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Review

Exploring Microbial Potential for Sustainable Agriculture

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Abstract: Microbes play diverse roles in agriculture. They are present in soil, in or on plant parts, and are also found associated with livestock. Soil microbes regulate biogeochemical cycles and cycling of organic matter and nutrients. They secrete compounds that promote growth of the plants by direct or indirect pathways. Many microbes possess catabolic genes that can degrade pesticides. Microbes also work against phytopathogens by inducing resistance in plants, hyperparasitism, antibiosis, competing for nutrients or space, or by producing secondary metabolites. Microbial balance in the gut of the ruminants influences their health and thus their productivity. More recently, in order to improve agricultural production, role of microbes has been explored for developing agricultural practices like organic farming and Climate Smart Agriculture.
An understanding of these diverse roles of microbes can aid in the development of microbial interventions for sustainable agriculture, such as development of biofertilizers, bioremediation techniques, use as biocontrol agents or plant growth promoters. Sustainable agricultural production is essential to beat hunger, improve health and well-being and it also contributes towards the economic growth of a nation. In this article, we explore the diverse roles of microbes in agriculture, including modern agricultural practices. We discuss the role of 'omics' technologies, to study the microbial communities that have opened a wide arena for designing and developing microbial interventions for sustainable agricultural production. In view of these roles, it is proposed that a greater emphasis needs to be laid on framing policies which incentivize use of microbes in agriculture, as it is the only way forward to ensure sustainable agricultural production and good health of ecosystems and humans.

Keywords: Microbiome, Sustainable agriculture, Biofertilizers, Plant Growth Promoters, Biocontrol, Omics

Introduction

Agriculture has played an important role in the evolution of human civilization. To feed an ever growing population, an increase in production of agricultural crops is essential. Concomitant with a five- fold increase in the area under cultivation in the last five decades, there has also been a seven fold increase in use of chemical fertilizers [1]. Many microbes flourish in the soil when natural fertilizer in the form of animal and plant waste is used in agriculture.

However, increased use of chemical fertilizers and pesticides changes the soil and plant associated microbiota, consisting of bacteria, fungi and algae, which may lead to severe disruption of associated ecosystem services [2]. Livestock has also been subjected to hormonal and antibiotic abuse in a quest to enhance production [3] leading to a change in the composition of microflora in these organisms.

With an increasing focus on sustainable practices, use of microbes in agriculture is imperative. Use of microbes is not only environmentally safe, but is a technology which can be easily made available even to marginal farmers and can help them in increasing agricultural and livestock production [4]. Microbial interventions in agriculture forms a prominent component of Sustainable Development Goal (https://sdgs.un.org/goals) of Zero Hunger and is also important for attaining many other Goals, such as those of Good Health and Well-being, Clean Water, Climate Action and Life on Land. Here, we review the role of microbes in cultivation of crops and raising of livestock, the understanding of which can help in designing and developing microbial interventions for sustainable agricultural production. We also emphasize the role of 'omics' technology in understanding the microbial communities, that can aid in this development.

Microbiota associated with Plants and Livestock

The capacity of soil to support agricultural plants is dependent not only on its physical and chemical characteristics but also on its microbial components. Microbes are present in soil as well as in/on different parts of plants. Rhizosphere, a narrow zone that surrounds the plant root is the most abundant and complex niche in microbial diversity [5], which is dependent on the organic and inorganic exudates of plant roots [6]. A diverse variety of microbiota termed endophytes is harbored in organs like leaves, stems, roots, flowers, fruits and seeds. The diversity and composition of microorganisms in the plant endosphere is dependent on the plant species, the physiological conditions of the specific tissue, stage of growth of the plant, as well as the environment [7]. The surface of plants, termed phyllosphere is also a home to a variety of epiphytes, including bacterial species. There exists a great variation in the microbiota of the phyllosphere, within and between plant species and over different stages of the life cycle as well as seasons of growth [8].

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Livestock forms an important part of agriculture. The rumen microbiome consists of bacteria, archeae and eukarya, where, majority of microbes in the bacterial community belong to phyla Firmicutes and Bacteriodetes [9]. The composition of rumen microbiome is not only essential for survival of the host, but also influences the animal health in a significant manner [10]. Table 1 lists some of the microbial genera found associated with different parts of the plants and livestock.

Table 1: Microbial genera associated with different parts of plants and livestock. Names of the plant species/livestock with which the specific microbes are associated are provided in the brackets.

