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REVIEW ARTICLE

A comprehensive view to deciphering of beneficial microbes' status - A review

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Abstract

Even with advancements in technology, rapid population growth, soil degradation, loss of soil nutrients and a scarcity of food supply coupled with high demand are intensifying global crises like mortality, malnutrition, the rise of new diseases and widespread hunger. Consequently, global scientific efforts are increasingly focusing on using microorganisms in agriculture and related fields, often referred to as "green" or "organic agriculture." This approach encompasses a wide range of microbial applications, including biocontrol agents, biofertilizers, biopesticides and fermenters. It also leverages synthetic additives (e.g., *Saccharomyces*, *Penicillium*, *Aspergillus*), microbes for bioenergy and biogas production (*Proteobacteria*, *Actinomycetes*, methanogenic *Archaea*) and for enhancing nutrient content in foods (e.g., rice, maize, wheat). Furthermore, microorganisms are crucial for developing vaccines and medicines (*Clonorchis sinensis Streptomyces spp.*, *Saccharomyces cerevisiae*, *Penicillium chrysogenum*) and facilitating bioremediation processes (*Agaricus bisporus*, *Ganoderma lucidum*, *Phlebia radiata*). These beneficial microbes are utilized based on their unique biometabolic pathways, offering a natural and eco-friendly solution that helps maintain food safety and ecological balance.

Keywords : *Aspergillus* spp; *B. cereus*; *C. sinensis*; *Nitrosomonas*; *Pseudomonas*; *S. marcescens*

Introduction

Worldwide, a rising population is driving demand for sustainable food production, making its effective distribution a critical challenge. However, in recent decades, while the global population has soared, food production has rapidly declined in both quantity and quality. This decline is largely due to the modernization of agriculture that often neglects native crops and sustainable practices. Such trends negatively impact the health of current generations (1). With the advent of globalization, the use of chemical fertilizers, pesticides, synthetic growth nutrients and pre-mixed chemical solutions significantly increased. This surge directly affected crop production and created an imbalance within natural ecosystems. For instance, only a tiny fraction (2 %) of the nitrogen used in agriculture globally comes from biological methods, while a substantial 40 % relies on chemical fertilizers. This heavy reliance has degraded natural resources, leading to infertile soil, reduced cropping diversity and the displacement of native crop varieties. It has also indirectly altered food supply chains, impacted natural habitats and accelerated changes in allied agricultural sectors.

Over the past fifty years, the combined effects of population growth and environmental damage have contributed to the emergence of new human diseases (representing 40 % of such diseases), often by altering pathogen behavior within crop ecosystems. Therefore, sustainable alternative strategies are crucial to maintain agricultural output without compromising food quality or quantity (2). Building on this pressing need, this review will summarize the importance, current status, principles and applications of beneficial microbes in agriculture, along with highlighting the significance of natural sources and their role in human health.

Current status

In natural ecosystems, organisms that benefit humans through agriculture and allied sectors are termed beneficial organisms. Historically, this category included certain bacteria like *Lactobacillus* species and yeasts such as *Saccharomyces cerevisiae*, which were crucial for fermentation processes in the dairy and wine industries. More recently, a wider range of microbial species has been recognized for their diverse applications. In agriculture, these include biofertilizers (*Azotobacter*, *Nitrosomonas*, *Nitrobacter*, *Azospirillum*, *Nostoc*, blue-green algae, *Rhizobia* species), biofungicides (*Trichoderma* species, *Bacillus* species, *Pseudomonas* species) and biopesticides (*Bacillus* species, *Pseudomonas* species, *Cordyceps* species, *Clonostachys* species and *Beauveria bassiana*). Beyond crop protection and nutrient provision, beneficial microbes also play roles in processes like jute retting (*Bacillus pumilus*), paper industries (*Aeromonas aerogenes*) and bio-fortification (*Bacillus* and *Pseudomonas* species). Furthermore, certain microbes like *Streptomyces* and *Penicillium* species have contributed to vaccine development. These organisms, due to their inherent capabilities, are silently integrated into agriculture and allied sectors with a multidisciplinary approach (Table 1), as further detailed in Fig. 1 (3). Current global research is focused on discovering new beneficial microbes, identifying their bioactive compounds and functional genes and developing efficient culture and mass propagation techniques. This includes exploring non-cultivable microbes through metagenomics to devise affordable and easily applicable methods, ultimately aiming to transfer these innovations from laboratories to farmers through national programs (4).

In agriculture

The crop environment is broadly categorized into two distinct microbial habitats: the phyllosphere, which encompasses the aerial parts of the plant and the rhizosphere, the soil region immediately surrounding the roots. Both zones are crucial for supporting plant growth and development. The phyllosphere is an active site for key plant physiological processes like respiration, photosynthesis, evaporation and transpiration. Within this habitat, various active bacteria, known as endophytes, reside within the plant's internal tissues (both intercellular and intracellular spaces). The diversity and activity of these phyllosphere microbes are significantly influenced by the specific crop genotype and prevailing environmental conditions (5).

