start with microbes, leading to an increase in undesirable compounds and a decrease in microbial diversity (2). Providing food to an increasing population amidst a rapidly evolving environment, where cultivable land is becoming smaller is a monumental task that cannot be dealt with in a straightforward manner. This has led to the pressing need to identify solutions to mitigate the impact of warming climate on agricultural production (3).

The exploitation of the functionality of plant-related microbiomes is now regarded as one of the best approaches to counteracting the short to medium-term effects of climate change on the agricultural productivity. Utilising crop microbiomes via sustainable agronomic practices is crucial given the relationship between microbiomes in particular habitats and climate-smart agriculture as well as the relevance of microbiomes in accomplishing the sustainable development goals (SDGs) (4). Soil microbes are needed to ensure that the ecosystem is in balance, essential nutrient cycles and ideal crop growth. In addition, agronomic practices, including reduced tillage, crop rotation, proper use of fertilisers and effective utilisation of water, boost agricultural production and improve the microenvironment of farmland to influence native soil microbes and pave the path to climate-smart agriculture (5).

Microbiome-based approaches can be advantageous in climate-smart agriculture in several ways. First, they can mitigate reliance on chemical fertilisers and pesticides by enhancing natural nutrient cycling and disease suppression mechanisms (6). Second, they can improve crop-based stress resistance by using microbiome-mediated stress resistance mechanisms (7). Third, they will be able to reduce climate change by reducing greenhouse

gases (GHGs) emissions and increasing soil carbon capture (8). Lastly, the microbiome management methods can be integrated with other sustainable agroecosystem management strategies because of their compatibility and complementation.

Microbiome compartments and structure

The microbiome concept is linked to the various types of microbes that are related to larger ecosystems including humans, animals and plants. Plants have been demonstrated to co-exist with a diverse collection of microbes as opposed to living alone and these microorganisms are primarily those that are bacteria and fungi which can be in the phyllosphere or endosphere between plants and soil. To date, thousands of bacterial and fungal species in plant tissues have been identified (9). The microbiome can be categorised into two main groups: aboveground and belowground (Fig. 1). The microbial community that exists in the soil and interacts with plant roots either nearby (rhizospheric microbiome) or far away (non-rhizospheric microbiome) is referred to as the “belowground microbiome.” The phyllosphere, endosphere and spermosphere microbiomes that circulate above the soil in plant components and interact with plant functions are included in the “aboveground microbiome” (10).

The crop microbiome in natural ecosystems, which is made up of a broad spectrum of bacteria, fungi, actinomycetes and nematodes that live in biological environments comprising the rhizosphere, rhizoplane and endosphere, is greatly influenced by the composition of the rhizosphere microbiota (11). The phyllosphere, where wide variety of microbial communities living includes epiphytes (on the leaf surface) and endophytes (colonise inside leaves), which component is essential for plant growth, development and resistance to both abiotic and biotic stresses. In addition, the phyllosphere microbes was significantly influenced by the environmental factors (12).

Microorganisms in the phyllosphere influence on plant health through various kinds of processes, such as defence against foliar diseases, immune response regulation and physiological

impacts through the synthesis of volatile organic molecules and other metabolites. An emerging field in microbiome-based agriculture is the comprehension of phyllosphere microbiome interactions and how they can be managed (13).

Plant microbe interactions and its effects

Plant-microbiome interactions have evolved over millions of years in the rhizosphere, endosphere and phyllosphere, with plants exploiting phytochemical characteristics, root exudates and plant biology to selectively lure useful microorganisms. These activities promote and stabilise beneficial microbial communities by preventing possible infections and influencing the formation of a good microbiome (14). The plant-microbiome interactions can be classified into 3 types which include plant-microbiome, plant-plant and microbiome-plant interactions.

Plant-microbiome interactions

Plant roots can synthesise wide range of primary and secondary metabolites, that change microbial communities by creating selective niches in the rhizosphere and endosphere (15). Whereas certain compounds that are products of exudates function as biochemical filters inhibiting or killing non-adapted microbial populations, in a same way some other compounds facilitate the coexistence of complementing microbial guilds that enrich one another and benefit the host plant in general (16). Benzoxazinoids, as an example, are a broadly studied group of metabolites present in maize and are involved in the construction of the microbiome as both antibacterial and signalling molecules. These benzoxazinoids influence root- and rhizosphere-associated microbial networks, namely the relative abundance and co-occurrence patterns of bacterial groups like Actinobacteria and Proteobacteria, which are gatekeepers to community structure (17).

Plant-plant interactions

The coexistence of two or more plant species leads to various forms of communication, both within or between the species, which can be supportive or intensely competitive. These interactions are mediated by chemical signalling as well as