	Microbial Genera (Plants/livestock)	**References**
Rhizosphere	*Pseudomonas, Acinetobacter, Ensifer, Rhizobium (Solanum* lycopersicum L.)*; Rhizobium, Allorhizobium, Mesorhizobium, Sinorhizobium Bradyrhizobium, Ochrobactrum, Azorhizobium (legumes); Enterobacter (Arachis hypogaea, Glycyrrhiza uralensis),Curtobacterium luteum (Trifolium pratense), Arthrobacter (Lespedeza sp.), Mycobacterium (Sphaerophysa salsula), Microbacterium (Glycyrrhiza sp), Agrobacterium (Phaseolus vulgaris), Blastobacter, Micromonospora (Pisum sativum), Bosea (Ononis vaginalis), Devosia, Pantoea (Hedysarum carnosum), Enterobacter (Arachis hypogaea), Bacillus (Cajanus cajan)*	[11, 12]
Endosphere (Non –root)	*Acinetobacter, Enterobacter, Pseudomonas, Bacteroides, Pantoea, Xanthomonas, Methylobacterium, Sphingomonas (Solanum* lycopersicum L.)	[11, 13]
Phyllosphere	Acinetobacter, Enterobacter, Rosenbergiella, Bacteroides, Pantoea, Pseudomonas *(Solanum* lycopersicum L.), *Micrococcus, Propionibacterium, Paracoccus and Delftia, Proteobacteria, Firmicutes, Bacteroidetes, and Actinobacteria, Actinobacteria, Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, Sphingobacteria, Pseudomonas (Quercus robur* L.)	[11, 14]
Livestock	*Prevotella, Succiniclasticum, Treponema, Ruminococcus, Mogibacterium, Acetitomaculum, Acinetobacter, Butyrivibrio, Campylobacter, Desulfobulbus, Anaerovibrio, Prevotella (*Gastrointestinal tract of Cattle*)*	[15]

Role of microbes in agriculture

Soil microbes are responsible for regulation of biogeochemical cycles, cycling of organic matter and nutrients, and therefore, are drivers of soil ecosystem. Microbes can directly or indirectly promote crop yields and these associations are labeled as Soil-Plant-Microbe interactions. Some of the key roles played by microbes are detailed below.

a) Microbes as Biofertilizers

The concept of enhancement of productivity with the help of microbes is termed as biofertility. Replacing mineral fertilizers by organic material derived from agricultural, industrial and municipal processes and supplanting it with root associated microbes that have the ability to mineralize nutrients bound to organic matter, can be the first step towards sustainable agriculture [16]. Microbes in the soil are essential for breakdown of cellulose, hemicellulose, pectin, xylan and other complex molecules found in the plant organic waste [17]. Some microbes possess genes that metabolize organic molecules and make available the nutrients like N,P and S for plant growth [2].

Nitrogen fixation is an anaerobic process. Nodulation and mycorrhizal interactions play a key role in instituting mutualism between plants and microbes [18]. Members of the family *Rhizobiaceae* often called as Plant Growth Promoting Rhizobacteria (PGPR) are associated with nodulation in leguminous plants [18]. The plant growth promoting Rhizobacteria (PGPR) not only help in nitrogen fixation, iron sequestration, phytohormone regulation etc., but also in inhibiting or controlling pathogens [19]. Many PGPR genes for promoting plant growth such as nif for Nitrogen fixation, phl for phloroglucinol synthesis etc. have been identified [20] Nevertheless, many free-living nitrogen-fixing bacteria like *Azatobacter*, *Azomonas*, *Mycobacterium*, *Clostridium*, *Rhodospirillum* etc. are also responsible for non-symbiotic nitrogen fixation in plants [21].

The efficiency of PGPR as inoculants is dependent on the colonizing efficiency of microbes,, the types of exudates released by the roots and also the soil health. The association between *Bradyrhizobium elkanii*, *Bradyrhizobium japonicum* and soybean display a good example of Biological Nitrogen Fixation [22]. *Azospirillum* has also been shown to increase the nutrient uptake and also the yield in wheat and maize [23]. Rhizobia and *A. brasilense* inoculants also show good results with soybean and common bean [24]. Endophytes also increase the acquisition of nutrients by plants, simultaneously stimulating their growth, and also aid in increasing stress tolerance, as well as in defense against pathogens and insects [25].