Conversely, the rhizosphere is a dynamic interface where roots interact with the soil. It plays a critical role in nutrient uptake, competition against plant pathogens, regulation of plant growth and yield, protection of root infrastructure and the overall maintenance of the rhizobiome (6). Both the phyllosphere and rhizosphere are extensively colonized by numerous bacterial species. These include symbiotic nitrogen-fixing bacteria such as *Rhizobium*, *Bradyrhizobium*and *Mesorhizobium* species, as well as asymbiotic bacteria like *Pseudomonas*, *Bacillus*, *Klebsiella*, *Azotobacter*, *Azospirillum* and *Azomonas* species (7). These bacterial genera exhibit a wide array of eco-survival strategies and plant-beneficial traits. They can acquire plant nutrients from root exudates, synthesize hydrogen cyanide and siderophores, produce various secondary metabolites, induce systemic resistance, generate lytic enzymes, detoxify heavy metals in the soil and stimulate the production of phytohormones. Such capabilities enable them to thrive in the ecosystem by competing for nutrient sources, establishing robust colonization through quorum sensing (cell-to-cell communication), surviving by utilizing available nutrients, modifying soil pH and texture, balancing reactive oxygen species and ultimately promoting overall plant growth and yield (8).

Modern agriculture extensively utilizes a diverse collection of microbes through multidimensional approaches. These applications include their use as biocontrol agents, biofertilizers and sources of pesticidal, herbicidal and nematicidal compounds. Specific examples of their applications include; *Pseudomonas* species, *Bacillus* species, *Ampelomyces quisqualis* and *Trichoderma* species (Biocontrol agents); *Azospirillum*, *Azotobacter*, *Rhizobium* species, *Nitrosomonas*, *Nitrobacter* and Arbuscular Mycorrhizal Fungi (AMF) (Bioferilizers); *Phytophthora palmivora* (used against *Mikania odorata*) and *Colletotrichum gloeosporioides* f. sp. *aeschynomene*; *Bacillus thuringiensis* (Bt), *Beauveria bassiana*, *Clonostachys rosea*, *Metarhizium* and *Paecilomyces* species (Biopesticides) and *Streptomyces avermitilis*, *Bacillus firmus* and *Pasteuria* species (Bionematicides) (9). During crop production, these beneficial microbes exhibit multifaceted mechanisms, contributing significantly to improved crop growth and development by mitigating both biotic and abiotic stresses.

Table 1. Modern applications of beneficial microbes to the better development of agriculture, medicine and environment

Microbes	Sectors	Beneficial traits	Biological functions	References
P. putida, Pseudomonas spp., *P. aeuroginosa, Klebsiella sp., Enterobacter asburiae, Rhizobium sp., Bacillus* spp., *Bradyrhizobium sp., Mezorhizobium sp., Azotobacter sp., Azospirillum amazonense, Nitrosomonas, Nitrobacter, P. jessenii, Proteus vulgaris, Rahnella aquatilis* and *Trichoderma* spp., *B. bassiana, Glomus, Clonostachys* spp., *Serratia marcescens, Saccharomyces* spp. and VAM	Agricultural microbiology	Growth promotion, biotic & abiotic stresses.	Alleviation of seed dormancy, seedling germination, pest & disease resistance, yield induction, postharvest management, salt & drought tolerance	(9, 10)
Lactobacillus, E. coli, Acetobacter, Candida spp., A. bisporus, *V. volvaeae, L. edodes, Pleurotus sp. Spirulina*, *Caulerpa lentillifera* & *Chlorella*.	Food microbiology	Additives & foods.	Biochemicals, organic acids, alcohols, nutritional supplements & foods	(55)
Cordyceps spp., Penicillium spp., *Streptomyces* spp., *Ganoderma* spp., *Trametes versicolor, Inonotus obliquus, Grifola frondosa, Hericium erinaceus*, *A. tumefaciens* & *E. coli*	Pharmacology & Biotechnology	Humans' health & livelihood, Bio-fortified foods.	Pharmaceutics for vaso-relaxants, diabetes, neural disorders, enhancing immunity, nutritional fortified food products.	(56 - 60)
Phlebia radiata, Arbuscular Mycorrhizal Fungi (AMF), *Cupriavidus necator*, *N. frowardii*, *P. chrysosporium* and *A. bisporus*	Eco-conservation	Waste management, Bioremediation in polluted natural resources.	Reclamation from salinity & heavy metals in soil and water sources.	(61)
M. frisius, M. barkeri, M. formicicum, Proteobacteria, Chloroflexi, Firmicutes & *Actinobacteria*	Bioenergy	Biofuel production.	Methanol & ethanol production.	(62)