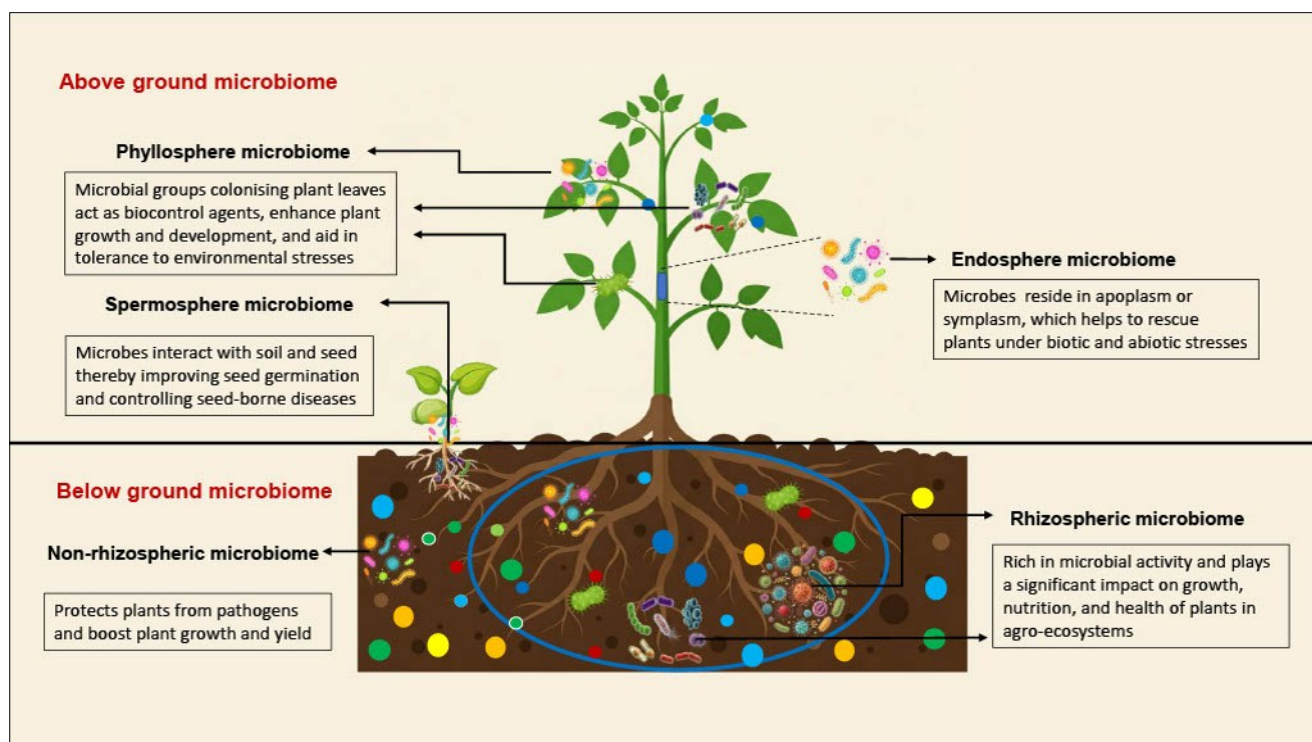


Fig. 1. The plant microbiome interactions with various microbiota in aboveground and belowground and its function (10).

physical variables, including light interception and root overlap. Chemically mediated plant-plant interactions are fundamental variables in species interactions, niche differentiation and the formation of plant communities throughout ecosystems, according to an expanding array of evidence. Allelopathy and allelobiosis, which both depend on the synthesis and release of specialised metabolites into the surrounding environment, are the traditional frameworks for chemically mediated plant-plant interactions (18).

Microbiome-plant interactions

The plants harnessing microbiomes that coexist with them and help defend plants against diseases by competing with pathogenic bacteria, producing antimicrobial compounds and stimulating the immune system of the plant to attack the bacteria (19). These positive interactions are due to a heterogeneous and dynamic set of microbes and individual microbes are metabolically related to each other, which results in a community-scale net metabolism that includes several microbial trophic levels and functional groups (20). Mutualistic relationships, e.g., rhizobia and arbuscular mycorrhizal fungi (AMF) in leguminous plants, illustrate this metabolic integration in which coordinated microbial activities increase the biological fixation of nitrogen and phosphorus uptake increasing the productivity of the host and influencing the structure of plant communities in nitrogen-limited habitats (21). These tripartite interactions between microbes, plants and microbes in a more general sense show how interactions between microbes and their hosts are essential to the development of individual plants but also the diversity of plant species and health of ecosystems of natural environments.

Sustainable agronomic practices that shape microbiome

Sustainable agriculture mainly focuses on optimal use of on-farm resources such as farmyard manure (FYM) and crop residues, while minimising the use of non-renewable inputs such as synthetic fertilisers and agrochemicals. This method is environmental friendly, economically viable and increases the living standard of rural communities (22). In this system, a wide range of microorganisms is contributing for nutrient acquisition and plant health via rhizospheric, endophytic and phyllospheric associations, including both symbiotic and free-living microbial interactions. Beneficial bacteria are used as bio-pesticides and bio-fungicides to protect plants, highlighting their importance in developing sustainable agroecosystems (23).

Sustainability also requires integrated farm waste management and use of animal manures which reduce the use of external agrochemicals. In this instance, production risks are minimised by planting crops that include cereals, oilseeds and pulses including rice, soybean and green gram that are adapted to the prevailing climate and water supply levels (24). These practices enhance biodiversity and improve the ecological balance of the soil. Some of the methods employed in sustainable farming systems include agroforestry, intercropping, crop rotation, green manuring, conservation tillage, use of cover crops as well as biofertilisers (22). The detailed processes by which sustainable farming practices shape the microbiome is discussed in the below sections.

Conservation tillage and soil microbial communities

Conservation tillage practices like no-tillage, reduced tillage and strip tillage reduce disruption of soil when compared to traditional

intensive tillage and a high level of impact on soil microorganisms. Reduced tillage causes microbes dwelling in layers to accumulate organic matter close to the soil surface and maintain soil structure in good condition. Similarly, it has a substantial effect on the bacteria community of the soil (25). No-tillage alters the microbial communities in the soil radically because it ensures that the habitats remain uninterrupted and the carbon sources are increased at the soil surface. Experiments repeatedly show higher microbial biomass and fungal dominance and enhanced microbial functional diversity when no-till is used in place of conventional tillage (Fig. 2). Farming methods that conserve soil have an impact on soil and bacteria in rice-wheat-green gram farms in eastern Indo-Gangetic Plains. Beneficial bacteria that help with nutrient cycling and soil health enhanced by the combination of reduced tillage, residue retention and crop diversification. These results are stronger in the farms that have used conservation agriculture longer (27). In detailed field study comparing conventional and organic management under different tillage intensities, it was observed that soil bacterial communities were primarily structured by tillage, root-associated bacteria were more strongly influenced by management type while soil fungal communities responded primarily to management type with additional effects by tillage. For example, the close clustering of these samples in the ordination is reflected in the high number of soil bacterium operational taxonomic units (OTUs) that were shared between the intensive tillage. Two OTUs from the genus *Gibberella* (fOTU57 and fOTU32, family Nectriaceae) that were sensitive to tillage intensities and had greater abundances in samples with no and reduced tillage were noteworthy among soil fungi (25).