Phosphorus is the second most essential element required for the growth of plants. Use of phosphorus fertilizers to increase crop production leads to depletion in soil fertility, water pollution, eutrophication [26]. Phosphate Solubilizing Microorganisms (PSM) can solubilize as well as mineralize insoluble soil phosphorus, thus bringing it back for utilization by plants. Bacteria like *Pseudomonas* and *Bacillus* secrete organic acids like formic, acetic, propionic, lactic and succinic acids that help to bring insoluble phosphates in their soluble form in soils [27]. Fungi like *Penicillium* and *Aspergillus* are also involved in solubilization of phosphates [26].

b) Microbes as plant growth promoters

Microorganisms secrete non-volatile (NVM) (cytokinins, organic acids, auxins) as well as volatile organic compounds (VOCs) like 2,3-butanediol, 3-hydroxy-2-butanone (acetoin), 2-pentylfuran, dimethyl hexadecylmine, that stimulate plant growth by direct or indirect pathways [28]. Microbial VOCs are low molecular weight, lipophilic signal molecules, with high vapor pressure and low boiling point, which can be transported through water, soil and air [30]. These molecules lead to activation of signals, which regulate plant health by modulating various physiological processes [31]. Specific microorganisms release compounds like Sulphur, alkanes, alkenes, ketones, esters and alcohols, that are derived from various metabolic pathways [28].

The important pathways influenced by VOCs include phytohormones pathways, photosynthesis, metabolic pathways etc., but their indirect influence is also reported in gene expressions and various biological functions [29]. VOCs released by microbes provide a sustainable solution as these compounds are cost effective, efficient, and eco-friendly. VOCs released by bacteria like *Arthrobacter, Pseudomonas* help in increasing the weight of roots and shoots [28].

c) Microbes as Degraders

Chemical pesticides often contaminate the soil and are responsible for its infertility. Many microbes possess catabolic genes that can degrade pesticides. Microbial bioremediation is an efficient method which utilizes microorganisms to reclaim environment contaminated with heavy metals. The efficacy of bioremediation is dependent on the type of organisms, environmental conditions and the concentration of pollutants [32]. Bioremediation can be carried out by supplanting microorganisms with nutrients or by genetically engineering the indigenous microorganisms to improve their ability of contaminant degradation.

A great variety of chemicals can be bioremediated by different microbes, for example *Pseudomonas fluorescens* and *Pseudomonas aeruginosa* are involved in bioremediation of Fe^{2+}, Zn^{2+}, Pb^{2+}, Mn^{2+} and Cu^{2}+ [33]. *Pseudomonas putida* is used for degradation of monocyclic organic hydrocarbons [34]. *Bacillus, Klebsiella, Acinetobacter, Flavobacterium, Alcaligenes,* and *Staphylococcus* are known to help in remediation of Endosulfan [35, 36], while *Bacillus sp., Streptomycetes* and *Cupriavidus* help in remediation of Chlorpyrifos using *opd* genes [37, 38, 39]. Sphingomonads possess *lin* genes for degrading Hexachlorocyclohexane (HCH) [40] and other catabolic genes for degradation of anthranilate, phenol, chloroform and homogentisate. Involvement of *tfdA* gene in degradation of phenoxyacetic acids has also been reported [41]. Microbial enzymes such as monooxygenases, dioxygensases, oxidireductases, halolkane dehalogenases, phosphotriesterases etc. have been reported to catalyze the degradation of pesticides. Thus, the use of microbial population should be used as an effective solution in clearance of chemical pesticides.

d) Microbes as Biocontrol agents:

Phytopathogens are a threat to agriculture as they cause severe damage to crops. Soil disinfestation is a biotechnological method which exploits indigenous microbes for eliminating soil-borne plant pathogens. Microbes work against phytopathogens inducing resistance in plants, hyperparasitism, antibiosis, competing for nutrients or space, or by producing secondary metabolites [42]. Microbial inoculants can be used to control insects, fungus, pathogens and weeds by a variety of mechanisms, namely, secretion of hydrolytic enzymes, or metabolites toxic to pathogens of plants and competition for nutrients on induction of defense response [43].

