Proc. Natl. Acad. Sci., India, Sect. B Biol. Sci. (January–March 2013) 83(1):1–14
DOI 10.1007/s40011-012-0059-4

REVIEW

Rhizospheric Flora and the Influence of Agronomic Practices on Them: A Review

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Received: 19 April 2012 / Revised: 5 July 2012 / Accepted: 12 July 2012 / Published online: 29 July 2012

Abstract Plants and most of the microorganisms in the rhizosphere have symbiotic relationships. While rhizodeposits (root exudates having lysates, mucilages) provide the food and influence the structure and number of microorganisms in the rhizosphere, the latter benefit the plants through secretion of a number of growth promoting hormones, organic acids and siderophores that help in increased availability and uptake of nutrients by plants. The interactions of roots and microflora may influence the plant growth positively through a variety of mechanisms, including fixation of atmospheric nitrogen by different classes of proteobacteria, increased biotic and abiotic stress tolerance imparted by the presence of endophytic microbes, and direct and indirect advantages imparted by plant growth-promoting rhizobacteria. The soil microorganisms affect plant growth, and are affected by plant growth, but there is incomplete understanding of their cumulative and interactive effects on plant performance, especially under varied crop production regimes. The diversity of cropping systems in both time and space (by rotations, intercropping, and so on) creates a mosaic of soil resources and niches, which in turn, enhances belowground biodiversity and improves the resilience of the system as a whole. Therefore, agronomic practices such as crop rotation, tillage, addition of organic manures, chemical fertilizers and mulches influence the structure and number of microorganisms in the rhizosphere. However, very little data are available on this subject. There is a need to generate such data to develop a strategy for sustainable agriculture.

Keywords Agronomic practices · Bacteria · Exudates · Fungi · Plant growth hormones · *Rhizobium* · Rhizodeposits · Rhizosphere · Root nodules

Introduction

Rhizosphere is defined as the volume of soil around living plant roots that is influenced by root activity. The whole range of root activities makes the rhizosphere a unique environment. The underlying changes in biochemical, chemical and physical properties of soil surrounding the root, compared with the bulk soil, arise from either processes for which roots are directly responsible, and/or activities of microorganisms that are stimulated in the vicinity of the roots as a consequence of the release of rhizodeposits by roots [1]. This is the so-called rhizosphere effect-stimulation of microorganisms that may be either beneficial or deleterious (e.g. pathogenic microorganisms). Much attention has been focused on the biological properties of the rhizosphere [2, 3] and there is a rich literature on the bacterial and fungal colonization of roots and root

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surfaces, and on pathogens. Advances in understanding the movement of water and nutrients to roots has led to the realization that roots may alter the immediate environment to assist the capture of these resources [4, 5].

The roots of living plants fuel a complex network of microbial interactions, involving both root-infecting and free-living microorganisms and connected food-webs of microbial grazers. These microorganisms affect plant growth, and are also affected by plant growth, but currently there is only limited understanding of their cumulative and interactive effects on plant performance, since the present knowledge is mainly based on isolated investigations of single organism groups. In recent years, the recognition of bacterial communication networks, the common exchange of microbial signals with roots and the fact that these signals are used to enhance the efflux of carbon from roots has revolutionized the views on rhizospheric processes. Plants allocate a great portion of their photosynthetically fixed carbon to root-infecting symbionts [6], such as mycorrhizal fungi, while some part is released as exudates fuelling mainly free-living rhizobacteria. Rhizobacteria are strongly top-down regulated by microfaunal grazers, particularly protozoa. Most importantly, effects of rhizobacteria on root architecture seem to be driven in large by protozoan grazers and the protozoan effects on plant root systems stand in sharp contrast to effects of mycorrhizal fungi.