Intercropping and plant diversity effects

Intercropping is the simultaneous growth of two or more types of crops in the same field and it leads to greater variety of plants and creates a much more complex environment for rhizospheres,

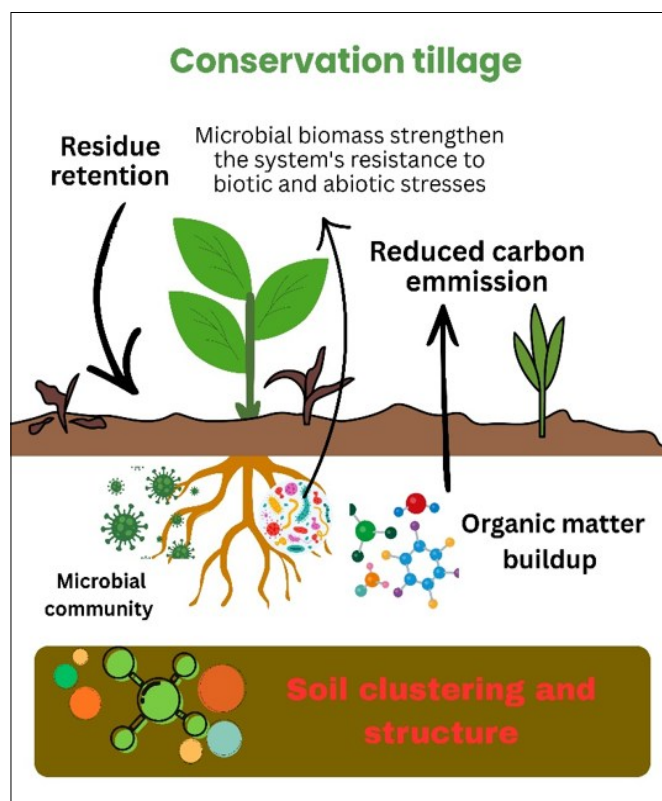


Fig. 2. Effects of conservation tillage practices on soil microbial communities (26).

which increases the number and diversity of microorganisms within the rhizosphere. While the presence of many different plants growing closely together creates greater diversity in the microorganisms found in that intercropping environment and allows for greater functional diversity among those microorganisms due to their spatial cohabitation (28). Intercropping also facilitates environments, which enable microorganisms to facilitate ecosystem services, reduce effects of pests and diseases and enhance how crops utilise the resources within their environment. The addition of legumes in intercropping systems, helps to enhance nitrogen content in the soil and diversity of the microorganisms in rhizospheres. Legumes have been found to alter the chemical property of soil and root exudates, which enhance the microbial communities present in the soil (29). For example, planting legumes alongside sugarcane would be able to improve the properties of the soil and the microbial diversity present in the soil without negatively affecting the sugarcane yield (30).

The processes of solubilisation of zinc in soils by microorganisms may increase the availability of zinc in soils by approximately 25 % in intercropping systems of maize or chickpea because the roots of legumes release the organic acids and phytosiderophores, which chelate and make zinc more available to the crops. In a same way, the root-exuded chemicals and microbial siderophore activity, which are particularly beneficial under alkaline soil conditions, lead to a 30 % increase in the iron uptake when wheat and lentils are interplanted (31). These agronomic practices may also enhance the synergistic gains and achieve improved soil resilience and sustainable intensification. Plant interactions in different populations can result in the creation of emergent characteristics that influence microbial assemblages. These complex relationships need to be understood to design efficient intercropping systems that can optimise the benefits of microbes (32).

Microbial diversity and cover cropping

One farming practices that could contribute to sustainable agriculture is cover crops which include legumes, Brassicaceae, cereals and other broadleaf plant species. Studies indicate that green manure such as cover crops have the potential to improve crop yield and recycling of nutrients. They may also enhance the biological health of soil by ensuring that it is a favourable environment to the growth of useful soil bacteria (33, 34). Soil fertility, structure and biota may all be significantly altered by cover crops, especially when they are incorporated back into the soil. Higher microbial biomass, enhanced microbial enzymatic activities and consistency of relative abundances within bacterial taxa are only a few of the positive effects of cover crops on the soil microbiome that have been studied (35).

Recent findings indicate that the effect of cover crops on the soil microbiome could help decrease infections from plant-parasitic nematodes. The use of resistant *Brassica* species for cover crops has been shown to influence the bacteria and fungus that infect cysts, consequently affecting the infectivity of the *Heterodera schachtii* nematode population (36). Cover cropping in maize field experiments conducted in Germany showed several advantages. These benefits arise from an extended period of vegetation cover, an increase in nitrogen-fixing bacteria and changes in local soil conditions caused primarily by root exudates. The root exudates, contribute to increased carbon inputs into rhizosphere. Diversity in cover crops increases the availability of

carbon and promotes soil microorganisms during the cover crop growth period (37).

Irrigation management and microbial population

Irrigation methods like flood, drip and sprinkler systems affect how water is spread in the soil and how much water is available, thereby controlling microbial diversity, composition and interactions (38). Compared with flood irrigation, deficit and drip irrigation systems often promote distinct bacterial communities and a more even distribution of bacterial taxa. These conditions favour oligotrophic bacterial taxa like *Actinobacteria* and *Acidobacteria* to grow, while decreasing the prevalence of copiotrophic species like *Proteobacteria* and *Bacteroidetes*. The depth of the soil also makes a difference. The top layer (0–5 cm) of soil below the surface changes a lot when the moisture levels change. Deeper layers of soil (15–25 cm) are dominated by the types of microbes that can withstand stress. The quality of the water used for irrigation is also important. The use of treated wastewater, it can introduce types of microbes to the soil, some of which might be harmful while others might be helpful. When we use deficit irrigation it helps the types of microbes that can survive with water like *Actinobacteria* and *Firmicutes*. It hurts the types of microbes that need more water, like *Proteobacteria*. This makes the soil around the roots can enhance rhizosphere more stable (39).