Aspergillus fumigatus, *Aspergillus niger*, *Trichoderma koningii*, *Penicillium citrinum* are some of the bacterial species effective against pathogenic fungi *Phytophthora infestans* [44]. Pseudomonads exhibit control on *Fusarium* wilts [45], while *Mitsuaria* sp. exhibits biocontrol on bacterial leaf spot [45]. Herbicidal activity is exhibited by *Colletotrichum coccodes*, which is a mycoherbicide of Striga [46], and velvet leaf and biofungicide of *Fusarium* spp. [47]. Microbes can also be used as bioinsecticides. *Bacillus thuringenesis* is the most common microbe that has been used predominantly in agriculture to target lepidopterans.

Some nematodes are also considered as pathogenic to plants and are called Plant-Parasitic Nematodes (PPNs). These nematodes cause severe damage to agricultural crops worldwide, leading to major economic losses [48]. Chemical methods employed to control PPNs cause damage to soil and environment. Nematophagous microbes can be used effectively to control PPNs. These microbes are usually fungi and bacteria that exploit different mechanisms to target nematodes. Fungi can either trap nematodes or kill nematodes by spore adhesion; whereas bacteria can secrete toxins to kill them [49]. *Bacillus firmus* is a Gram-negative bacterium that can parasitize eggs and larvae of nematodes [50].

Microbial BioControl Agents (MBCAs) can prime plants or induce resistance in them without interacting directly with the pathogen. The resistance inducing stimuli produced by microorganisms are called Microbe-Associated Molecular Patterns (MAMPs) [51]. The induction of defense mechanisms leads to formation of physical barriers like cell wall and cuticles, or production of proteins related to pathogenesis or phenolic compounds, phytoalexins, reactive oxygen species [52]. Microbes can modulate growth condition of pathogen by adopting tactics like nutrient competition [53]. The saprophytic stage of necrotrophic pathogens is dependent on exogenous nutrients present in the environment. In order to reach high population levels, the bacterial pathogens often exhibit dependency on exogenous nutrients. Microbes which are able to rapidly utilize the resources necessary for pathogen infection such as plant exudates, pollen, sugar, will outcompete the pathogens [53].

Some MBCAs directly interfere with pathogens by antibiosis or hyperparasitism [53]. Antagonists acting through hyperparasitism and antibiosis directly interfere with the pathogen by producing interfering metabolites, enzymes and signaling compounds at low concentration [53]. Hyperparasitism will result when a plant pathogen is parasitized by another microbe. *Bdellovibrio bacteriovorus* derives nutrients from cytoplasm of Gram-negative bacteria like *Agrobacterium tumefaciens*, *Erwinia herbicola*, *Xanthomonas vesicatoria* [54]. Low molecular weight, organic metabolites, produced by microorganisms, that are deleterious to metabolic activities or growth of other microorganisms are termed as antimicrobial metabolites and play an important role in microbial interactions in plant and soil surfaces [55].

e) Microbes in livestock health

Livestock farming constitutes an important component of agriculture and involves raising of animals for meat, milk, wool, hides etc. In general, microbial diversity in adult ruminants is high, while newborn's rumen has simple microbiota which grows and diversifies with time. The difference in rumen bacteria between different ages of calves and adult is particularly due to the diets viz. colostrum, milk, milk supplemented rations and total mixed rations [56].

It has been established that inclusion of probiotics in diet could improve the overall health of the animals and also enhance their productivity. This is brought about by an improvement in the microbial balance of the intestine, leading to an increase in the absorption and utilization of feed and increase in body weight of animals like goats, sheep, cattle, horses, turkeys and chickens [57]. The bacteria most commonly used as animal-feed probiotics include *Lactobacillus*, *Bacillus*, *Bifidobacterium Streptococcus*, *Pediococcus* and *Enterococcus*. Rumen microbes aid in digestion of plant fiber and cellular material into high grade animal protein and nutrients [58]. Microbes are also reported to produce vitamins B, especially B12 and K [59]. Factors which play an important role in shaping the rumen microbiome are possibly, diet, animal age and health [56].

Two challenges of livestock production, namely, methane emission and use of antibiotics has raised a serious concern which upstretched the use of alternative or additional strategies to rear livestock with a better quality. As per the studies, innovative and newer feed additive combinations could serve as a possible alternative for safer environment and wellbeing of people's health. Such feed additives include fermented feed, probiotics or prebiotics, as in symbiotics, algae and products from plant origin which have shown to have a positive effect on production both in terms of quality and quantity and improved health status of the animal [60]. More specifically, fermented feed obtained from agricultural waste, soyabean meal, wheat straw and rapeseed can improve the nutrient digestibility and thus, also reduce the mandate of conventional feed (Figure 1).