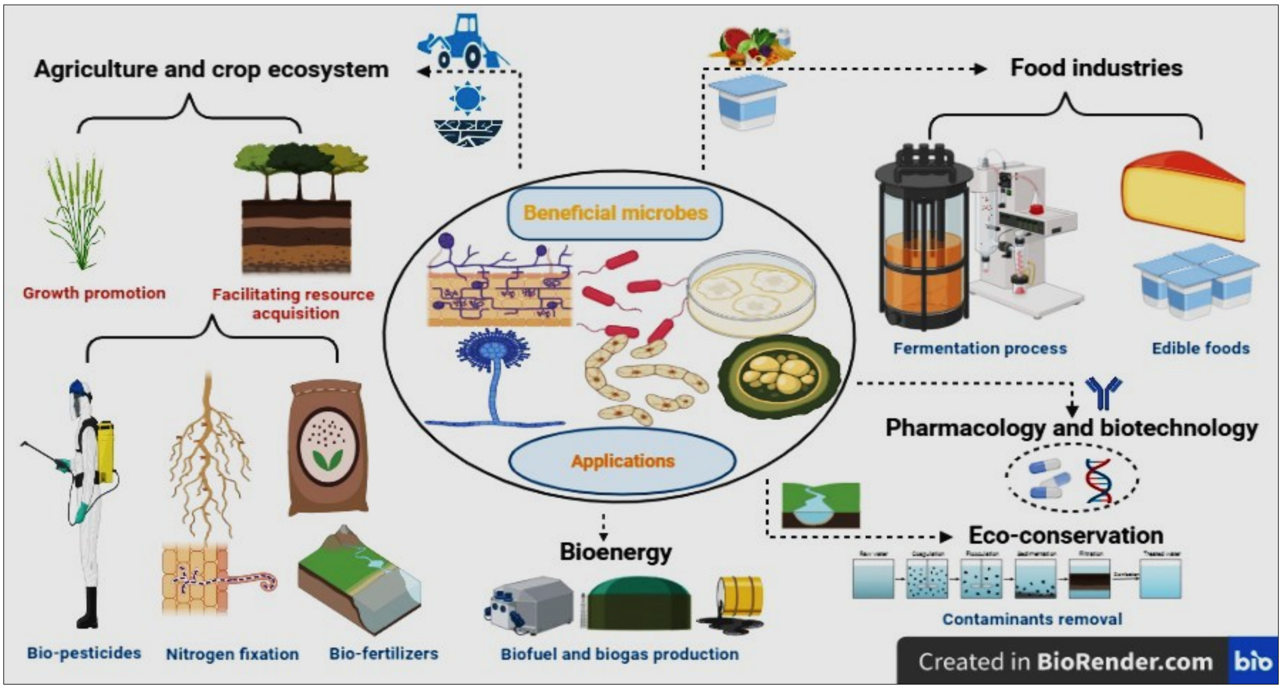

Fig. 1. Multi-dimensional applications of beneficial microbes in livelihood of humans and environment.

Methodology

A detailed review of notable scientific databases, such as PubMed, Google Scholar and Science Direct, was carried out for this study, with an emphasis on papers released in the previous five years. The search utilized specific keywords such as “beneficial microbes and applications’. These approaches give substantial information about the beneficial microbes and their applications, mode of actions and potential uses. Additionally, the gathered resources were studied to obtain key information on beneficial microbes.

Growth promotion

The rhizosphere, the dynamic zone of soil influenced by plant roots, is home to various free-living bacteria that can colonize the root surface (rhizoplane) or even reside within the root tissues (as endophytes). These beneficial microorganisms are collectively known as Plant Growth Promoting Rhizobacteria (PGPR) (10).

PGPR encompass a wide array of bacterial genera, including well-studied rhizobacteria such as *Pseudomonas* (including fluorescent *Pseudomonads*), *Bacillus*, *Rhizobium* species, *Azospirillum*, *Azotobacter* and *Klebsiella*. Beyond bacteria, other microbial groups also contribute to plant growth promotion. These include various actinomycetes, exemplified by *Streptomyces*, *Nocardia* species, *Microbispora*, *Amycolatopsis*, *Actinomadura* and *Saccharothrix* (11). Furthermore, diverse yeast species are found in the rhizosphere, which can be broadly categorized into pigmented yeasts (e.g., *Saccharomyces* species, *Cystobasidium*, *Rhodotorula*, *Rhodosporidiobolus*, *Sporobolomyces* and *Vishniacozyma* species) and non-pigmented yeasts (e.g., *Bannozyma*, *Colacogloea*, *Curvibasidium*, *Serratia* species, *Hamamotoa* and *Oberwinklerozyma*) (12). In fertile or managed soils, the population density of these beneficial microbes typically ranges from 10^8 to 10^9 Colony Forming Units (CFU) per gram of soil. However, in unfertilized or nutrient-poor soil conditions, their populations can be significantly lower, often around 10^4 CFU per gram of soil. The specific organisms present in these diverse communities vary in their natural functions, production of bioactive compounds, survival strategies and potential for parasitism (13). When applied via seed treatment or soil amendment, these beneficial microbes trigger or produce various plant growth hormones, such as auxins, gibberellins and cytokinins. This hormonal modulation plays a crucial role in regulating seed germination, alleviating seed dormancy and promoting overall plant growth and development (14).

Facilitating resource acquisition

In general, plants require essential soil nutrient elements, particularly nitrogen (N), phosphorus (P) and potassium (K), for optimal growth. When these elements are deficient or in unavailable forms in the soil, plant growth suffers, leading to reduced yields. While synthetic chemical fertilizers effectively boost plant growth by supplying these nutrients, their production often relies on non-renewable resources and its energy-intensive. Moreover, exclusive or improper reliance on chemical fertilizers can negatively impact long-term soil health, microbial diversity and physical structure, rather than holistically sustaining them. Therefore, to mitigate these environmental and soil health concerns, the integration of PGPR holds significant importance for improving soil resource management and promoting sustainable agriculture (15).

Nitrogen fixation

Nitrogen, primarily in the form of proteins and nucleic acids, is a fundamental component of all living organisms. While atmospheric nitrogen (N_2) is abundant, most organisms cannot directly utilize this gaseous form. Therefore, its conversion into biologically available compounds is essential for all life. This crucial conversion is largely facilitated by Biological Nitrogen Fixation (BNF), a process carried out by diazotrophic microorganisms (16). BNF broadly occurs via two main types: This involves a close mutualistic relationship, most notably between *Rhizobium* species and leguminous plants. Here, N_2 is fixed within specialized root nodules, directly supplying the host plant with usable nitrogen, which significantly promotes its growth and development (symbiotic). On another process occurs independently of a plant host. Examples of asymbiotic nitrogen fixers include certain Cyanobacteria (e.g., *Anabaena*, *Nostoc*), as well as bacterial genera such as *Azotobacter*, *Beijerinckia* and *Clostridium*. These organisms possess specialized nitrogenase enzymes, whose function is controlled by specific *nif* genes (17). The overall nitrogen fixation process requires the intricate coordination of factors like the assembly and activity of iron-containing proteins, the biosynthesis of iron and molybdenum cofactors, electron donation and precise gene regulation (18). The *nif* genes are generally grouped within a 20-24 kb region and arranged into seven operons, which collectively encode around 20 distinct proteins crucial for nitrogenase function and its regulation in asymbiotic systems (19).