Drip irrigation systems, especially when used with film mulching help keep the soil moist and reduce the salt levels and pH compared to flood irrigation which also creates an environment for microbes to grow, especially in dry areas. However, drip irrigation can also limit how far the roots can spread and the amount of biomass they can produce. This reduces the amount of food for the microbes, which can affect the whole ecosystem (40). Studies on microbial network (Table 1) show that drip irrigation supports a wider variety of microbes but flood irrigation supports a core group of microbes that work well together and are important, for the carbon and nitrogen cycles.

Addition of organic amendments

Organic amendments contain carbon and nutrients that enable the microorganisms to survive in the soil and make the soil healthier. The quantity and composition of organic amendments introduced into the soil may have an influence on the small microorganisms which reside in the soil. It explains how some compounds favour microbial consortia based on their chemical composition, carbon : nitrogen (C : N) ratio and decomposability (43). The use of biochar is one of the most successful microbial management strategies of the phyllosphere and rhizosphere, through the amplification of microbial populations. Biochar is a carbon-dense by-product produced through the pyrolysis of agricultural waste products which makes the soil better in many ways. Because of its large surface area, high porosity and stable chemical properties, it effectively enhances soil structure, promotes nutrient retention and cultivates microbial species (44). Experiments in rice production systems indicate that the use of biochar reduces crop failure by controlling the taxonomic composition of soil microorganisms. The diversity of the soil bacterial population rose when biochar was added, but it was reduced when biochar was applied excessively. In contrast, higher biochar concentration applications result in the richest and most diverse soil fungal communities (45).

Table 1. Impact of different irrigation methods on microbial population and microbial diversity

Irrigation type	Enriched taxa	Reduced taxa	Effect on microbial diversity	References
Flood irrigation in rice fields	<i>Actinobacteria</i> , <i>Proteobacteria</i> and <i>Latescibacteria</i>	<i>Firmicutes</i> , <i>Planctomycetes</i> and <i>Cyanobacteria</i>	Decrease in the diversity	(41)
Furrow irrigation in maize-tomato rotation	<i>Acidobacteria</i> and <i>Gemmatimonadetes</i>	<i>Actinobacteria</i> and <i>Proteobacteria</i>	Optimum diversity	(38)
Sub-surface drip irrigation (SDI) in maize-tomato rotation	<i>Actinobacteria</i> and <i>Acidobacteria</i>	<i>Gemmatimonadetes</i>	Shifts decrease in diversity	(38)
Drip irrigation in cotton	<i>Actinobacteria</i> and <i>Acidobacteria</i>	<i>Proteobacteria</i> and <i>Bacteroidetes</i>	Increase in the diversity / slightly decrease in richness	(40)
Drip irrigation wheat - maize rotation	<i>Actinobacteria</i> , <i>Acidobacteriota</i> and <i>Methyloirabilota</i>	<i>Gemmatimonadota</i> , <i>Myxococcota</i> and <i>Chloroflexi</i>	Increase in the diversity / slightly decrease in richness	(42)

When organic amendments are applied, soil microbial communities experience unique temporal dynamics that are mostly affected by the availability of labile carbon. These dynamics are characterised by an initial quick surge in activity followed by long-term stabilisation. Long-term improvements in soil health and productivity can result from cumulative changes in soil organic matter pools and microbial community composition brought about by repeated treatments over several years (46).

Integrated nutrient management (INM)

To maximise nutrient availability and increase crop productivity while enhancing beneficial microbial communities, INM is a comprehensive strategy that combines the incorporation of chemical fertilisers, organic manures, biofertilisers and crop residues (47, 48). Overuse of synthetic fertilisers, especially the addition of urea as soil fertiliser, raises pH initially because of urea hydrolysis and later lowers pH because of ammonia (NH₃) oxidation. According to reports, soil pH is the most important element regulating the makeup of soil bacterial communities among biomes and creating differences in niche specialisation among soil microbes (49). At the same time, more diverse microbial communities with more functional capacity are facilitated by balanced nutrient management that includes organic sources. Long-term nitrogen fertiliser generally lowered the pH of the soil, reducing bacterial diversity and changing the composition of the community to include less diverse but acid-tolerant species. The obtained production decline under high nitrogen input was probably caused by these microbial changes that impacted nutrient cycling capacities (50).

The way we use phosphorus is important for a type of fungus called mycorrhizal fungi. These fungi are essential for plants to get the phosphorus when they need. If we use much phosphorus fertilizer, it can inhibit these fungi from colonisation, reducing the positive aspects of these interactions (51). The nature, time and quantities of nutrient intakes influence the responses of the microbial population. Although it is true that boom-bust cycles of microbial populations can arise due to blend application of the readily available nutrients, slow-release fertilisers and organic amendments offer a constant supply of nutrients and this can support sustainable microbial communities. A variety of sources of nutrients and adding it at different times should be used to maintain the communities healthy and working well depending on the needs of the crops. This aids in maintaining the microbes as stable and in good operation (52, 53).

Mechanisms of plant-microbiome interactions

Plant-microbiome interaction can influence the crop resilience

and performance through chemical signalling, symbiotic exchanges of nutrients, immunological control and stress-adaptation pathways. Root exudates, which are composed of organic acids, amino acids, sugars and secondary metabolites, are essential chemical signals, carbon sources and chemo attractants that regulate microbial community organisation as well as promote root colonisation in the rhizosphere (54, 55). Plants use specific exudates like flavonoids, coumarins and amino acids to inhibit phytopathogens and attracting beneficial microbial communities like rhizobia, AMF and plant growth promoting rhizobacteria (PGPR), plants can "filter" their microbial partners. Additionally, it has been demonstrated by integrative analyses of metabolites (metabolomics), rhizobacterial communities (metagenomics) and RNA transcripts (transcriptomics) that root exudates actively regulate bacterial consortia to improve nutrient acquisition, stress resistance and disease defence in addition to responding to environmental stimuli (56).

At the symbiotic interface, rhizobia and legumes produce nodules and many crops develop arbuscular mycorrhizal associations, wherein densely branched fungal arbuscules or bacterial bacteroids exchange fixed nitrogen or mobilised phosphorus for carbon derived from plants (57). These symbioses increase the effective root absorptive surface, which improves nutrient and water use efficiency (WUE) under limiting conditions by increasing the uptake of relatively immobile nutrients and water from beyond depletion zones (58). Associative nitrogen fixers, phosphate-solubilising bacteria and siderophore makers, which mobilise nutrients by organic acid secretion, chelation and enzyme formation, all indirectly improve plant nutrition (59).