Plant Roots and Rhizospheric Flora

The root system is fundamentally important for plant growth and survival because of its role in water and nutrient uptake. It attracts many soil organisms in its vicinity. Major rhizospheric flora are bacteria, fungi, actinomycetes and algae. In general, root growth leads to substrate loading in the root zone, which in turn promotes rhizobacterial proliferation, leading to the root growth, a concomitant increase in root exudation that leads to substrate loading, and so on. Root–microbial exchanges can be considered a form of allelopathy [7] and include those biochemical interactions, both inter- and intraspecifically, that involve microbial- or plant-produced secondary metabolites (allelochemicals) that influence growth and development of biological systems in the soil. Consequently, phyto-microbially governed plant growth is a form of beneficial allelochemical response that shares many of the characteristics of a "feedback" system. The plant initiates an allelopathic cascade of which it is also the final recipient. An analogous process can be found in autotoxicity, where phytochemical autoinhibitors collect in the root zone and inhibit similar or dissimilar species' growth and development [8].

The term allelopathy was originally introduced to describe the injurious effects of one plant upon the other [9]. However, the term has now been generally accepted to include both inhibitory and stimulatory effects, and the definition has been extended to include "any process involving secondary metabolites produced by plants, microorganisms, viruses and fungi that influence the growth and development of agricultural and biological systems (excluding animals), including positive and negative effects" [10]. Thus in its broadest sense "plant-directed" microbial communities can provide the host plant with a distinct ecological advantage through the increase of beneficial allelopathies [11]. Microbially generated secondary metabolites have been shown to aid plant growth [12, 13], increased availability of minerals and nutrients [14], improve nitrogen economy [15, 16], change plant susceptibility to frost damage [17], enhance plant health through the direct biocontrol of phytopathogens [18], induce systemic forms of plant disease resistance [19], and secure plant establishment [20].

By contrast, detrimental allelopathies occur where bacterially produced secondary metabolites adversely affect plant growth and development. These detrimental effects occur in the absence of any pathogenic symptomology [21], although affected plants, in their weakened state, can subsequently become susceptible to phytopathogen attack [22]. Accordingly, such organisms have been termed deleterious rhizosphere microorganisms and include the deleterious rhizobacteria.

Rhizodeposition and Soil Microflora (Root–Microflora Interaction)

Some microbes have a direct interaction with crop plants in a mutually beneficial manner, whereas others colonize the plant only for their own benefit. In addition, microbes can indirectly affect plants by drastically altering their surroundings. Understanding the complex nature of plant–microbe interactions can potentially offer new strategies to enhance plant productivity in an environmentally friendly manner [23].

Rhizodeposition has received considerable attention considering its major impact on soil microorganisms and on the fate of carbon in terrestrial (and even aquatic) environments [1, 2]. Rhizodeposition includes exudates (small soluble or volatile organic molecules released passively by living cells), lysates (compounds actively released by plant roots) and mucilages (organic compounds such as polysaccharides, amino acids, etc. of diverse origin) [24]. After secretion mucilages are modified by microorganisms in the rhizosphere and the final substance consists of high molecular weight gelatinous material containing mineral soil particles, soil organic matter and sloughed root tissues [25].

Rhizodeposition from roots stimulate the growth of the microorganisms in the rhizosphere. Generally the microbial diversity is higher in the rhizosphere than in the bulk soil and it can be expressed as rhizosphere: soil (R:S) ratio. The different groups of microorganisms may be classified on the basis of R:S ratio and these are with decreasing ratio:bacteria > actinomycetes > fungi > protozoa > algae. The R:S ratio for bacteria may range between 10 and 20, but may reach as high as 100 [26]. Thus chemical components of rhizodeposits may deter one organism while attract another, or two very different organisms may be attracted with differing consequences to the plant. A concrete example of diverse meanings for a chemical signal is the secretion of isoflavones by soybean roots, which attract a mutualist (*Bradyrhizobium japonicum*) and a pathogen (*Phytophthora sojae*) [27].