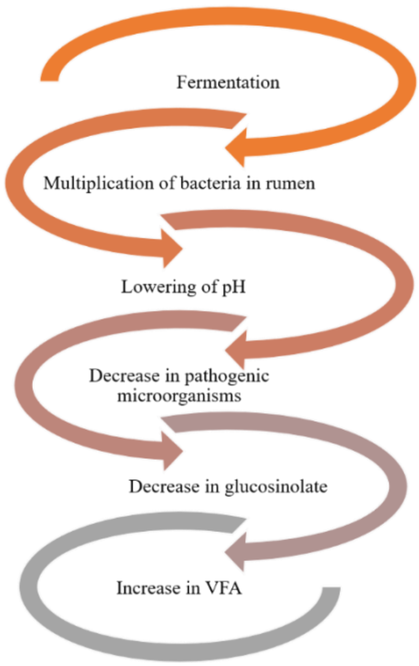

Figure 1: Scheme of fermentation and effects of fermented feed [48]. VFA- Volatile Fatty Acids

Role of Microbes and Modern Agricultural Practices

Transformation in agricultural practices is essential for climate change mitigation, improving resilience, combating desertification and meeting the increased demand of food production for the growing population [61]. Thus 'intensive agriculture' or 'modern agricultural practices' including procedures such as crop rotation, intense tillage, abundant irrigation, use of synthetic chemical fertilizers and pesticides, genetic manipulation of plants etc. are paving way for sustainable agriculture practices. Although in nascent stage, increasingly, these techniques are projected to exploit microbes as the plausible natural means for improving production. Some of these sustainable modern practices where role of microbes has been suggested are discussed below:

a) Microbes in Climate Smart Agriculture

Climate Smart Agriculture (CSA) is an integrated approach which aims at managing landscapes by increasing productivity, improving resilience and mitigating climate change [62]. As explained above, microbes play diverse roles as biofertilizers, biopesticides, plant growth-promoting rhizobacteria etc., hence, appropriate management of such microbes can help in accomplishing sustainable goals [63]. For example, greenhouse gases like CO_2 and CH_4 contribute to global warming. Microbes can be exploited to consume greenhouse gases and can contribute to climate change mitigation. Methanotrophs are well known to mitigate methane emission [64]. Apart from this, plants that can cope with elevated levels of CO_2 can be preferably planted. It is observed that some strains of mycorrhizal fungi help C4 plants to survive at higher levels of CO_2 [65]. Some *Rhizobia* species also help several plants to cope well under abiotic stress conditions. These strains can be further genetically manipulated to increase their efficiency.

b) Organic Farming

Organic farming is now a very familiar term which maximizes the efficient use of local resources while reducing the use of non-renewable resources, without depending upon agrochemicals, GMOs and synthetic additive compounds to enhance soil fertility [66]. Soils that are managed organically are found to have high water holding capacity and increased soil pH [67]. Microbes are an integral part of this system as it is seen that organic agriculture leads to increased microbial abundance and diversity [66]. Enriched microbial populations in turn help in nutrient cycling and in promoting plant growth.

Organic farming is increasingly being employed in many modern farming techniques such as, permaculture, which is a sustainable design system that mimics the natural environment and includes banishing waste in all its forms and increasing natural productivity [68]. Effective Microorganisms (EM) which are mixed cultures of naturally-occurring beneficial organisms can be used as bioinoculants to increase the biodiversity of the soil ecosystem. A greater ecosystem diversity is linked to an increase in food production. Permaculture agroecology is still in its early stages and need time and more research to finely monitor agroecosystems towards ideal biodiversity, higher resilience and quality food and habitat production.

c) Urban farming

Urban cities have their own environmental issues like generation of excessive wastes, pollution, population etc. especially with high amounts of toxic metals like copper and lead. Increased denitrification has also been reported in Urban systems [69]. Urbanization impacts microbial diversity as well, and, the microbial diversity found in such areas include both beneficial and harmful microorganisms. These microbes are involved in waste treatment, pollutant biodegradation, nitrogen fixation as well as in causing infection to plants and animals [70]. Hence, by target selection of plants and microbes, greenhouse effect and degradation of pollutants in urban area can be modulated.