Systemic acquired resistance (SAR) or induced systemic resistance (ISR) is activated by microbial initiators and microbe-associated molecular patterns that are established by the plant immune system. To prime defence genes and improve protection in distal tissues without incurring significant metabolic costs, beneficial rhizobacteria and fungi primarily activate the ISR through the jasmonic acid and ethylene pathways (60). In contrast, pathogen infection causes SAR, which is marked by the buildup of salicylic acid and long-range mobile signals that frequently interact with the microbiome structure in leaves and roots. This immunity-tolerance balance can be adjusted by root-derived compounds, which suppress extreme reactions while permitting mutualists to be accommodated steadily (61).

Microbiome-mediated stress tolerance involves ion homeostasis, osmotic adjustment, antioxidant defence and control of plant hormone profiles under drought, salinity, heat and heavy-metal stress (7). Drought-adapted microbial taxa and AMF

help to improve the root architecture of plant, hydraulic conductivity and osmolyte accumulation in water-limited environments, protecting photosynthesis and reducing oxidative damage (62). Microbes that generate siderophores and exopolysaccharides helps to improve soil aggregation, facilitate balanced intake of essential nutrients and immobilise or sequester ions under hazardous or saline conditions (58). The schematic representation of overall mechanism of plant microbiome interactions presented in Fig. 3.

Climate resilience in microbiome-mediated ecosystem services

The crop-associated microbiome, including the phyllosphere, endosphere and rhizosphere, is generated through the combined activities of bacteria, fungi, protozoa and archaea and performs a broad spectrum of ecological functions. Some of these functions are nutrient cycling, maintenance of soil structural health, pathogen control, modulation of plant stress responses and control of GHG fluxes, which are of critical importance in climate-smart agriculture (2). The agroecosystem level is the interaction of the soil and rhizosphere microbiome with carbon, nitrogen and water fluxes by functioning as a biological interface between plants and soil-atmosphere system (63). Microbiome driven activities can preserve ecosystem multifunctionality by reducing impacts of climate change, including warming, changes in rainfall patterns and extreme events (64).

Increased nutrient use efficiency (NUE)

Sustainable agriculture requires the improvement of nutrient use efficiency (NUE) because it reduces the use of fertiliser, minimises environmental pollution and maximises farm profitability. Crop microbiomes can enhance NUE in different ways, including biological fixation of nitrogen, solubilisation of phosphates,

mineralisation of nutrients by organic matter and increased nutrient uptake by an increased root surface area. These microbiome-mediated processes can be enhanced by sustainable agronomic systems that can greatly improve NUE without the need of relying on synthetic fertilisers (65).

A large quantity of nitrogen input into agroecosystems is provided by biological fixation of nitrogen by rhizobia on the root nodules of legumes and by free living diazotrophs on soil and plant tissues. Crop rotations that incorporate legumes can be of great benefit in terms of nitrogen to the crops that occur after them because of decomposition of the residues and increased pools of nitrogen in the soil (66). Management practices such as tillage, organic supplements and crop rotation influence the diversity and activity of fixation of nitrogen by the nitrogen-fixing bacteria and hence there is the opportunity to increase the biological fixation of nitrogen. Much of the phosphorus present in agricultural soils exists in forms that are not readily available to plants. Phosphate-solubilising bacteria and fungi can improve the availability of phosphorus by synthesising organic acids, phosphatases and other compounds which releases phosphorus in both inorganic and organic pools (67). Crop rotations have been shown to alter the genes that are involved in the phosphorus metabolic processes within the soil microbiomes; even certain rotations have been shown to enhance the ability to mineralise organic phosphorus (68). The presence of diverse microbial communities to recycle phosphorus can be used to increase the efficiency of phosphorus utilisation and reduce fertiliser requirements. Besides, crop rotation of rice-oilseed under the same conditions contains much more accessible phosphorus content compared to rice-wheat rotation. This observation states that microorganisms were more capable of mineralising phosphorus in the rice-oilseed rotation compared with the

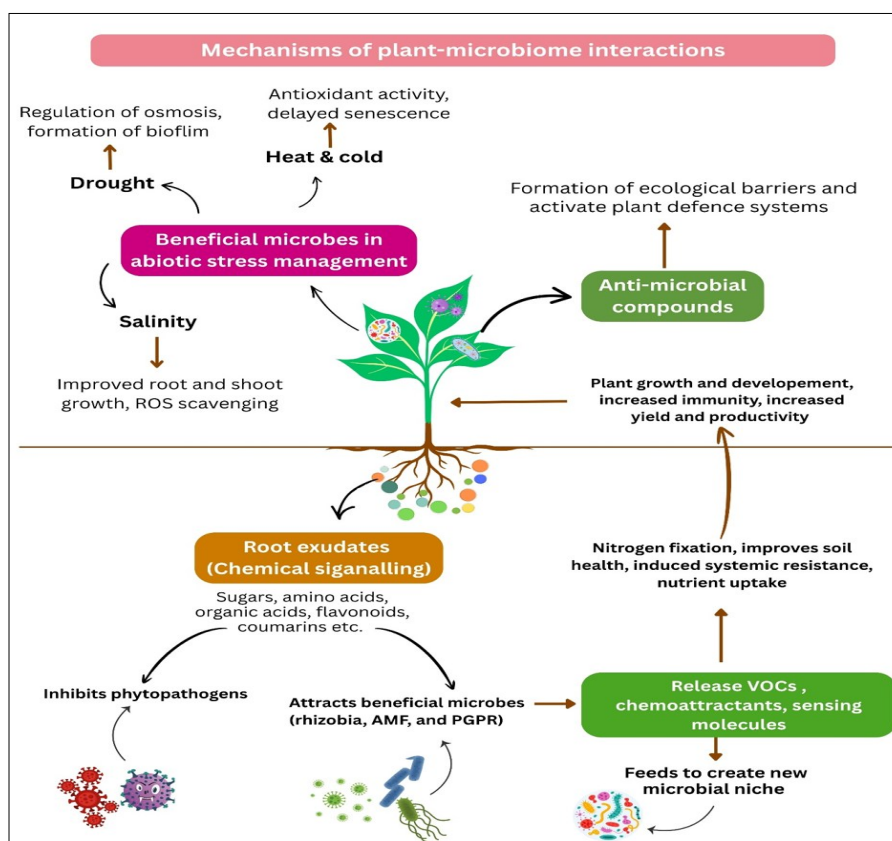


Fig. 3. The overall mechanism of plant microbiome interactions (15, 58, 60).