Nitrogen fixation is an energetically demanding process, requiring a significant amount of ATP. Bacterial carbon resources are channeled towards oxidative phosphorylation to generate this ATP. Research on the balance between carbon storage and nitrogen fixation efficiency is ongoing. For instance, a strain of *Rhizobium tropici* with a deleted glycogen synthase gene, when inoculated onto bean plants, led to increased nodule formation and higher plant biomass compared to the wild-type strain. However, this mutant exhibited reduced survival in the soil environment, highlighting a trade-off between host-beneficial functions and free-living persistence (20). A key challenge for root -nodulating *Rhizobium* species is that while they require oxygen (O_2) for respiration, the nitrogenase enzyme is highly sensitive to O_2 and can be irreversibly inactivated by it. Within root nodules, this "oxygen paradox" is managed by specialized proteins like leghemoglobin, which maintains a micro-aerobic environment conducive to nitrogenase activity. Furthermore, genetic engineering has shown that introducing respiratory hemoglobin genes (e.g., from *Vitreoscilla* sp.) into *Rhizobium etli* can boost nitrogenase activity by 68 %, indicating strategies to optimize oxygen delivery for enhanced nitrogen fixation (21). Plant hormones also play a regulatory role in nodule formation. Ethylene, for instance, is generally known to inhibit nodule development at higher concentrations. However, some *Rhizobium* species produce the enzyme ACC deaminase, which degrades 1-aminocyclopropane-1-carboxylate (ACC), a precursor to ethylene in plants. By reducing the plant's ethylene levels, these bacterial strains can alleviate ethylene's inhibitory effect on nodulation. For example, the production of ACC deaminase by *Rhizobium leguminosarum* bv. *viciae* has been shown to result in increased nodule numbers and higher alfalfa plant biomass (22).

Phosphate solubilization

Phosphorus (P) is the second most essential macronutrient for plant growth, playing crucial roles in metabolism, protein and nucleic acid synthesis and kinase regulation. It constitutes approximately 0.2 % of the Earth's crust and 0.05 % of a plant's dry weight, existing primarily in two forms: inorganic phosphate (Pi) and organic phosphate (Po). However, plants can typically utilize only about 0.1 % of the total phosphorus present in the soil, as most of it is in unavailable forms. Phosphate anions (PO_4^{3-}), commonly supplied by chemical fertilizers, are highly reactive in the soil. They readily become immobilized through interactions with Ca^{2+}, Fe^{3+} and Al^{3+} ions, forming insoluble phosphate complexes that accumulate in the soil. Consequently, the plant utilization efficiency of applied phosphorus from chemical fertilizers is often low, ranging from only 5 % to 25 % (23).

This low efficiency reduces soil productivity and contributes to phosphorus enrichment in the soil, which can lead to environmental issues. To address this challenge, optimizing soil phosphorus availability using microorganisms, specifically Phosphate Solubilizing Bacteria (PSB), is critical. These bacterial communities transform unavailable forms of phosphorus into plant-available forms through various mechanisms, including dissolution and mineralization. PSBs are broadly categorized based on their phosphorus-dissolving mechanisms: Pi-solubilizing microorganisms that secrete organic acids to dissolve inorganic phosphate compounds; Po-mineralizing microorganisms that secrete phosphatase enzymes to enzymatically mineralize organic phosphate compounds (24). The combined action of both classes of PSB in the rhizosphere leads to localized acidification and increased availability of phosphorus around the plant roots (25). In addition to bacteria like *Bacillus*, *Pseudomonas*, *Arthrobacter*, *Agrobacterium*, *Micrococcus*, *Enterobacter*, *Vibrio*, *Serratia*, *Rhizobium* species, *Pantoea*, *Aeromonas* and *Burkholderia*, various fungi such as *Sclerotium*, *Penicillium*, *Aspergillus* and *Trichoderma* also exhibit significant phosphate-solubilizing activity, thereby enhancing plant vigor (26).

Siderophore production

Iron is one of the most abundant elements in the Earth's crust and soil; it is seldom present in its elemental state or in a freely soluble form. It plays a vital role in microorganisms, plants and animals, primarily existing in two common oxidation states: ferric (Fe^{3+}) and ferrous (Fe^{2+}). Iron is involved in numerous critical biological processes, including cell morphology, nucleic acid synthesis (DNA/RNA), sporulation, the TCA cycle, nitrogen fixation, photosynthesis, chlorophyll and vitamin formation and serving as a cofactor for various enzymes such as Peroxidase (PO), Superoxide Dismutase (SOD), DAHP synthetases, ferredoxins and flavoproteins.

