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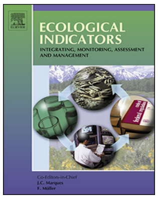

Original Articles

Connecting microbial capabilities with the soil and plant health: Options for agricultural sustainability

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ABSTRACT

Microorganisms are the key players in every agro-ecosystem. They are the natural inhabitants of all the soil and plant systems, in which they represent dominant presence in terms of their vast diversity and multipronged functional capabilities. Multifarious physical, chemical and biological factors usually represent good soil fertility status as a guaranty of sustainable agro-ecology, plant health and crop productivity. Since healthy soils are largely characterized by their profound biological and chemical behavior, microbial functionalities related to nutrient fixation, recycling, acquisition, sequestration, solubilization, mobilization, decomposition, degradation and remediation may act as definitive indicators. Functional capabilities of microbial communities associated with soils and plant parts have been critically identified and characterized in the past few decades. Application of individual microbes or their consortia in many crops established their role in finding out a supplement and/or substitute in the existing agricultural practices which are largely dependent on synthetic chemical inputs in present time. We are presenting here a detailed account of microbial community functions, their relation with the soil and plant health and the potential indicative roles they play to establish a sustainable soil ecological environment for supporting crop growth, development and yield in long term.

1. Introduction

At the time when we are looking for advances in producing more and more crops to feed the ever-increasing population and harvesting benefits from agricultural economy (Zhang et al., 2010), the adversities of the agro-ecosystem and socio-economic challenges are becoming severe. Farmers are facing issues of unpredictable climate, shrinking agricultural lands, depleting natural resources, balanced nutrition in soil and diminishing crop responses to agrochemicals. Therefore, the concerns for sustainable soil and plant health improvement are rising.

Soil is the ultimate nutrient hub and bioresource reservoir for agricultural crops. Among the all biological entities, soil harbors huge diversity of microbial life forms. The microorganisms serve as active agents for nutrient sequestration, recycling and supply to plants. Wide array of benefits are extended to the plants by the rhizosphere microorganisms that fix dinitrogen (Brahmaprakash and Sahu, 2012; Gothandapani et al., 2017), improve phosphorus uptake (Ahilandeswari and Maheswari, 2016), degrade xenobiotics and sequester heavy metals (Ahemad and Malik, 2011; Pant et al., 2016), suppress phytopathogens and pests (Feng et al., 2013; Cheng et al., 2016), improve soil aggregation (Van Veen et al., 1997; Yilmaz and Sonmez, 2017), help plants tolerate abiotic stresses (Meena et al., 2017), remediate problematic soils (Yao et al., 2010; Tiwari et al., 2011) and chelate minerals like Fe, B and Zn (Ghosh et al., 2015). The microenvironment of plant rhizosphere is a major hub for microbial diversity and functionalities that contribute enormously to the plant and soil health.

As microorganisms play crucial roles in the soil processes, any physical, chemical or biological changes happening in the soils clearly affect the microbiota. Microbes respond quickly to any changes happening in the soil ecosystem and act as true indicators for specific functions in the soil environment. Having seen the prospects and perspectives of microorganisms as critical biological players that can even play role of indicators, we elaborately described their potential functions as prominent soil and plant health indices in the agroecosystem.

2. Microbes connect roots with the soils

2.1. Nutrient cycling and organic matter decomposition

Rhizosphere is a chemically complex region having a dynamic

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microbiome (Haldar and Sengupta, 2015). This region is helpful in controlling physicochemical properties of the soil, plant growth and development activities and chemical signals that are exchanged between microbial communities and inhabiting plants (Lareen et al., 2016). Arable soil system is under continuous modifications due to microbial community functions. Adhesive properties of the extracellular compounds produced by soil microorganisms help in aggregating mineral nutrients around the roots. This aggregation facilitates increased nutrient uptake. The organic materials produced by microbes also act as protective coating against desiccation of the organisms along with improving soil aggregation. Total soil organic matter and mineral aggregates are majorly modulated by inhabiting microbial communities which improve soil structure and chemical properties in order to support plant growth and thus, are strong indicators of soil health (Kibblewhite et al., 2008).

Enzyme catalyzed microbial processes that constitute the basis for cycling of vital minerals like C, N, P, K, Fe, B and S are important for functioning of fertile soils (Alkorta et al., 2003a; Johnston et al., 2009). Nutrients assimilated by microbial biomass are added to the soils in the form of valuable organic matter embedding minerals which, are slowly released to improve soil quality (Kaschuk et al., 2010; Shahbaz et al., 2017; van der Wal and de Boer, 2017). Therefore, such microorganisms directly assimilate, sequester or adsorb mineral nutrients for continuous and slow release. These can act as positive indicators of key soil functions in nutrient cycling. Vital soil enzymes in different biogeochemical cycles are also being used as indicators for proper nutrient recycling and management in the soil ecosystem (Bastida et al., 2006; Nayak et al., 2007). Microbes are crucial entities to provide broad range of enzymes for organic matter decomposition (Wallenstein and Weintraub, 2008). Complete or partial degradation of plant residues (Castellano et al., 2015) adds the organic matter back to the soils.

In a sustainable ecosystem, nutrients flow across different tropic levels via soil macro and microorganisms (Chen et al., 2003). If we talk about climax forests, nearly 95% nitrogen re-circulates in the soil–-plant-microbe continuum (Rosswall, 1976). However in the agricultural soils, continuous depletion of nutrients by crop harvest, losses by leaching and evaporation removes substantial amount of nitrogen and other nutrients which otherwise, supports crop production (Brussaard, 2004). Microbial communities in association with other flora and fauna, play significant role in fixing biological nitrogen making it available to the plant roots and releasing organic nitrogen by decomposing N-rich plant residues (Barrios, 2007). Therefore, in the soils naturally rich in nitrogen, the microorganisms for nitrogen cycling may be considered as indicators for maintaining and improving soil nitrogen content. In fact, major advances in molecular tools readily applied for analyzing microbial communities and defining community level functional characteristics propelled the implication of such tools as biomarker for indicating and monitoring ecosystem processes associated with the soil health at global scale (Trivedi et al., 2016).