OMICS approaches in understanding microbial community

Owing to the diverse role microbes play in agricultural production, as revealed in the previous sections, it becomes necessary to understand not only the composition but also the dynamics of the microbial communities of soil, plants and livestock. This understanding will help in designing efficient microbial interventions for sustainable agriculture production. OMICS techniques help in understanding the complex interactions between host and microbes. One such example is Genome-Wide Association Studies (GWAS) which determined the role of host genome in shaping gut-microbiota in mice and humans [71]. Information obtained from hundreds of omics studies in the past two decades addressed different aspects of rumen microbiome which includes feed additives and their impact on gut microbiota, early and late colonization of ruminants, diversity of enzymes, especially, glycoside hydrolases and other functional roles [72].

The understanding of plant microbiome and characterizing their functions can help in designing the strategies to enhance quality and production. Also, it helps in improving the existing knowledge of microbial habitants in different parts of various plant species. For instance, in a study, the compatible and incompatible interactions between *Solanum tuberosum* and *Phytophthora infestans* were analyzed using transcriptomic and proteomic methods [73]. In another study, root microbial communities of wheat and soybean were compared and interestingly, 60-70% rhizospheric bacteria were found to be similar, with Pseudomonas and Bacillus being in highest proportion. Recently, a study on sorghum associated root microbiome [74] has revealed a huge change in bacterial community of rhizosphere against early drought stress. Notably, drought stress enhanced Gram-positive bacteria especially Actinobacteria and Firmicutes [74]. Using plant microbiome, it has been shown that microbes controls root diffusion of minerals and maintain nutrient balance, which promises application in plant and human nutrition, food quality and safety [75]. In addition to this, microbial profiling has shown to decipher host stress even better than studying host transcriptomes [76].

However, lack of reference genomes and extensive information on different niches is a shortcoming. This can be overcome by adding more data on assembled accurate reference genome, followed by their classification under accurate operational taxonomical units (OTUs). Also, constant updates on the data and its availability to scientific community is critical for revealing the hidden potential of varied microbiota across animal world [77]. Thus, the ultimate goal of omics studies is to enhance the knowledge of roles of microbes and designing strategies for sustainable development in agriculture and livestock production.

Gaps and challenges

Though application of microbial inoculants has given successful outcomes in research, the requirement of large amounts in field conditions imposes a limitation on their use. Another factor which limits the use of microbial inoculants is their limited shelf life and a very high cost of storage of microbes [78].

Organic farming systems have been using biofertilizers for some time, however, there occur gaps in the knowledge about the strategies used by plants to recruit microbes. Also, there is a deficiency in information regarding the types of microbes which will be best suited to enhance plant nutrition from organic sources. Also, PGPR affects only specific targeted organisms, resulting in inconsistency in efficacy [79].

Microbes show a great biocontrol potential, yet challenges of efficacy in field and cost still need to be overcome. There are lacunae in the knowledge about the biology of microbes, pests and pathogen and their interaction with other microbes, host plant and environment. Unless this gap is filled, mass scale application of these microbial agents for biocontrol will not be feasible. Also, the effect of microbial inoculants on non-target organisms needs to be researched thoroughly before they are used in fields, as they could be toxic and pathogenic to them [80].

With the advent of meta-omics technologies, namely, metagenomics, metatranscriptomics, metaproteomics and metabolomics, new perspectives and newer knowledge on microbiota interactions has been revealed, however, much is yet to be deciphered. Further, the understanding of rumen microbiomes and characterizing their functions can help in designing the dietary combinations to enhance livestock quality and production.

Conclusion

Microbes play a significant role in agriculture production and thus exhibit an immense potential in developing sustainable agri-production strategies. Modern agricultural practices focus primarily on two outcomes – increase in productivity and profit for the producers. However, as per the need of the times, they need to be environment friendly too. The knowledge of microbial impact on agricultural crops can be carefully employed to achieve desired outcomes, as is discussed in this paper. For example, use of biofertilizers is rapidly replacing use of synthetic, chemical-based fertilizers and pesticides. Moreover, microbes are applied to restore fertility of soils and promote plant growth. Modulation of the gut microbiota by altering the feed, for example, is adopted to improve livestock health and increase productivity. To build up on this knowledge, multidimensional research initiatives need to be undertaken. Interventions at the policy level for example incentivizing the use of microbes for agri-production are also required. Metagenomic studies of soil microbial communities, supplanted with field studies on role of various microbial species, need to be undertaken on a global scale. In conclusion, microbes have immense potential to transform the agri-production in an eco-friendly manner for sustainable development.

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Conflict of interest

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Availability of data and material

Not applicable

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