The optimal iron concentration for plant tissues typically ranges from 12 - 24 ppm (27). During the growing season, crop plants may require approximately 5-10 kg/ha of iron. However, at a neutral pH of 7.0, a common soil condition, iron primarily exists as insoluble ferric hydroxides, such as $Fe (OH)^3$. This insoluble form is largely unavailable for direct plant uptake. Consequently, plants have evolved diverse mechanisms to facilitate iron uptake and overcome its limited solubility (28). One such strategy involves the production of chelators, which are compounds that bind to iron, making it more soluble and available. These chelators can be broadly classified into phytosiderophores (produced by plants) and microbial siderophores.

Plants, particularly Strategy II plants (e.g., grasses), produce phytosiderophores like Nicotianamine (NA) and Deoxymugineic acid (DMA) to chelate and mobilize iron (29). Microorganisms, on the other hand, synthesize a wide variety of siderophores, which are high-affinity iron-chelating compounds. These microbial siderophores are broadly categorized into classes such as, catecholates or phenolates, hydroxamates (including citrate hydroxamates), peptide-based siderophores (which can overlap with the above classes), mycobactins (specific to mycobacteria) and carboxylates (e.g., citric acid derivatives). Fungal siderophores specifically include examples such as ferrichromes, coprogens, rhodotorulic acid and fusarinins (30). Some Plant Growth Promoting Fungi (PGPF) also generates siderophores to aid plant iron acquisition.

Production of signal molecules

Microbial communication is a crucial mechanism influencing movement, survival, colonization and population density within localized environments. Rhizobacteria, a diverse group specialized for plant growth promotion, thrive by establishing successful colonization and increasing their population density through the production of signaling molecules (31). These molecules act as chemical messengers within the bacterial community and facilitate interactions with the host plant. This specialized form of communication is termed 'Quorum Sensing' (QS), a process that regulates collective behaviors, including colonization and antagonistic activities (32).

A common class of these messenger molecules is N-acyl Homoserine Lactones (AHLs). Through quorum sensing and the production of various signaling molecules, rhizobacteria mediate a range of beneficial functions (33). These include survival strategies, such as competition for food sources, secretion of secondary metabolites, including Hydrogen Cyanide (HCN) and siderophores. They contribute to the solubilization of inorganic phosphate (PO_4) and heavy metals (e.g., by *Bacillus* and *Pantoea agglomerans*), nitrogen (N_2) fixation (e.g., by *Rhizobium* species), modulation of phytohormone levels, including the production or stimulation of auxins (IAA), cytokinins, gibberellins and ethylene. Additionally, they reduce ethylene levels via of ACC deaminase activity (which reduces ethylene levels), production of microbial antibiotics, such as phenazine, pyrrolnitrin, surfactin, iturin, fengycin, 2,4-diacetylphloroglucinol (DAPG) and zwittermicin A and finally, triggering of Induced Systemic Resistance (ISR) in plants, often mediated by signaling pathways involving ethylene (ET) and jasmonic acid.

Many of these functions, particularly those involved in antagonism against soil-borne pathogens, are biologically regulated by AHLs (33). A wide array of bacterial genera and species are known to engage in these complex interactions, including *Pseudomonas* (e.g., *P. fluorescens*, *P. aeruginosa*, *P. chlororaphis*, *P. putida*, *P. protegens*), *Bacillus* (e.g., *B. amyloliquefaciens*, *B. cereus*, *B. megaterium*, *B. mojavensis*), Cyanobacteria, *Clostridium*, *Escherichia coli*, *Ensifer*, *Enterobacter*, *Azospirillum*, *Azotobacter*, *Anabaena*, *Klebsiella*, *Agrobacterium*, *Nitrosomonas*, *Nocardia*, *Nostoc*, *Rhizobium*, *Bradyrhizobium* and *Streptomyces* (34).

Production of ammonia

Soils are primarily composed of organic residues and debris from organisms, which are rich in nitrogen. A significant portion of soil nitrogen, approximately 60 %, is found within the cells of plants and microorganisms, incorporated into various protein residues containing amino acids and structural components like chitin and peptidoglycan (35). The decomposition of these organic residues is a vital process. Traditionally, soil organic matter is degraded by a diverse range of microorganisms, including many species of *Pseudomonas* and *Bacillus*. During this decomposition, complex organic nitrogen compounds, such as amino acids, are mineralized to produce ammonia (NH_3). This process is known as ammonification. Subsequently, ammonia is converted into nitrite (NO^{2-}) through the action of chemoautotrophic soil bacteria like *Nitrosomonas* species. The nitrite is then further oxidized to nitrate (NO^{3-}) by other chemoautotrophs, such as *Nitrobacter* species (36).

Regulating phytohormones

Phytohormones play crucial roles in regulating plant growth from seedling to maturity, while also mediating plant responses to abiotic and biotic stresses (37). Key phytohormones include Cytokinins (CKs), Gibberellins (GAs), Auxins (Indoleacetic Acid - IAA), Abscisic acid (ABA) and Ethylene (ET) (38). A broad group of microorganisms are known to modify plant hormone levels within the environment or directly interact with plant hormonal pathways. These include bacterial species such as *Arthrobacter, Bacillus* spp., *Enterobacter, Pantoea, Pseudomonas, Rhizobium* spp., *Cellulosimicrobium, Mycobacterium, Ochrobactrum, Paenibacillus, Azospirillum, Stenotrophomonas, Mycoplana, Rahnella, Klebsiella, Leifsonia, Achromobacter xylosoxidans, Streptomyces* spp., *Microbispora* and *Micromonospora* (39).