Recycling and degradation of organic matter is a vital biological process through which soil regains its lost nutrients. These nutrients are essential for the growth and development of plants in addition to soil fertility. Similarly, physical and chemical functions of soils rely majorly on biological properties that are usually regulated by diverse microbial population (Anderson, 2003). For better understanding of bacterial and fungal metabolism and dynamics in the process of organic matter decomposition, ^{13}C labeled stable isotopic analysis of mineralized C and phospholipid was performed. Radiolabeled (^{13}C) wheat residues incubated in the soil for 120 days revealed that priming and microbial enzymes are responsible for mineralization processes (Shahbaz et al., 2017). The study indicated that both bacteria and fungi worked together for phosphorus bioavailability. Here, fungi converted litter C and bacteria assimilated supplied C into biomass or recycled it back to the environment (Fabian et al., 2017). Since microbial population is cumulatively responsible for decomposition processes, they can directly add to soil fertility, crop productivity and therefore, are good indicators for improved soil health.

2.2. Nutrient acquisition

In unmanaged forest ecosystem, biological nitrogen (N) fixation is crucial for plant nutrition (Wang et al., 2010). Cyanobacteria contribute to the N economy in the soils of forest ecosystem (DeLuca et al., 2002). In paddy cultivation, various N fixing cyanobacteria fulfill N needs of the crop plants by fixing atmospheric dinitrogen. For example, *Azolla-Anabaena* symbiosis has been estimated to contribute around 600 kg N ha^{-1} (Syiem et al., 2017). Cyanolichen *Peltigera aphthosa* significantly contributes to N-fixation using vanadium nitrogenase enzyme instead of common Mo-nitrogenase in molybdenum limited forest soils (Darnajoux et al., 2017). Thus, *P. aphthosa* can be considered as an indicator organism that utilizes alternate nitrogenase system in Mo-limited conditions.

Paddy soils rich in N-fixing cyanobacterial population may reduce dependency of crops on external supply of N inputs. Many unicellular, filamentous, non-filamentous, heterocystous and non-heterocystous cyanobacterial species like *Aphanothece, Synechococcus, Gloeocapsa, Nostoc, Anabaena, Aulosira, Calothrix* and *Lyngbya* represent prominent N-fixing communities in the paddy soil. Their application could be a viable biological option for enhancing nitrogen in the soils and maintaining crop N-requirements (Singh et al, 2016). Microalgae are integrated component of paddy fields and play crucial role in rice cultivation. These organisms supplement nitrogen, other minerals and phytohormones and add biomass to the soil (Dineshkumar et al., 2017). Excessive fertilizers used in paddy cultivation may partially be replaced by the application of microalgae including cyanobacteria for crop enhancement and better grain quality (Singh et al., 2011).

In agroforestry systems, biological N fixation is a proven N fertilization method in intercropping tree species. Hybrid walnut trees intercropped with alfalfa indicated 35% improvement in light use efficiency (LUE) by alfalfa and stimulated N fixation in plant rows close to trees (Querne et al., 2017). Similarly, co-inoculation of *Enterobacter* sp. with *Microbacterium arborescens* in wheat resulted in higher N fixation (9.32 mg Ng^{-1} carbon oxidized), IAA production (27.06 TP 100 µg mL^{-1}) and P-solubilization (112.27 µg mL^{-1}) (Kumar et al., 2017). Enhanced yield was recorded with higher plant uptake of N, P, Zn, Cu and Mn. These microorganisms are indicative of sustainable N nutrition in the crop plants.

Various bacterial and fungal species facilitate belowground phosphorus (P) solubilization and mobilization. P-solubilization may not be due to phosphate solubilizing bacteria (PSB) alone (Pii et al., 2015), interaction among different rhizobacteria, PSB and mycorrhiza may also account for prominent results (Antoun, 2012). Bacteria adhered to the hyphae of mycorrhiza add to P mobilization by the mycorrhizal organisms (Sieverding et al., 2014), which in turn help these bacteria to proliferate by providing attachment surface and nutrition (Taktek et al., 2015; Kaiser et al., 2015). Mycorrhiza solubilize more phosphorus in presence of PSB (Taktek et al., 2015) and bacteria like *Burkholderia anthina* Ba8 and *Rhizobium miluonense* Rm3. Biofilm forming mycorrhiza, hyphobacteria and mycorrhizobacteria enhanced solubilization of igneous phosphate rocks, which are rather slow to solubilize and therefore, facilitate steady release of P to the plants (Taktek et al., 2017).

2.3. Production of phytohormones

Microorganisms have inherent capability to produce phytohormones like indole acetic acid (IAA) (Spaepen and Vanderleyden, 2011), gibberellins (Baca and Elmerich, 2007), cytokinins (Pieterse et al., 2012) and ethylene (Gamalero and Glick, 2015) that influence plant growth and development. Improvement in host immunity against pathogens in plants treated with IAA producing *Azospirillum* sp. is reported by Spaepen et al. (2007). Similarly, gibberellic acid (GA)