AMF: arbuscular mycorrhizal fungi; PGPR: plant growth promoting bacteria; VOCs: volatile organic compounds.

rice-wheat rotation (69). Siderophore producing bacteria increase the availability of iron in iron restricted environments and other bacteria employ chelation and redox processes to mobilise zinc, manganese and other micronutrients (70). The process of controlling a series of microbial communities which complement each other in terms of nutrient cycling can enhance crop nutrition and general nutrient utilisation efficiency.

Plant immunity and disease suppression

Crop microbiomes are beneficial in the inhibition of plant diseases in different ways, such as competitive removal of pathogens, synthesis of antimicrobial compounds, direct antagonism and stimulation of plant resistance. These microbiome-mediated disease suppression technologies can offer a sustainable alternative or supplement to synthetic pesticides by reducing environmental impacts and increasing crop protection. One of the important prospects of sustainable agriculture is the understanding and control over disease-suppressive microbiomes (71). The rhizosphere microbiome suppresses pathogens by competing with them through resource depletion, secreting antimicrobial chemicals, e.g., antibiotics, lipopeptides, volatile organic compounds and directly antagonising them by mycoparasitism and predation (72). The beneficial taxa are *Bacillus*, *Pseudomonas*, *Trichoderma* and *Penicillium* species which are particularly important in disease suppression. Agriculture can enhance the natural disease suppression capacity by favouring these beneficial taxa (71).

Crop rotation is particularly effective in controlling soil-borne disease as it disturbs the life cycle of pathogens and enhances disease-repressive microbial communities. In comparison to monocropping, it was found that crop rotation formed more successful microbial assemblies that prevented peanut root rot disease (73). Plant diseases may be repressed through cover crops through microbiome processes. Ryegrass rotation improved the advantageous soil microbiota through the OSLRR-RLK-MAPK-WRKY-JA signalling cascade, which directly reduced the infectivity of nematodes and induced the immunity of plants. In addition, it has been demonstrated that the cyclic dipeptide Cyclo(L-Pro-L-Leu), which is produced from *Pseudomonas simiae* strain MB751, exhibits strong nematocidal action against RKN *Meloidogyne incognita*. Similarly, *Bacillus cereus* Bc-cm103's dimethyl disulphide and S-methyl ester butanethioic acid are poisonous and repulsive to *M. incognita* (36). Additionally, some microbial consortia which enhance disease suppression are enlisted by resistant plant types. Experiments on banana cultivars found that resistant cultivars selectively attracted specific taxa of bacteria and fungi, including *Penicillium* and *Trichoderma*, which, in combination, prevented disease. Root exudates (stearic acid and shikimic acid) mediated this selective recruitment. The potential of microbiome-based disease-management methods was evidenced by the fact that these beneficial microbiomes could be transferred between resistant and susceptible types to generate more resistance to diseases (74). This shows that cover crops have the potential to influence diseases both directly and indirectly via immune priming and regulation of the microbiome.

Abiotic stress tolerance

Environmental stresses such as water deficiency, salt, extreme temperatures, nutrient availability and metal toxicity are likely to be worsen by climate change which intensely impacting crop production. Plant microbiomes are being used as a natural approach to support this mitigation and build resilience in

agriculture, via multiple mechanisms including the production of compounds protective against stress, regulation of plant hormones, increasing root system architecture and direct effects on pathways regulating plant stress responses (75). Bacteria and fungi can inhabit the roots, stems, leaves and even fruits and seeds of plants, which results in a symbiotic and protective relationship, particularly in drought. Beneficial microbiomes improve plant resilience under drought, salinity and temperature stress by supporting physiological stability and maintaining crop productivity under adverse environmental conditions. In addition, endophytic microbes may also promote the antioxidative defence in the plant, reducing the accumulation of reactive oxygen species (ROS), normally elevated in drought stress. Lowering cellular damage and maintaining cellular structure in the drought like situation, this antioxidative effect also boosts plant drought tolerance (76).

Water use efficiency and drought resilience

Water scarcity is a major limitation to agricultural productivity and climate change exacerbates water stress by altering rainfall patterns and increasing evaporation rates. To support climate-smart agriculture, improving crop drought-resistance and WUE is required (77). The crop microbiomes facilitate WUE and drought resilience in several ways, such as by improving water absorption, reducing transpiration, promoting root growth and activating plant drought response mechanisms (78). Mycorrhizal fungi are important for water relations because they enhance plant water conductance and create a network of hyphae that can access more water in the soil. Arbuscular mycorrhizal fungi colonisation can improve water uptake and alter water relations of the host plant to enhance their tolerance to drought in several crop species. Low-tillage and light phosphorus fertilisation are two cultivation practices that encourage AMF establishment and enhance resistance to drought (79).

Exopolysaccharides are high-molecular-weight polysaccharides produced by microorganisms (particularly bacteria) increase soil aggregation and soil moisture holding capacity, which increases soil water content. These bacteria also form biofilms on the roots enhancing water absorption and preventing dehydration (80). No-tillage, cover cropping, organic fertilisers and crop rotation all have been shown to boost soil microbial activity and diversity, resulting in improved soil fertility and structure and WUE (81). These practices also influence the number of bacteria that produce exopolysaccharide. Similarly, cover crops enhance water circulation in soil through several mechanisms including soil structure, evaporative loss and water infiltration. These benefits are in turn supported by the microbes associated with cover crops by producing chemicals which bind the soil and promote aggregation (82).