Root-microflora interactions can positively influence plant growth through a variety of mechanisms, including fixation of atmospheric nitrogen by different classes of proteobacteria [28], increased biotic and abiotic stress tolerance imparted by the presence of endophytic microbes [29], and direct and indirect advantages imparted by plant growth-promoting rhizobacteria [30]. Bacteria can also positively interact with plants by producing protective biofilms or antibiotics operating as biocontrols against potential pathogens, or by degrading plant- and microbe-produced compounds in the soil that would otherwise be allelopathic or even autotoxic. However, rhizosphere bacteria can also have detrimental effects on plant health and survival through pathogen or parasite infection. Secreted chemical signals from both plants and microbes mediate these complex exchanges and determine whether an interaction will be malevolent or benign.

Root colonization is important as the first step in infection by soil-borne pathogens and beneficial associations with microorganisms. In addition to providing a carbon-rich environment, plant roots initiate cross talk with soil microbes by producing signals that are recognized by the microbes, which in turn produce signals that initiate colonization. Chemical attraction of soil microbes to plant roots, or chemotaxis, is a well understood mechanism involved in initiating cross talk between plant roots and microbes [31]. Root–microflora interactions may be positive or negative.

Positive Root–Microflora Interactions

Nodulation of Legumes by Rhizobia

Rhizobium–legume interactions represent one of the most important entry points of nitrogen into terrestrial ecosystems. Nitrogenase from rhizobia and other N-fixing bacteria reduces atmospheric dinitrogen. Rhizobia form symbiotic associations with leguminous plants by fixing atmospheric nitrogen in root nodules. Scientists have always wondered whether plants outside the Fabaceae family might be manipulated to form associations with rhizobia. However, rhizobia-legume interactions are very specific, allowing specific rhizobial strains to nodulate with specific host legumes. *Sinorhizobium meliloti* effectively nodulates species of the genera *Medicago, Melilotus*, and *Trigonella*, whereas *Rhizobium leguminosarum* bv *viciae* induces nodules in the genera *Pisum, Vicia, Lens*, and *Lathyrus*. Not all members of the legume family form nodules. Of the three subfamilies of legumes, Caesalpinoideae, Mimosoideae, and Papilionoideae, members of the basal subfamily Caesalpinoideae are mainly non-nodulating. The signal components largely responsible for these specific host-microbe relationships belong to a class of compounds termed flavonoids [32]. More than 4,000 different flavonoids have been identified in vascular plants, and a particular subset of them is involved in mediating host specificity in legumes [33].

Biological nitrogen fixation may act as a sustainable source of N and can complement or replace fertilizer inputs [34]. The two main cultural practices to benefit from biological N fixation are crop rotation involving legumes and intercropping legumes with cereals or other non-N fixing plants. These have been practised since the ancient times, even if the basis for the benefit derived was not understood [35]. Most of the N fixed in legumes is harvested and fed to animals, but evidence from a number of experiments using different methodologies indicates that legumes can deposit significant amounts of N in the soil during growth [36, 37]. Fixed N can also be transferred to associated intercropped nonlegumes in the case of mixed cropping systems, or to the succeeding crops in the case of crop rotation. Not only N fixation benefits, but the leguminous cover crops also have a significant influence on the soil chemical and microbial properties [38]. Besides the use of legumes in crop production, other biological sources to take advantage of N_2-fixing micro-organisms include the utilization of the symbiosis between the fern *Azolla azollae* and the N_2-fixing cyanobacterium *Anabaena azollae* as a green manure in rice wetlands, and the use of free-living N_2-fixing bacteria such as *Azopirillum* inoculated into the rhizosphere of grasses [39].

Mycorrhizal Associations

Unlike the selective legume-rhizobial associations, arbuscular mycorrhizal fungi (AMF) and plant roots form associations in more than 80 % of terrestrial plants. AMF are able to extend plant root systems and increase root accessibility to nutrients with low mobility in soils, including phosphorus [40]. Plant roots are interconnected by mycorrhizal hyphal networks that allow the exchange of resources [41], and up to 90 % of phosphorus and 80 % of nitrogen demands can be supplied by mychorrhizal fungi [42].