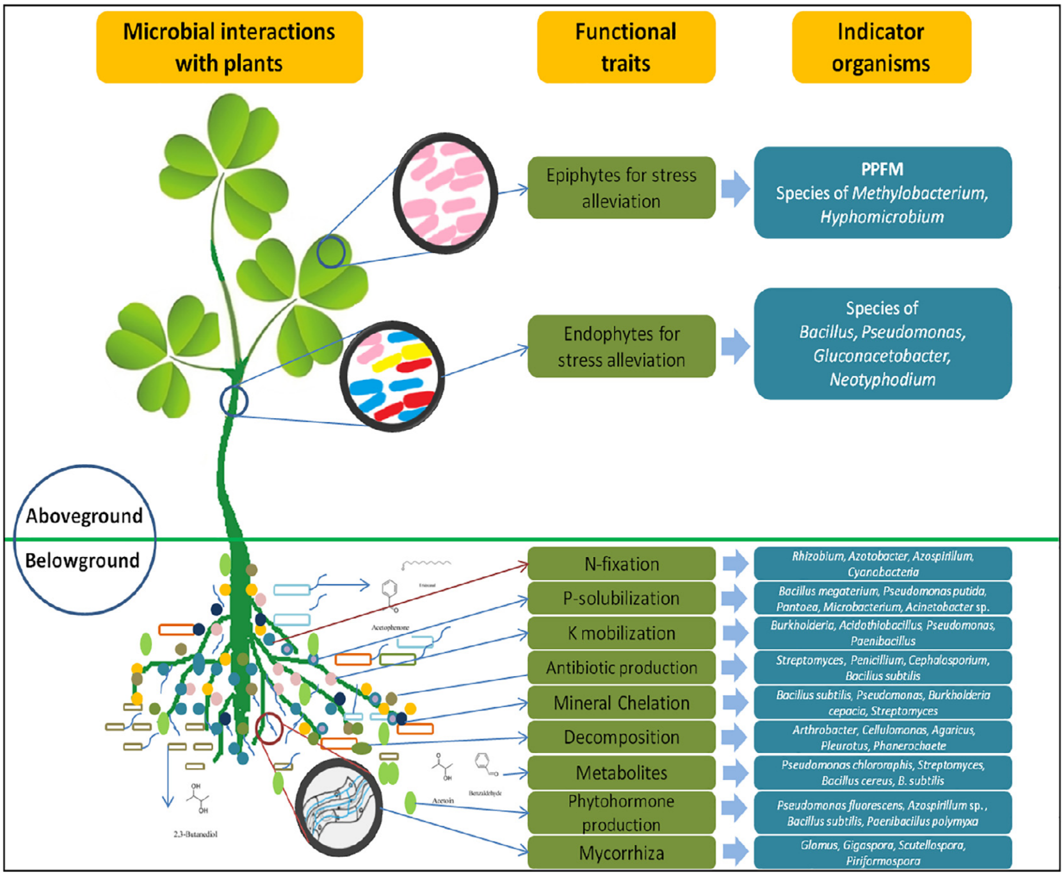

Fig. 1. Microbial associations with plants and soils and their inherent functional attributes that make them potential indicators for plant and soil health management.

producing *Azospirillum brasilense* and *A. lipoferum* was reported to promote shoot elongation, reverse dwarfism and enhance root hair density in rice and maize (Baca and Elmerich, 2007). GAs are reported to contribute towards germination and elongation in plants (King and Evans 2003) and also regulate plant growth by degrading DELLA proteins (Pieterse et al., 2012). Cytokinins play important role in cell division and defence responses against biotrophic plant pathogens (Pieterse et al., 2012). Microbe-mediated increase in the level of cytokinins in the plants is widely reported (Arkhipova et al., 2005; Ortíz-Castro et al., 2008). Microorganisms also produce ACC (1-aminocyclopropane-1-carboxylate) deaminase that reduces ethylene levels in plants in order to alleviate secondary effects of stress (Glick, 2014; Gamalero and Glick, 2015). In this way, phytohormone producing microbial communities entwined with plant growth promotion can be used as indicators in plant health management practices (Fig. 1).

2.4. Plant growth promotion

Bacterial capabilities for different functional traits [like fixation, solubilization and mineralization of N, P, K, Zn and production of siderophores and hydrocyanic acid (HCN)] make them prominent plant growth promoting microorganisms (Singh et al., 2011; Meena et al., 2017; Felestrino et al., 2017). Studies on microbial metabolic multifunctionalities have paved the way for developing microbial inoculants for plant growth promotion, biological control of pests and pathogens, bioremediation of contaminant soil sites and decomposition and degradation of agricultural wastes (Singh et al., 2016a,b). Thus, the soils richly inhabited by organisms like N-fixers, P-solubilizers, phytohormone producers and bioremediators are supposed to support plant health. The surge of ecofriendly approaches in agriculture inspires and promotes usage of microbial biofertilizers. Worldwide, functional trait rich microorganisms have been used to perform their specific functions for making soils fertile, productive and sustainably performing for plant tolerance to stresses and crop productivity (Bhardwaj et al., 2014).

Use of plant growth promoting biofertilizer BioGro by rice farmers in Mekong Delta, Vietnam reduced usage of chemical fertilizers by 52% (Nguyen et al., 2017). The results are based on the application of inoculant for fifteen years in more than twenty experiments in Vietnam and Australia on different aspects of nutrient use efficiency, plant growth promotion, biochemical and molecular parameters. Coupled application of fertilizers and biofertilizers improved sweet potato yield in Uganda. Arbuscular mycorrhizal inoculation in sweet potato cultivar NASPOT 11 with NPK fertilizers enhanced yield by 12.8–20.1 T ha^{-1} as compared to 4.5 T ha^{-1} of existing yield (Mukhongo et al., 2017). Inoculation of host specific bacteria, especially endophytic and rhizospheric microflora promotes growth in mandarin orange (Thokchom et al., 2017). In fennel, improvement in the growth and essential oil content was observed due to application of biofertilizers and cold water extract (El-Azim et al., 2017). The findings has supported the fact that microbial inputs can not only support plant growth but also bring qualitative and quantitative changes in the produce quality and content.

Growth enhancement by the use of PGPRs doesn't add to the greenhouse gas emission. An experiment conducted to assess the impact of biofertilizers on growth of paddy and green house emission from alluvial soils of Indonesia showed that emission of N_2O, CH_4 and CO_2 was reduced after application of biofertilizer 'Biotara' and 'Biosure' in rice. It indicated that biofertilizers enhanced yield with only 75% of recommended dose of chemical fertilizer without any further enhancement of greenhouse gases (Hadi and Nur, 2017). The application of *Trichoderma* enriched biofertilizer enhanced plant growth and yield up to 12.9% when a 100% biofertilizer and compost mixture was used. This further improved mineral content and antioxidant level (ascorbic acid, β-carotene and lycopene) in plants and fruits (Khan et al., 2017).

Growth promotion, harvest index and nutrient use efficiency was reported using nitrogen fixing and P-solubilizing biofertilizers in sesame (Asl, 2017). Examples prove that the inoculation of trait-specific microbial formulations has potential application on growth and nutritional health in the crop plants.

2.5. Soil health management

The goal of enhanced crop productivity could not be fulfilled without sustainable soil health management. Soil health means to maintain its inner physicochemical and biological capabilities to support all life forms and sustain their growth and development (Doran and Safley, 1997). Microorganisms provide a great strength to the soil health by influencing physical, chemical and organic conditions at a time. The preference for minimum tillage over conventional tillage provides much better soil and moisture conservation options to improve soil quality because it increases the population of aerobic and facultative aerobic microorganisms significantly as compared to deeply ploughed soils. Content of organic C, organic N, potentially mineralizable N, water, phosphatase and dehydrogenase enzymes were also high in zero till soils (Doran, 1980). Results reflected altered positive physical and chemical parameters due to enhanced biological activity regulated by microorganisms and microfauna (Kaschuk et al., 2010). Therefore, for monitoring health and quality parameters of any soil, microbial population and functions can be employed.