Cytokinins (CKs), for instance, have been detected in cell-free media of microbial strains like *Azotobacter, Rhizobium, Pantoea agglomerans, Rhodospirillum rubrum*, *Pseudomonas fluorescens, Bacillus subtilis* and *Paenibacillus polymyxa*. Hormones produced by these microbes can break seed dormancy during sowing, alleviate seed coat hardness, facilitate adaptability to soil moisture conditions and enhance seed uptake. This collectively triggers seed germination, allowing plants to resist salt stress and high pH conditions and aiding in the avoidance of seed-borne pathogen induction (40).

Auxins are well-known for inducing and promoting functional cell division, elongation and differentiation. IAA is biologically significant and derived from tryptophan. Moreover, microbial production of auxin has been shown to improve stress tolerance in various crops, such as rice (e.g., *Serratia marcescens* 90 - 166) and soybean (e.g., *Bacillus aryabhattai* SRB02), by influencing host signaling pathways, including membrane-bound transcription factors (like NTM2) and IAA30 gene expression. Microbial auxins significantly affect taproot and lateral root elongation, leading to increased biomass. Specific strains like *Pseudomonas brassicaerum* STM196 and *Bacillus* spp. LZR216 both express IAA synthesis genes, resulting in increased endogenous IAA levels in the main root (41). Conversely, some PGPR species can modulate auxin-like effects; for example, *Pseudomonas aeruginosa* strains might suppress auxin responses by producing cyclopeptides (e.g., LasI and Rh1). Other strains, such as *Bacillus subtilis* GB03 and *Bacillus amyloliquefaciens* IN937, stimulate homeostatic effects on plant growth and can improve auxin expression by producing volatile compounds like acetoin and 3,4-butanediol, even if endogenous auxin concentrations decrease in shoots and roots. Additionally, organic volatiles like albuterol and 1,3 - propanediol can stimulate plant growth by modulating specific tomato plant genes (e.g., *SlIAA3/SlIAA1*) (42).

ET is an important gaseous plant hormone involved in diverse developmental processes, including root and shoot apical meristem function, hypocotyl swelling, fruit ripening, leaf senescence and stomatal formation and function. Plants regulate ethylene levels through the expression of genes and enzymes involved in its synthesis, such as ACC synthase and ACC oxidase, crucial for maintaining hormonal homeostasis (43).

Some beneficial microbes, like *Paraburkholderia phytofirmans* PsJN, can increase the expression of plant genes related to stress tolerance and growth, an effect observed in crops such as tomato, potato, maize, lupin and grapevine. This beneficial interaction can occur even in the presence of plant colonization by pathogens like *Pseudomonas syringae* pv. *tomato* (44). Importantly, several species of rhizobacteria, including *Bacillus cereus* AR156 (wheat), *Azospirillum brasilense* FP2, *Pseudomonas putida* (tomato), *Bacillus subtilis* (tomato) and *Variovorax paradoxus* (for *Arabidopsis thaliana*), can increase ACC deaminase activity. This enzyme degrades ACC (ethylene precursor), leading to a reduction in plant ethylene levels, which can enhance plant tolerance to stress and promote growth, often accompanied by the accumulation of PR proteins in leaves and fruits (45).

Drought tolerance

During cultivation, crops are often impacted by various abiotic stresses, including high temperatures, drought (resulting from reduced soil water-holding capacity), unfavorable soil pH (acidity/alkalinity), heavy metal contamination, nutrient deficiencies and general soil infertility (46). These challenging agroclimatic conditions can severely diminish plant biological function and yield, retard overall growth, impose nutritional limitations and lead to poor root and shoot development. In response to such stresses, the stimulation and induction of phytohormones by PGPR play a crucial role in modulating plant physiology. PGPR can influence various physiological processes that enhance stress tolerance. For instance, they can aid in the synthesis of protective compounds like polysaccharides (e.g., trehalose and fructose), which act as osmolytes. Additionally, phytohormones like auxin and ethylene regulate processes such as stomatal opening, which is critical for managing water loss (47).

Salt tolerance

Under saline conditions, plant stress tolerance is significantly enhanced by a diverse group of rhizobacteria. This enhancement is often mediated by the activity of ACC deaminase, an enzyme produced by various genera and species, including *Pseudomonas, Bacillus* spp., *Burkholderia, Azospirillum, Serratia marcescens, Rhizobium* spp., *Ensifer meliloti, Acinetobacter, Achromobacter, Agrobacterium tumefaciens, Alcaligenes, Enterobacter, Ralstonia* and *Halomonas maura*, as well as *Ochrobactrum intermedium*. These rhizobacteria utilize the ethylene precursor ACC and convert it to 2-oxobutanoic acid and ammonia (NH_3), thereby reducing the plant's endogenous ethylene levels. This reduction of stress-induced ethylene can mitigate its inhibitory effects on plant growth, allowing for increased resistance. Furthermore, some of these bacterial species also promote plant growth by optimizing nutrient availability in the soil or by enacting beneficial changes under other soil stress conditions (48).

Competition

In ecological communities, all living creatures, including microorganisms, rely on other species for sustenance, survival, colonization and reproduction. This interdependence is particularly evident and crucial for the sustainability of beneficial microbes. Within the plant rhizosphere, a large and diverse collection of PGPR competes for nutrients and can antagonize crop pathogens. One of the primary mechanisms by which PGPR prevent plant pathogen invasion is through biological control, particularly parasitism or hyperparasitism. In these antagonistic interactions, PGPR can employ specialized structures, such as mycelial pegs, to extract nutrients directly from host plants or, more commonly, from pathogens. They can also disintegrate antagonistic organisms by secreting lytic enzymes (49).