During drought stress, many 1-aminocyclopropane-1-carboxylate deaminase (ACC) deaminase producing PGPR strains in effect increase growth of various plants by reducing ethylene and preventing stress-induced growth arrest and maintain root growth to enhance water uptake. These bacteria also increase the production of osmoprotectants and antioxidants to increase plant tolerance to the stresses induced by the water deficit (83). Furthermore, the field study on *Ocimum basilicum* L. indicates that the microbial consortium, consisting of a mixture of PGPB and *Trichoderma* with ACC deaminase activity, enhances plant productivity and soil fertility, promotes growth and reduces drought stress, as well as the concentration of stress ethylene and malondialdehyde (MDA) (84). A summary of interactive effects of

plant microbe association on nutrient uptake, plant growth and crop performance on various crops is presented in the Table 2.

Greenhouse gas mitigation and carbon sequestration

The agricultural sector is a major source of GHG through carbon dioxide loss as soil carbon, emission of nitrous oxide from fertiliser application and methane release from cattle and rice production. However, carbon dioxide emissions from agriculture can be mitigated by soil carbon sequestration enhanced in agricultural ecosystems. The crop microbiome plays a key role in the production of GHGs and carbon sequestration and represents an opportunity for microbiome manipulation to tackle climate change (90). The balance between carbon addition (residues, root exudates) and carbon removal (respiration, degradation) is strongly influenced by the microbial community composition. In addition, microbial communities with more fungi tend to be associated with more carbon storage because fungal communities produce complex carbon compounds such as lignin-derived substances and promote stable soil aggregate formation, which enhances long-term carbon storage (91).

Cover crops fix atmospheric carbon dioxide and increase soil structure and diverse crop rotations increase carbon inputs over time, avoiding carbon losses. Organic amendments support aggregate and carbon stabilisation, through increased microbial biomass, availability of carbon substrates and aggregate formation (92). Conservation agriculture practices rebuild stable soil organic matter pools with microbes that stabilise carbon through increased organic carbon inputs. Higher biomass production and production of extracellular polymeric substances that aggregate soil particles into stable aggregates, which physically protects organic matter from decomposition are the mechanisms (93). Soil nitrous oxide emissions are a major source of GHGs with a high global warming potential. Emission is controlled by microbial processes like nitrification and denitrification, the level of nitrogen fertilisation, soil water content and the microbial community structure (94).

Knowledge gaps and future perspective

The study of plant microbiomes is rapidly evolving but still has to overcome several limits to be applied for climate-smart agriculture. It is difficult to predict how reduced tillage, rotation, cover crops, irrigation and organic inputs affect microbes in different soils and climates because a large part of this research is site specific, short term and focuses on specific practices or crops. There are less long-term, multi-zone experiments in tropical and smallholder agriculture, where climate risk is greater. Also, there are disconnects

between process understanding and descriptive omics. While investigations of changes in microbial diversity and functional genes under sustainable management are common; there remains a need for practical validation of their relationships with NUE, resistance to pests and diseases, stress tolerance, carbon sequestration and greenhouse mitigation.

Existing technology of microbiome engineering (e.g., single-strain inoculant, simple consortia, or generic biofertiliser) shows high biotic competition, inconsistent establishment and limited yield or resilience improvements in different environments and seasons. The rationale of establishing microbial consortia that are compatible with certain cropping systems, soil constraints and management practices (e.g., no-till with high-residue cover crops (e.g., wheat, rice) versus intensive vegetable production with drip irrigation) is unclear. Adverse or negative interactions of inoculants with other agronomic techniques such as fertiliser, water or residue management, which are finely tuned in combination may occur.

Research should focus on 5 main areas for microbiome-based climate-smart agriculture. First, conduct long-term and multi-site trials that monitor changes in the microbiome in addition to yield, nutrient efficiency, soil carbon and GHG before and after evidence-based trials of methods such as tillage, crop rotation, cover crops, organic soil amendments and irrigation. Second, integrate direct measurements and models with multi-omics data (such as metagenomics and metabolomics) to develop predictive tools and key microbiome indicators that link to performance. Third, create crop- and farm-specific microbiome consortia (such as stress-tolerant microorganisms for dry irrigation or AMF-PGPR sets for no-till legume rotations) to ensure they are well adapted in the field. Fourth, ensure microbiome traits are incorporated in crop breeding for cultivars that work in partnership with beneficial microorganisms such as mycorrhizae and those that exude beneficial compounds. And finally, to support policies that recognise the value of microbial services, ensure fair compensation of our invisible partners, integrate microbial factors into farm management, carbon credits and soil health.

Trade-offs and context dependence

The beneficial aspects of microbiome-mediated practices are claimed but not always. For instance, organic amendments and inputs of nitrogen-rich residue can encourage beneficial microbial processes and enhance soil carbon cycles but can also accelerate denitrification and increase nitrous oxide emissions in poorly oxygenated or nitrogen-fertilised soils. Similarly, drip irrigation can promote certain microbial groups adapted to drought and

Table 2. Interactive effects of plant microbe association on nutrient uptake, plant growth and crop performance

Plants	Microbial association	Effects	References
Rice	<i>Bacillus</i> sp., <i>B. megaterium</i> (PB50), <i>B. altitudinis</i> (FD48), <i>Azotobacter chroococcum</i>	Increase IAA, GA and ABA content in plants, enhance N fixation, facilitate stomatal closure and promote plant growth, inflorescence and seed growth	(85, 86)
Wheat	<i>Bacillus subtilis</i> , <i>Azospirillum brasilense</i>	Secrete IAA, GA, CK and ABA to promote plant growth and increases phosphorus uptake	(56, 87)
Maize	<i>Pseudomonas fluorescens</i> , <i>Bacillus subtilis</i> , <i>Arthrobacter arilaitensis</i> (MG547869)	Increased N uptake, improved plant growth and root elongation	(88)
Soybean	<i>Pseudomonas putida</i> H-2-3 sp.	Induced tolerance against abiotic stress	(22)
Cotton	<i>Pseudomonas putida</i>	Promotes better plant growth and pest resistance and enhances nitrogen fixation	(56)
Pearl millet	<i>Bacillus amyloliquefaciens</i> (MMR04)	Improve seed germination and seedling vigour, regulate ethylene content	(88)
Bengal gram	<i>Mesorhizobium</i> sp.	Enhance nutrient acquisition, drought tolerance and increase the yield	(22)
Mung bean	<i>Pseudomonas aeruginosa</i>	Secrete ACC deaminase, inhibit ethylene synthesis	(89)