Microbial inoculants improve plant growth and restore soil fertility (Singh et al., 2016a,b). Improved aggregate stability and organic carbon content were observed in clay loam soil due to the application of vermicompost clubbed with microbial inoculants like *Glomus* sp., *Chlorella* sp., *Bacillus megaterium, B. subtilis, Panibacillus azotofixans* and *Pantoea agglomerans* in various combinations (Yilmaz and Sonmez, 2017). Soil health improvement using composted straw and bioformulation containing *Trichoderma* resulted in significant decline in brown spot, sheath blight and bacterial leaf blight disease owing to induce systemic resistance (ISR) and enhancement in yield up to 0.8–3.0 ton ha^{-1} in rice (Simarmata et al., 2016). Enhanced soil fertility, luxuriant growth and yield in tomato were also reported by the inoculation of biofertilizer containing *Bacillus* sp. and *Burkholderia* sp. in biochar and flyash based bioformulation (Tripti Kumar et al., 2017). These studies reflect similar line of impact of microbial application on different crops and soil conditions.

Soil aggregation, a vital feature for plant growth is likely to be affected by biotic and abiotic factors (Asano and Wagai, 2014). A huge network of fungal hyphal mesh, as in case of arbuscular mycorrhizal fungi (AMF) that makes symbiosis with roots of most of the plants is crucial for formation and stability of soil macroaggregates ($> 250\,\mu m$) (Oades, 1984; Miller and Jastrow, 2000). AMF also have extraradical mycelium and secrete organic substances which help in the formation of microaggregates ($< 250\,\mu m$) (Tisdall and Oades, 1982; Rillig and Mummey, 2006) that significantly contribute soil aeration and particle structure. Influence of AM on aggregate stability was assessed in semiarid vertisols of India in *Sorghum bicolar,* in which inoculation showed higher soil stability and larger particles (Bearden and Petersen, 2000). Relationship of glomalin (protein secreted by mycorrhiza) content and soil aggregate stability was further assessed in five plant species where higher glomalin content showed more aggregate stability suggesting that different plant and AM species e.g. *Rhizophagus irregularis, Septoglomus deserticola*, and *Gigaspora gigantea* influence aggregate capacity of soils differently (Leifheit et al., 2014; Kohler et al., 2016). Soil aggregation is also affected by specific plant root, rhizospheric microflora and mycorrhizal interaction (Rillig et al., 2015). Mycorrhiza infection in the soil is indicative of good soil aggregation. In coarse grained soils on the slopes of Swiss Alps, studies on the impact of mycorrhizal inoculation on soil aggregate stability, plant survival and fine root development showed that repeated inoculation of AM improved aggregate stability in soils and the practice was demanded for long term inoculation to maintain mountain slopes (Bast et al., 2016).

2.6. Biocontrol activity

Healthy soils represent minimum retention of disease causing biotic agents within them to facilitate infection-free conditions for the seeds during germination and early stage plant development. This could be achieved by application of effective microbial inoculants. Inoculation of *Bacillus* sp., *Paenibacillus* sp., *Enterobacter* sp. and *Klebsiella* sp. showed growth inhibition of pathogens *Colletotrichum fulcatum* and *Macrophomina* sp. (Arthee and Marimuthu, 2016). Report confirms that due to the production of salicylate and catechol-type siderophores along with HCN, lipopeptide, iturin and surfectin, microbial inoculants succeeded to suppress phytopathogens. Microorganisms or their key products can be used as indication of healthy and disease-resistive soils. Besides *Bacillus thuringiensis, Metarrhizium anisoplae* and *Baeuveria bassiana* were useful in the management of insect-pests. Application of *Pseudomonas fluorescens*, *Bacillus subtilis*, vermicompost and humic fertilizers also reduced incidence of tomato leaf miner (*Tuta absoluta*) (Mohamadi et al., 2017). Reduction in adult longevity period of *Myzus persicae* was shown in bell pepper and chili pepper by application of *Glomus intraradices* + *Bacillus subtilis* treatment. Enhanced plant growth was also reported from *Bacillus subtilis* and $ZnSO_4$ application (Mardani-Talaee et al., 2017). These microorganisms are known biocontrol agents and their application was sufficient to significantly reduce net reproductive rate, increase intrinsic rate of natural population and final rate of increase of *T. absoluta*.

Similarly, the inoculation with arbuscular mycorrhizal (AM) fungus affect the expression of defense related genes like β-1, 3 glucanases, chitinases and oxalate oxidase in wheat infected with *Fusarium oxysporum*. Improvement in growth, yield and β-1, 3 glucanase expression was reported (Sabbagh et al., 2017). Successful suppression of root knot nematode (*Meloidogyne incognita*) in Pusa Ruby cultivar of tomato was also observed by the application of microbial inoculants. Application of biofertilizer (*Azospirillum*, *Azotobacter* and PSB) with balanced dose of NPK (125:50:100 kg ha^{-1}) resulted in 74.8% reduction in nematode population in the soil along with reduction in root knot (75.8%) and increase in plant dry weight (62–64%) (Patra et al., 2017). Biocontrol of *Ralstonia solanacearum* was reported by the use of chitosan obtained from *Cunninghamella elegans* (Oliveira et al., 2017). In banana, treatment of *Bacillus amyloliquefaciens* NJN-6, which suppressed the growth of *Fusarium* and *Ralstonia* like pathogens under field conditions, also caused plant health promotion (Fu et al., 2017). These studies helped to establish new roles of PGPRs as biocontrol agents against pests and nematodes and as biological indicators for disease and pest suppression.

2.7. Alleviation of abiotic stress

Microbes have evolved diverse weapons (genes, proteins and metabolites) to fight challenges posed by abiotic factors due to their adaptive behaviour in adverse abiotic conditions and evolutionary diversification. These functions could be of great help for plants to combat abiotic stresses if exploited judiciously (Rojas-Tapias et al., 2012; Shilev et al., 2012, Bashan et al., 2014; Bacilio et al., 2016; Meena et al., 2017). Application of *Pseudomonas stutzeri* with humic acid forming ability improved K^+/Na^+ and Ca^{2+}/Na^+ ion ratio and growth in bell and chili pepper indicating mitigation of negative impacts of salinity stress (Bacilio et al., 2016). Biochar based *Bradyrhizobium* inoculation was beneficial for lupin under abiotic stress, where it enhanced nodulation and N and P uptake under drought conditions (Egamberdieva et al., 2017).

Table 1
Microbial functional traits that can act as indicator soil functions.