Production of lytic enzymes

Beyond direct competition, a key secondary process involves beneficial microorganisms binding to pathogens and inhibiting their biological activity through the synthesis of hydrolytic enzymes. During these interactions, PGPR and plant growth-promoting fungi (PGPF) produce numerous cell wall lytic enzymes. These include, cellulases, chitinases, lipases, proteases and β-1,3-glucanases. These enzymes are secreted by a wide range of microbial species, such as *Pseudomonas fluorescens* (e.g., strains Pf1, LRB3W1), *P. chlororaphis* (e.g., strain CPs3), *P. putida*, *P. aeruginosa*, *Bacillus cereus*, *Burkholderia cepacia*, *B. megaterium*, *B. coagulans*, *B. thuringiensis*, *B. subtilis*, *Cellulomonas* sp., *Beauveria bassiana*, *Clonostachys* sp., *Cordyceps* sp. and *Trichoderma* spp. Through the action of these enzymes, phytopathogens are effectively and completely degraded from within and around the host ecosystem (50).

Bacteriocins

Bacteriocins are micromolar proteinaceous substances produced by beneficial bacteria to gain a competitive advantage in microbial environments. They exhibit antimicrobial activity, often destroying or inhibiting the growth of closely related bacterial types, including those within bacteriocyanogenic cells. These compounds can inhibit early-stage pathogen survival, colonization and infection, typically acting within a narrow spectrum of target organisms. Examples of such bacteriocins include colicin (produced by *Escherichia coli*), megacin (from *Bacillus megaterium*), marcesin (from *Serratia marcescens*), cloacin (from *Enterobacter cloacae*) and pyocins (from *Pseudomonas aeruginosa*, not *P. pyogenes*) (51). Unfortunately, a significant concern with some of these compounds is their potential toxicity to humans and animals.

Antibiotics production

The production of antimicrobial compounds by beneficial microbes is widely accepted as one of their most significant roles in the overall eradication of pathogen invasion and enhancement of host survival. Antibiotics (Abs), defined as low molecular weight chemical compounds, act by inhibiting or suppressing pathogen populations, their biological functions and their survival. These multi-dimensional antibiotics are produced by diverse groups of microorganisms, including fungi, bacteria and actinomycetes. Historically, only about 2 % of soil microbes could be cultured in the lab, with the majority being characterized using techniques like rRNA gene sequencing and functional gene analysis (52). A wide array of well-known antibiotics are produced by various microbial genera (53); *Pseudomonas* is known for many antibiotics that include Phenazine-1-carboxylic acid (PCA), 2,4-diacetylphloroglucinol (2,4-DAPG), aerugine, rhamnolipids, pyocyanin, pyrrolnitrin, oomycin A, azomycin A, viscosinamide, cepafungins, kanosamine, pseudomonic acid, butyrolactones, karalicin, pyoluteorin and cepacimide A. *Bacillus* produce antibiotics like bacillaene, bacillomycin, basalin, Tas A, chlorotetain, subtilosin, iturin, surfactin, fengycin, subtilin, bacilysin, sublancin, polymyxin, circulin, colistin, mupirocin and zwittermicin A. *Stenotrophomonas* produces compounds like xanthobaccin and oligomycin. *Streptomyces* synthesise compounds such as streptomycin, oxytetracycline and chloramphenicol. *Trichoderma* produces gliotoxin, 6-pentyl-α-pyrone (6-PAP), viridian and gliovirin and *Beauveria* species (beauvericin and bassianin).

Induced systemic resistance

Induced systemic resistance refers to a deliberate method employed to enhance a plant's immune system, enabling it to better combat diseases and pests. This resistance can be categorized into two distinct types based on its functional expression during the induction of pests or diseases, as well as its association with resistance development through (1) systemic tolerance, where plants achieve tolerance via the immediate stimulation of the hormone salicylic acid; and (2) local tolerance. This process is further augmented by beneficial microbes and various signaling responses, such as MAMP (Microbe Associated Molecular Patterns), elicitors (including flagellin, chitin, Lipopolysaccharide (LPS) and phytohormone stimulation like JA and ET), volatile organic compounds, acetoin, 2,3-butanediol, siderophores and hydrogen cyanates (which encompass alkanes, alcohols, esters, terpenoids, sesquiterpenes and ketones). These diverse chemical signals are detected by host Pattern Recognition Receptors (PRRs). Biologically, the two types of resistance operate on different principles; for instance, systemic acquired resistance (SAR) functions by elevating salicylic acid levels and involves a wide array of pathogenicity-related genes (such as PR-1a, PR-1b, PR-1c, β-1,3-glucanase, chitinase, thaumatin-like proteins and lipid transfer proteins) that play a role in defense responses from the nucleus to the outer membrane. In the case of induced systemic resistance (ISR), the expression of the NPR1 gene is mediated by jasmonate and ethylene without the activation of PR genes, thereby triggering cytoplasmic signaling that extends to the outer membrane. For ISR, various species of rhizobacteria (isolated from native sources) are applied through manual soil application, seed enrichment and foliar application (54).

Other sectors

Food industries

Since ancient times, various microorganisms have been utilized in the food industry as additives and nutritious food sources to enhance taste, aroma and the fermentation process, thereby extending product shelf life. In particular, the production of organic acids involves *A. niger, Acetobacter sp.* and *A. oryzae*; wine and ethanol are produced by *S. uvarum, Dekkera*and *S. cerevisiae*; vanillin is derived from *P. cinnabarinus*; shelf-life determinants include *P. chrysogenum* and *C. spherospermum*; fermentation products are produced by *Lactobacillus, E. coli* and *B. bifidum*; dietary supplements consist of *Candida, Saccharomyces, Rhodotorula sp., Methanomonas, Bacillus* and *Hydrogenomonas*; and edible foods include *A. auricula, V. volvaceae, A. bisporus, C. lentillifera, Chlorella, Spirulina, L. edodes* and *Pleurotus sp.* (55).