IAA: indole-3-acetic acid; GA: gibberellic acid; ABA: abscisic acid; CK: cytokinin; N: nitrogen; ACC: 1-aminocyclopropane-1-carboxylate.

enhance WUE, but limited wetting fronts can suppress root proliferation and affect microbial interactions in ways that may limit ecosystem function. High phosphorus fertilisation levels may prevent arbuscular mycorrhizal colonisation, while excessive levels of biochar may not always have a positive effect on the diversity of microorganisms. The examples highlight the need to think of microbiome management as a dynamic balance, influenced by the crop species, soil characteristics, climate and intensity of inputs.

Conclusion

The microbial communities associated with crop plants are key mediators between agronomic management and the three dimensions of climate-smart agriculture productivity, resilience and mitigation; as suggested by the literature reviewed here (Fig. 4). Physical soil conditions, organic inputs, plant genomes and the water and nutrient cycles, which are influenced by management practices, impact on ecosystem functions and crop productivity. This in turn provides altered biomes in the rhizosphere, endosphere and phyllosphere. Across different agroecosystems, sustainable agricultural practices promote diverse and functionally active microbiomes, which reshape microbial communities in ways that improve nutrient cycling, plant health, stress tolerance and soil carbon dynamics. However, the effectiveness of microbiome-based strategies varies across environments and management systems, highlighting the need for context-specific approaches. Future research should prioritise long-term, multi-location studies integrating multi-omics tools with field-level validation. Additionally, understanding trade-offs such as greenhouse gas emissions and inconsistencies in microbial inoculant performance is essential. Advancing microbiome engineering, integrating microbial traits into crop breeding and developing predictive models will be key to achieving sustainable intensification and climate-resilient agriculture.

Authors' contributions

KS wrote the original draft of the text. HC made recommendations for overall adjustment and improvement. RB, SR, MB and TR helped with literature collecting and formatting. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Grammatical service to improve the spelling and grammar of the article. Biorender was used for making the pictorial presentation. After using these tools/services, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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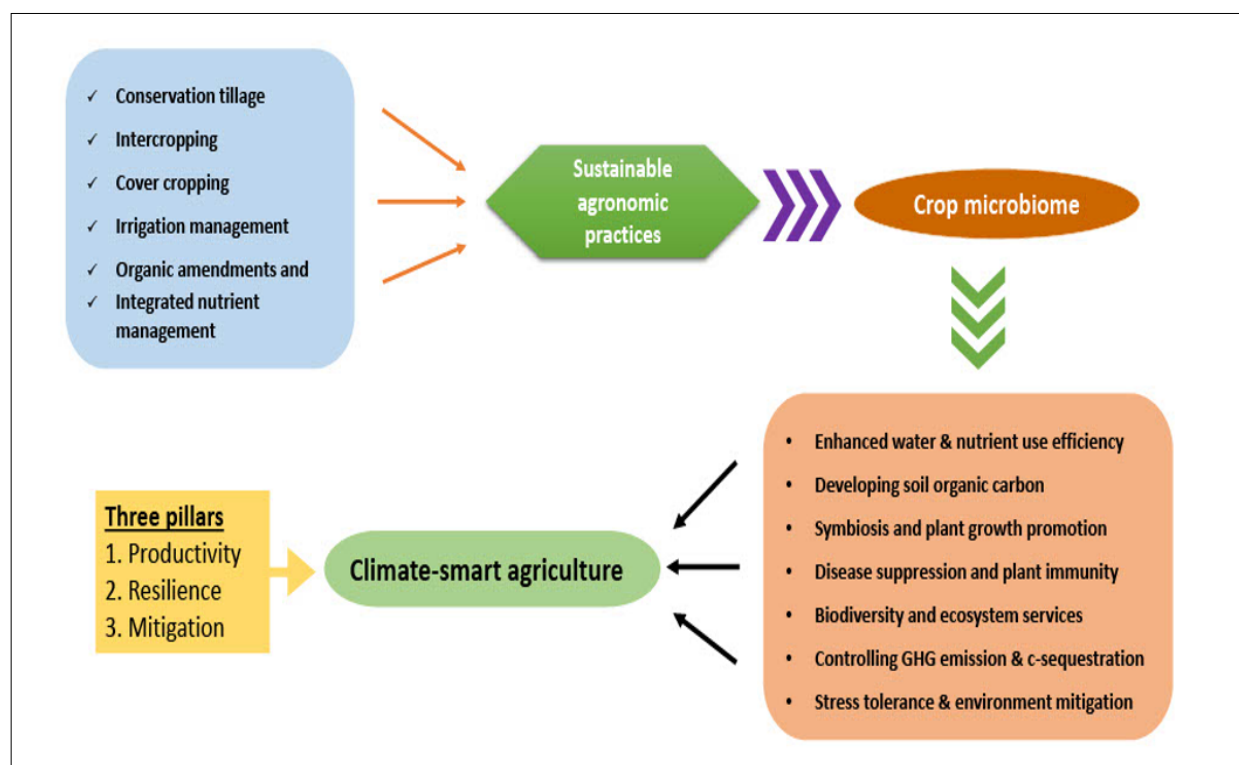


Fig. 4. Three pillars of climate-smart agriculture include productivity, resilience and mitigation. Sustainable agronomic practices balance the different steps in the biogeochemical cycles to builds a crop microbiome, which is the intrinsic player in nutrient recycling, symbiosis and plant growth and development. Through various physiological process crop microbiomes pays the way for three pillars of CSA to strengthen sustainability and environmental health (2).

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