S. No.	Functional Traits	Indicator functions	Indicator Microorganisms	References
1.	Toxicity in mining areas	Bioleaching, adsorption, bioaccumulation	*Arthrobacter globiformis*	Marques et al. (2014)
2.	Soil aggregate stability	Glomalin content	Arbuscular mycorrhizal fungi	Kohler et al. (2016)
3.	Nitrogen fixation	Nitrogen content and organic nitrogen	*Rhizobium, Azotobacter, Azospirillum, Cyanobacteria*	Hardy et al. (1973), Dabundo et al. (2014)
4.	Nitrogen removal	Nitrification, denitrification, ammonium removal	*Chlorella vulgaris*, microalgae, microbial communities	Delgadillo-Mirquez et al. (2016), Xu et al. (2017)
5.	P-solubilization	Organic and inorganic acids, phosphatase, phytase, siderophores	*Bacillus megaterium, Pseudomonas putida, Pantoea, Microbacterium, Acinetobacter* sp.	Pii et al. (2015), Sahu et al. (2016), Kumar et al. (2017)
6.	P-mobilization	Mycorrhizal infection	Mycorrhiza	Antoun (2012), Taktek et al. (2017)
7.	K-solubilization	Available potassium content	*Burkholderia, Acidothiobacillus, Paenibacillus* sp.	Singh et al. (2010), Parmar and Sindhu (2013)
8.	Nutrient status	High pH soils and desserts Nitrogen poor soils Nitrogen rich soils	Actinobacteria, Cyanobacteria *Azorhizophilus Nostoc, Chloronema, Phormidium* and *Microcoleus* Nitrosomonadaceae, Anaerolineae and Thermomicrobia	Shange et al. (2012), Sharma et al. (2014) Jiménez-Bueno et al. (2016) Jiménez-Bueno et al. (2016)
9.	Tillage practice	Zero tillage	*Actinomycetospora, Sphaerisporangium, Clavibacter* and *Mycobacterium*	Navarro-Noya et al. (2013)
10.	Crop residue management practices	Partially incorporated residues Completely incorporated residues No incorporation Removal of residual Burning of residues	Acidobacteria Burkholderiales Proteobacteria Gemmatimonadetes and Armatimonadetes *Chloroflexi, Bacillus, Alicyclobacillus,* Actinobacteria, Acidobacteria	Jiménez-Bueno et al. (2016) Jiménez-Bueno et al. (2016) Jiménez-Bueno et al. (2016) Jiménez-Bueno et al. (2016) Zhou et al. (2007), Yang and Ponce (2011)
11.	Competitive inhibition of pathogens by Fe-Chelation	Presence of siderophore	*Bacillus subtilis, Pseudomonas, Burkholderia cepacia, Streptomyces*	Loper (1988), Khamna et al. (2009), Frenkel et al. (2017)
12.	Sulfur metabolism and herbivore defense	Volatile organic compounds (VOCs)	*Bacillus amyloliquefaciens* GB03	Aziz et al. (2016)
13.	Plant growth promotion	VOCs: 13-Tetradecadien-1-ol, 2-Methyl-n-1-tridecene and 2-Butanone	*Pseudomonas fluorescens* strain SS101	Park et al. (2015)
14.	Draught alleviation	VOCs: 2,3-butanediol	*Pseudomonas chlororaphis* O6	Cho et al. (2008)
15.	Induced systemic resistance against *Botrytis cinerea*	VOCs	*Bacillus subtilis* GB03	Sharifi and Ryu (2016)
16.	Disease suppressive soils	VOCs	*Streptomyces* spp.	Cordovez et al. (2015)
17.	Soil borne fungal pathogens	VOCs	*Trichoderma* spp.	Dubey et al. (2007)
18.	Plant growth promotion	VOCs: albuterol, 1, 3-propanediole	*Bacillus subtilis* SYST2	Tahir et al. (2017)
19.	Soil sickness	Decreased maturity index and increased plant parasite index	Nematodes	Bongers et al. (1997)
20.	Biocontrol of *Colletotrichum fulcatum* and *Macrophomina* sp.	salicylate and catechol type siderophores	*Bacillus* sp., *Paenibacillus* sp., *Enterobacter* sp. and *Klebsiella* sp.	Arthee and Marimuthu (2016)
21.	Reduce infection of tomato leaf miner (*Tuta absoluta*)	Disease suppression	*Pseudomonas fluorescens*, *Bacillus subtilis*	Mohamadi et al. (2017)
22.	Abiotic stress tolerance	Stress alleviating metabolites and proteins	*Methylobacterium, Hyphomicrobium*	Lee et al. (2015), Meena et al. (2017)
23.	Biological control of *Ganoderma boninense*	Volatile and non-volatile compounds	*Penicillium citrinum* BTF08 (endophyte)	Cheong et al. (2017)
24.	Management of *Ralstonia solanacearum* in pepper	2,3-butanediol	*Bacillus subtilis* (endophyte)	Yi et al., (2016)

3. Microorganisms as indicators of soil health

3.1. Microbial indicators

Soil is a dynamic, vital and continuously changing reservoir of physical, chemical and biological factors. Various biotic and abiotic components interact with the soil to affect its composition. Microbial populations with distinct and definite functions are the major inhabitants that change structural and functional characteristics, which in turn is reflected in the biological properties of the soils. Such changes could be used as related parameters to measure soil health. As microorganisms reflect the status of soil and respond to the changes, they serve as a good biological indicator to monitor soil quality and health (Table 1).

Tremendous physiological adaptation with excellent metabolic versatility makes bacteria key agent to indicate changes in the soil ecosystem adjacent to the plant roots *i.e.* the rhizosphere. An accurate and sensitive correlation between microbes and their environmental factors can measure the behavior of the population and the impacts of population dynamics on edaphic factors to indicate soil health. Compared to other indicators, biological indicators exhibit the advantage of having easy and fast measurement technique making it cost effective and sensitive tool for monitoring soil quality (Alkorta et al., 2003a; Wessén and Hallin, 2011; Niemeyer et al., 2012; Cardoso et al., 2013; Dose et al., 2015) as they reflect rapid response to natural and anthropogenic changes. Pankhurst et al. (1995) studied biological parameters of soil in response to different agricultural management practices for plant growth and development as indicative of soil health in long term field trials. Load of different soil microbiota, macrobiota, enzyme activity and organic matter decomposition were analyzed in varied agronomic practices (Bending et al., 2002). Studies concluded that carbon mineralization and soil microbial biomass was significantly affected by tillage practice, stubble management, N-fertilizers and crop rotation which affected mycorrhizal fungi, soil protozoa, N nutrition, soil peptidase activity and cellulose decomposition (Pankhurst et al., 1995; Bending et al., 2002). Such studies directly linked soil biological properties with the population of mycorrhiza and other microbes that are dominant indicative organisms in the soil.