Pharmacology and biotechnology

In the realm of Pharmacology and Biotechnology, pressing global challenges such as the destruction of natural resources, shifts in food habits (often linked to the extinction of native plants and food sources)and the rise of accompanying diseases pose significant threats to human life (56). These factors can inherently reduce and suppress genetic immune responses. Thus, innovative approaches are being explored; gene editing combined with the consumption of biofortified foods can strengthen human immune systems. These foods are highly nutritious supplements, often fortified and enriched by beneficial microorganisms such as *Acinetobacter, Candida* species and *Fusarium venenatum* (immune system enhancement) (57). The endosymbiotic bacterium, Wolbachia is effectively utilized to reduce populations of *Aedes aegypti*, a mosquito species that transmits diseases like dengue and Zika virus, by inducing gene silencing in the mosquito host (vector control) (58) and polypeptides derived from *Cordyceps sinensis* have been explored for their potential in insulin production for diabetics (59). Furthermore, in cancer biology, bioactive compounds with anti-tumor properties, such as taxol, have been synthesized or found in association with fungi like *Ganoderma lucidum, Cordyceps sinensis, Metarhizium anisopliae* and *Colletotrichum gloeosporioides*, offering valuable alternatives to traditional antitumor agents (60).

Eco-conservation

A wide variety of microorganisms, such as heterotrophic bacteria, actinomycetes, faecal coliforms, thermophilic firmicutes, yeasts and fungi have been identified in the context of environmental management. A biologically active carbon filtration method was employed by *P. radiata, arbuscular mycorrhizae, C. necator, N. frowardii, P. chrysosporium* and *A. bisporus* to eliminate contaminants of heavy metal compounds, including mercuric, arsenic, sulphides, metalloproteins, benzopyrenes and polymers from contaminated soils and water (61).

Bioenergy

From both a national and international perspective, biofuels represent a promising alternative source to meet the growing demands of the fuel industry. Bioethanol and biogas are key products obtained through the anaerobic digestion of organic matter by microorganisms. This microbial conversion yields gaseous molecules such as methane (CH_4), carbon dioxide (CO_2), nitrogen (N_2) and hydrogen sulfide ($H2_S$). As the Earth's conventional fuel reserves are declining significantly, the role of microorganisms, including many non-cultivable species, in biofuel production is increasingly critical. These include diverse phyla like Proteobacteria, Chloroflexi, Firmicutes and Actinobacteria, as well as specific methanogenic archaea such as *Methanosaeta frisia*, *Methanosarcina barkeri* and *Methanococcus formicicum* (62).

Discussion

The global landscape post-COVID-19 pandemic has significantly heightened awareness among both farmers and the general public regarding the importance of sustainable agriculture, including organic farming practices that emphasize indigenous crop varieties and the integration of beneficial microorganisms. This shift is driven by a renewed focus on ecological health and food security. Consequently, the study of novel microorganisms and their diverse biotechnological potential is gaining critical importance in advancing microbiological sciences for human well-being. However, the comprehensive characterization and application of these microorganisms are inherently time-consuming and there is a recognized shortage of qualified personnel to undertake these complex tasks. Addressing these challenges will require concerted scientific effort and technological advancements to yield improved outcomes for future generations (63). Indeed, beneficial microbes are abundant and offer immense potential across a wide range of fields, including agriculture, healthcare, environmental remediation and bioenergy production (64). Their primary utility lies in their capacity to enhance plant growth, combat pathogens, break down pollutants and produce valuable compounds. Crucially, these microbial applications promote sustainable practices and support natural ecosystems by reducing dependency on synthetic chemical inputs (65).

Conclusion

Beneficial microbial applications are increasingly recognized for their multifaceted utility across various modern fields. However, the comprehensive utilization of microorganisms in each industry presents certain limitations, including challenges in their availability, accurate identification, detailed characterization, effective methods of application and the significant time investment required for research and development. These practical challenges are being addressed through continuous scientific advancements and improved methodologies.

Concurrently, as the global population continues to grow, so too will the demand for food. Historically, efforts to meet this demand have often involved conventional agricultural practices, such as the extensive use of chemical fertilizers, reliance on hybrid seeds and increased mechanization in rural farming globally. While effective in increasing output, these practices are now understood to have significant drawbacks. Their widespread application has led to the degradation of the soil's natural nutrient status, a reduction in agroecosystem diversity, inadequate production and supply in certain regions and has been implicated in emerging human diseases and disorders. These issues, alongside a general decline in rural livelihoods, pose a substantial negative impact on future generations. Despite these challenges and as scientific methodologies are continuously refined and innovated, the leveraging of native microbial communities in agriculture represents a crucial endeavor to foster sustainable food systems and ultimately sustain life on Earth.

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Authors' contributions

KK and PMS writes a full manuscript and over prepared a draft of outcome. All authors read and approved the final manuscript. ES carried out conceptualization. MJ and VS collected all literatures and framed the work outline (data collection). PA correction carried out in manuscript.

Compliance with ethical standards

Conflict of interest: Authors declare that there exists no conflict of interest.

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