Microbial soil enzyme activity is a proven indicator of soil health providing information of key soil-ecological processes in a better resolution than physical or chemical parameters (Alkorta et al., 2003b). Live or dead microbial cells in the soils are prominent sources of soil enzymes apart from the plants and animal resources (Baldrian, 2009). Therefore, they could be a rather sensitive indicator to be able to indicate even small changes in the soil physicochemical properties. Biological indicators, have an edge over other indicators in being very sensitive and reproducible (Dose et al., 2015). The resilience of microorganisms in the soil towards ecological disturbances and its relative sensitivity to respond to these changes can make these organisms suitable indicators. Dose et al. (2015) studied the reclamation of sodic soils for improving soil health, in which microbial indicators (gene copies of nitrifier and denitrifier, soil enzymes including nitrate reductase, arylsulfatase, alkaline phosphatase, ammonia monooxegenase, β glucosidase, fluorescein diacetate hydrolysis and urease) were proven to be highly sensitive even to the small changes to distinguish between land use and application of amendment in short term as compared to other physicochemical indicators which failed to distinguish such changes.

Omics, metaomics and bioinformatics based assessment of indicator microbial communities can provide multifold higher sensitive indication than others (Alkorta et al., 2003a; Wessén and Hallin, 2011). Assessing gene copies of indicator microorganisms clearly indicated that gene copy ratio of ammonia oxidizing archaea to ammonia oxidizing bacteria serves as a microbial indicator in order to assess nutrient status, disturbance in land use and climate change (Wessén and Hallin, 2011). In contaminated and non-contaminated (or degraded) soils, structure and function of microbial population vary distinctly and reflect clear and dominant presence of such microorganisms that qualitatively reflect the level of contamination (Singh, 2015). Enhanced microbial functions that may include biodegradation, bioaccumulation, sequestration, adsorption and biosorption may reduce the level of contaminants in the environment (Avidano et al., 2005) and thus, establish functional equilibrium in the degraded ecosystem for promoting ecosystem sustainability (Singh, 2015). The sites contaminated with heavy metals are not practically fit for crop production and food quality. In quality evaluation of heavy metal contaminated soils, indicator processes of microbial origin like soil respiration, microbial biomass, carbon and nitrogen, acid phosphatase and asparaginase activity, ammonifying and ammonium oxidizing microflora, nitrification and qCO_2 (metabolic quotient for CO_2) significantly assess elevated ecological risk parameters (Moreno et al., 2009; Niemeyer et al., 2012). These soil quality indicators can be used for monitoring the level of contaminants (Castaldi et al., 2004; Niemeyer et al., 2012), on the basis of which reclamation and restoration strategies could be developed (Nogueira et al., 2006; Clemente et al., 2007).

The parameters that relate to carbon and nutrient cycling can be exploited for better crop health in contaminated locations (Tu et al., 2006; Gülser and Erdogan, 2008). Also, from the contaminated sites, many bacterial and fungal species have been isolated and characterized. This can help plants in alleviating heavy metal stresses. Furthermore, metagenomic methods have led to the characterization of dominant microbial communities in contaminated soils and groundwater (Hemme et al., 2010). Such methods helped in revealing population dynamics as a marked divergence in the belowground structure of microbial communities and associated functions (He et al., 2010). These studies helped in generating deeper insights into potential microbial community structures and their associated feedback regulatory responses towards sustainability of elevated carbon dioxide in the terrestrial ecosystem of agricultural importance (Yang et al., 2012).

Deploying nematodes as candidate for soil health indicator is another good strategy as nematode composition reflects two vital ecological processes, nitrogen cycling and decomposition (Neher, 2001). The cultivation practices like tillage operation, crop rotation, water, nutrient and pest management affect soil organisms (Van Bruggen and Semenov, 2000). The shift in nematode community by short and long term disturbances have been studied (Korthals et al., 1996; Bongers et al., 1997) and it was found that the disturbance caused a decline first and then increase in the nematode maturity index whereas a permanent damage was observed in community structure leading to extinction of organisms in long run (Ettema and Bongers, 1993; Korthals et al., 1996). Decreased maturity index under enhanced nutrient conditions and increased plant parasite index was reported as characteristic indication of poor soil health (Bongers et al., 1997). As far as the microbial communities along with the nematodes are concerned, both vary with soil aggregate fractions but efficiently contribute towards whole soil food web system (Briar et al., 2011).

Microorganisms can also be used in advance weed management by deciphering relationship between weed soil seed bank and signature community shift associated with them. Studies reveal that impact of soil microbial population could structure plant community including seedling recruitment and species abundance by controlling their decay and germination (Schafer and Kotanen, 2004). In a rather specific outlook, these microbes do have impact on soil seed bank (Chee-Sanford et al., 2006). Great economical benefits can be drawn by identifying such strong connections with long lived weed seed bank in soil which can be one of the best tools to supplement modern weed control strategies. Metagenomic approach can be used as supplement in establishing relationship between soil seed bank of weeds and key impacting microbes on that. Such sets of microbial soil indicators could identify the areas with long lived weed seeds to stop sizable addition of weed seeds in the areas with low weed intensities.

3.2. Microbial functions in agronomic practices

Healthy agronomic practices help soils to produce healthy crops (Dias et al., 2015). As microorganisms are key participant in most of the biological processes in soils (Nicolas et al., 2012; Jiménez-Bueno et al., 2016) and their community composition keeps on changing with the developmental stages of the plants, frequent and abrupt changes in agricultural practices affect the microbial population buildup, disintegration or loss (Schneider et al., 2010; Lupwayi et al., 2012). The changes in microbial community behavior are an indicator of corresponding factors (Jiménez-Bueno et al., 2016) that help selection of sustainable agro-ecological practices. Higher number of actinobacteria is found in high pH soils and desserts (Shange et al., 2012; Jiménez-Bueno et al., 2016). *Azorhizophilus* and other diazotrophs like *Nostoc, Chloronema, Phormidium* and *Microcoleus* are indicative in poor N soils. Similarly, microorganisms belonging to Nitrosomonadaceae, Anaerolineae and Thermomicrobia dominate in nitrogen rich agricultural soils. Cyanobacteria can survive even in dessert and provide N, P and phytohormones to plants and shown their presence in nutrient poor soils (Sharma et al., 2014). Low population of actinobacteria like *Actinomycetospora, Sphaerisporangium, Clavibacter* and *Mycobacterium* are indicative of high tillage practices as their relative abundance increases in zero-tillage compared to conventional one (Navarro-Noya et al., 2013).

Microbial communities are also real players in crop residue management. Various practices used in the fields favor proliferation and dominance of different taxa of microorganisms with decomposition and degradation functions (Verhulst et al., 2011; Dias et al., 2015). Acidobacteria is indicator for partially incorporated residues whereas Burkholderiales indicate complete incorporation of residues up to final breakdown. Gemmatimonadetes and Armatimonadetes indicate partial removal of crop residues whereas various Proteobacteria dominate on leftover crop residues in the fields (Jiménez-Bueno et al., 2016). Bacterial indicator taxa such as *Chloroflexi, Bacillus, Alicyclobacillus,* Actinobacteria, Acidobacteria, Bacteroidetes and Verrucomicrobia indicate such soil conditions where the crop residues are burnt in the fields. These microbes can sustain high heat conditions by forming endospores and other resistant structures (Zhou et al., 2007; Yang and Ponce, 2011; Jiménez-Bueno et al., 2016).

3.3. Microbial volatile organic compounds (MVOCs)

Microbial volatile organic compounds are low molecular weight organic molecules of high volatility. The release of VOCs by bacteria is directly correlated with plant growth promotion (Bailly and Weisskopf, 2012). Their presence mediates microbe-plant interactions that drive plant nutrition (Hofmann, 2013). Production of 2,3-butanediol and acetoin by *Bacillus* strains GB03 and IN937a indicated that these volatile compounds induce plant growth and systemic resistance in cytokinin signaling mutant of *Arabidopsis* (Farag et al., 2006). VOCs secreted by *Pseudomonas fluorescens* SS101 augment plant growth *in vitro* and *in planta* studies indicating their key role in plant growth promotion (Park et al., 2015). MVOCs are used as info-chemicals in plant–microbe and microbe-microbe signaling (Aziz et al., 2016; Tahir et al., 2017) where these compounds enable plants sense microbial presence and understand complex ecological interactions. Since these compounds have profound applications in signal transduction, their presence indicates corresponding impact on soil and plant health (Park et al., 2015). Volatile molecules of bacterial origin can facilitate sulphur nutrition to their associated plants (Hofmann, 2013). Such studies are strong validation to the fact that microbes producing volatile molecules are good indicators of healthy microbial communities with distinct functions that attract plants for enhanced interaction, nutrition and mutual benefits.

4. Microbial management of nutrient use efficiency

The management of nutrients in the intensive cropping system is important because of the two prominent reasons, (i) the availability of the minerals, and (ii) the root/rhizosphere capability to uptake nutrients. In the last four decades, global consumption of nitrogenous fertilizers in agricultural crops increased 7.4 fold while the overall crop yield increased by 2.4 folds only (Hirel et al., 2011). It suggests that excessive use of fertilizers cannot guaranty efficient uptake of nutrients by the plants. Nutrients may be lost due to leach out, surface runoff and volatilization or degraded due to denitrification, eutrophication and other biological processes (Fageria and Baligar, 2005) causing environmental hazard and economic loss (Diaz and Rosenberg, 2008; Adesemoye and Kloepper, 2009). Various local strategies like use of neem cake, thiourea, split application of fertilizers, encapsulation, and other management practices can enhance nutrient use in plants (Fageria and Baligar, 2005), but more practical, reliable and applicable management strategies involves manipulation of soil environment, rhizosphere biology, plant features, fertilizer variables and application of microbial inoculants (Kumar et al., 2016).

Microorganisms have tremendous capacity to improve nutrient use efficiency. Four important groups of microbial inoculants that include i) PGPRs, ii) arbuscular mycorrhizal fungi (AMF), iii) N fixing rhizobia (non-PGPRs) and iv) free-living N-fixing cyanobacteria possess the capacity to facilitate plants to take up the nutrients more efficiently (Adesemoye et al., 2008). Role of microbial inoculants in enhancing nutrient use efficiency of plants have been demonstrated (Adesemoye et al., 2009; Richardson and Simpson, 2011; Dodd and Ruiz-Lozano, 2012; Sharma et al., 2013; Owen et al., 2015; Garcia-Gonzalez and Sommerfeld, 2016; Kumar et al., 2016). In the rhizosphere, microbial diversity, competitiveness and dominance influence efficient mobilization, acquisition and exploitation of soil nutrients (Shen et al., 2013). Microbial interactions with the rhizosphere therefore, can improve root growth, size, development, proliferation, root architecture, mineral dissolution, mobilization, conversion into usable forms and enhance supply through slow but steady release to facilitate plant growth (Zhang et al., 2010). The use of PGPRs with AM fungi as supplements to chemical fertilizers where reduced dose of fertilizers was used, showed promising results (Adesemoye and Kloepper, 2009). Vermicompost and chitosan from *Cunninghamella elegans* applied with recommended dose in banana showed that the organic matter could be a suitable additive to chemical fertilizers (Stamford et al., 2017).

4.1. Nitrogen use efficiency

N and P are the major soil nutrients essentially required by the crops. Their deficiency either due to unavailability or acquisition by the plants causes severe crop losses. Microorganisms like cyanobacteria, bacteria and AM fungi improve utilization and enhance end-use efficiency of N and P in soils (Briones et al., 2003; Adesemoye et al., 2009). PGPR inoculation in oil palm seedlings in Malaysian nursery resulted in higher uptake of N and P (Amir et al., 2005). Two *Pseudomonas fluorescens* strains (ACC50 and ACC73) applied in wheat with different levels of N, P, and K enhanced 27% higher N and P use efficiency over control with 100% recommended dosage of NPK fertilizers. The performance for improving nutrient use efficiency was better in case of ACC50 as compared to ACC73 in pot and field trials (Shaharoona et al., 2008). PGPR inoculated plant roots reflected enhanced N uptake in three years of field study, which further showed increased plant N content due to improved utilization of fertilizers as a part of integrated nutrient management (INM) system (Adesemoye et al., 2008).

Field experiments with microbial consortium containing *Azotobacter chroococcum, A. brasilence, Glomus mosseae* and G. *fasciculatum* in pomegranate indicated that dual inoculation of strains led to increased uptake of N, P, K, Ca, and Mg apart from enhancing plant growth. Adesemoye et al. (2008) suggested that the dual inoculation of microbes provided more consistent results on nutrient uptake. A field experiment conducted to test nutrient use efficiency and produce quality in the crop showed that inoculation of *Gluconacetobacter diazotrophicus* and P solubilizing bacteria (PSB) with 75% of the recommended dose of N and P resulted in improved growth and production of two eye bud sets in sugarcane seed plot. This has verified that in sugarcane, microbial inoculants improved nutrient use efficiency and enhanced soil quality (Murumkar et al., 2017). The effect of fertilizer, biofertilizer and brassinosteroids on yield and economics of fenugreek was reported (Godara et al., 2017). Dual inoculation of *Rhizobium* with PSB resulted in higher yield attributes, seed yield and net crop return. Combined application of biofertilizer and brassinosteroids also saved almost 20% of chemical fertilizer for similar yield.

In nutrient poor soils also, microbial inoculants enhance efficiency and availability of nutrients to the plant roots (Souza et al., 2015). In oat grown in reclaimed sodic soil, application of *Trichoderma* and P solubilizing bacteria with combined nitrogen, phosphorus and potash (NPK) and farm yard manure (FYM) in integrated approach resulted in better growth (Kashyap et al., 2017). Such studies were also carried out in summer mung bean in which, integrated application of NPK with vermicompost, biofertilizer, Mo and Co facilitated high nutrient use and yielded crops with high protein content (Singh et al., 2017). Microbial inoculants can therefore, serve as novel candidates in integrated nutrient management to indicate improved nutrient use efficiency.

4.2. Phosphorus use efficiency

Despite of the fact that most of the soils possess high amount of total P, the pool of available P in the soil is quite limited (Margalef et al., 2017). Phosphorus is fixed into soil as stable complexes with metal ions like Al, Fe and Ca that make substantial amount (up to 75–90%) of P unavailable for plant uptake (Igual et al., 2001; Gyaneshwar et al., 2002). Therefore, a higher amount of P is required than that actually needed for crops (Ohno et al., 2005). Beneficial microbes solubilize unavailable P in the soils into available forms for plants (Collavino et al., 2010; Owen et al., 2015). Application of a mixture of organic and biofertilizer (*Pseudomonas putida* and *Bacillus subtilis*) that increased solubility of triple superphosphate (TSP) in alkaline soils improved P use efficiency in wheat. High available P content was reported from 75% TSP application, organic matter and *Pseudomonas putida* (Nosratabad et al., 2017). Mycorrhizal colonization, through its extended mycelial mesh, enhances P use efficiency in plants by mobilizing P in the soils and growth and extension of plant roots (Smith et al., 2011; Richardson and Simpson, 2011). Application of bacterial inoculants with organic fertilizers along with the AM fungi benefited plants. Improved N and P uptake was observed by co-inoculation of basidiomycetes fungus *Piriformospora indica* with *Pseudomonas* in *Vigna mungo* (Kumar et al., 2012). P solubilization is an important characteristics of many bacterial and fungal communities that when dominantly present in the soils may indicate for better P availability for plants.

4.3. Microorganisms improve use efficiency of other nutrients

Plant's efficiency to use of various other nutrients is facilitated by certain microbial species. Inoculation of PGPR *Pseudomonas fluorescens* and *Acinetobacter* sp. helps plants for higher uptake of N, P, K, Ca, Mg, Fe and Zn (Khan, 2005; Sahu et al., 2016). Arbuscular mycorrhizal (AM) fungi (*Glomus intraradices* and *G. mosseae*) and *Pseudomonas mendocina* improve the uptake of N, P, Ca, Fe and Mn in lettuce (Kohler et al., 2008). Significant improvement in Mg content in *Sesbania aegyptiaca* and *S. grandiflora* seedlings after inoculation of *Glomus macrocarpum* was observed in saline soils (Giri and Mukerji, 2004). Increased acquisition of Cu, Zn, Fe and Mn was achieved through mycorrhizal association in maize (Liu et al., 2000). Compost tea used with organic matter and inoculants enhanced uptake of macro and micronutrients by strawberry plants (Hargreaves et al., 2009).

Micronutrient uptake was also affected by plant growth promoting rhizobacteria. Improved Zn acquisition was observed in shoot, leaves and grains by the application of *Pseudomonas, Azospirillum* and *Rhizobium* that facilitated efficient nutrient uptake in wheat (Naz et al., 2016). Application of *Trichoderma harzianum* enhanced uptake of essential nutrients in salt affected mustard (*Brassica juncea*) in which oil content, antioxidant activity, osmolyte accumulation and NaCl exclusion was observed as mechanisms to alleviate salt stress (Ahmad et al., 2015). This is why selection, screening, characterization and application of stress tolerant microorganisms could be viable options to help overcome productivity limitations of crop plants in stress-prone areas.

5. Future trends in microbial soil–plant health indicators

Understanding and identifying microbial capabilities can benefit soil fertility, crop production and reduce the soil degradation due to excessive applications of agrochemicals, heavy metals and industrial wastes. Soil associated microbial community structure as deciphered by the metagenomics analysis of many agricultural, terrestrial and contaminated soils and taxa-linked relationships with the functional metabolic networks (as depicted by metatranscriptomics and metaproteomics strategies) present strong evidences to establish niche-specific microorganisms as indicators. Future leads in this area should come from the integration of sophisticated instrumentation, advanced technologies and high-throughput methods to establish new ecological indices for soil health at physicochemical, biochemical, metabolic, molecular and microscopic levels. Studies on microbial metabolites need to be intensified in order to track more signature molecules reflecting climate and stress responsive changes in the soil and plant health. Similarly, meta-omics studies on the soil and plant ecosystem can assess disturbances of several magnitudes in the degraded, contaminated or chemically-disturbed soils to reveal information on microbial successions and diversity changes. The richness of beneficial microbial communities in the soil system should be intensified for improving microbial environment that can support better soil and plant health. There is also a need to harness potentials of microorganisms as autonomous curing agents of the soils.

6. Conclusion

Many of the microbial functionalities relate to nutrient availability, accessibility, acquisition, recycling and remediation in the soils, hence the presence of dominant communities may be linked with the prominent indicators for characteristic ecosystem functions of the soils. Studies on habitat-specific functional microbial communities as prominent indicators raise hope for developing region or agro-climatic zone-specific microbial inoculants for successful implications in the agriculture and environment. Enhanced applications of microbial inoculants (biofertilizers, biofungicides, biopesticides, bioremediators, biodegraders, microbe-based decomposers) as a supplement to reduce dependency of farmers on chemical farm inputs can promote the scope of integrated nutrient and pest management practices for sustainable agriculture. This can help in designing nutrient doses, practices on nutrient use efficiency and amendments in Integrated Nutrient Management (INM) strategies for better crops. Understanding microbial behavior, their habitats and functions is also important for preparative prevention of disturbed management caused due to abiotic, agronomic and disease conditions before any non-repairable damage in the agroecosystem. Coupling the applications of high throughput polyphasic microbial identification and trait characterization with the metaomics approaches can generate deeper understanding on microbial communities characteristics, functions, interactions, signaling and communication processes in the soils and with the plants to offer real time diagnostics for sustainably maintaining soil health for better crops in a more sustainable manner.

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