This symbiotic relationship increases nutrient uptake, improves plant fitness, and in turn, the associated fungi extract lipids and carbohydrates from the host root [43]. AMF may recognize the presence of a compatible host through root exudates, similar to recognition by rhizobia [44]. The ability of AM fungi to enhance host–plant uptake of relatively immobile nutrients, in particular P, and several micronutrients, has been the most recognized beneficial effect of mycorrhiza. Rhizosphere interactions occur between AM fungi and other soil micro-organisms with effects on plant nutrient balances, such as nitrogen-fixing bacteria and plant growth-promoting rhizobacteria [45]. AM colonization may furthermore protect plants against pathogens. AM fungi interact with heavy metals/micronutrients. They can restore the equilibrium of nutrient uptake that is misbalanced by heavy metals [46]. AM fungi can alleviate Al toxicity. AM fungi improve water relations, especially under nutrient limitation. The extraradical hyphae of AM fungi contribute to soil aggregation and structural stability. Therefore, mycorrhizas are multifunctional in (agro) ecosystems, potentially improving physical soil quality (through the external hyphae), chemical soil quality (through enhanced nutrient uptake), and biological soil quality (through the soil food web).

Plant Growth-Promoting Rhizobacteria (PGPR)

Bacteria thrive on abundant nutrients in the rhizosphere and some of these rhizobacteria provide benefits to the plant, resulting in plant growth stimulation [30, 47, 48]. Root exudates also influence flagellar motility in some rhizospheric bacteria. Plants get benefit from microbes mainly through enhanced nutrient acquisition by fixing nitrogen [49, 50], solubilization of inorganic phosphate [51, 52] mineralization of organic phosphorus [53], and/or production of siderophores for iron uptake [54]. In addition, PGPR can increase root accessibility to minerals and water by synthesizing growth regulators including auxin [55] and gibberellins [56].

Some PGPR produce phytostimulators, which directly enhance plant growth. In addition to fixing atmospheric nitrogen, *Azospirillum* spp. secrete phytohormones such as auxins, cytokinins, and gibberellins [57–59]. There is the exciting possibility that most PGPR are capable of producing growth regulators continuously, provided that precursors of phytohormones are available in the rhizosphere. Some bacteria (and fungi) produce siderophores, which contain reactive groups such as hydroxamates that chelate iron (Fe) and make them available to plants [60]. Physiological responses of PGPR on growth and yield parameters of selected crop plants are given in Table 1.

Plant diseases can be controlled by certain rhizobacteria through the production of antagonistic compounds against phytopathogens (e.g. antibiotics, siderophore competition) [75, 76] and/or by priming. Priming is the process whereby the plant defense metabolism is enhanced and resistance against pathogens is induced [77]. When this mechanism is mediated by non-pathogenic rhizobacteria, it is referred to as induced systemic resistance (ISR) [78]. Numerous bacterial traits have been identified as triggers of ISR, such as flagellae, components of the cell envelope, siderophores, phenolic compounds, quorumsensing molecules and antibiotics [79].

Certain rhizobacteria create “suppressive soils” by controlling plant diseases caused by soil fungi and bacteria. The biocontrol agents that are best characterized at the molecular level belong to the genus *Pseudomonas.* Most of the identified *Pseudomonas* biocontrol strains produce antifungal metabolites, of which phenazines, pyrrolnitrin, 2,4-diacetylphloroglucinol, and pyoluteorin are most frequently detected. However, antifungal metabolites belonging to the class of cyclic lipopeptides, such as viscosinamide [80] and tensin [81], have also been discovered. Viscosinamide prevents infection of *Beta vulgaris* L. (sugar beet) by *Pythium ultimum* [82]. *Arabidopsis thaliana* ecotype Columbia plants (Col-0) treated with the PGPRs *Serattia marcescens* strain 90–166 and *Bacillus pumilus* strain SE34 developed minor disease symptoms upon infection with the Cucumber mosaic virus [83]. Also, it was reported that some of the known gram-positive biocontrol PGPRs (such as *B. subtilis* 6051 strain) assist plants in evading a gram-negative plant pathogen, *Pseudomonas syringae* pv. tomato DC3000, by forming a protective biofilm on *A. thaliana* roots limiting pathogen access to the root surface and by producing an antimicrobial cyclic lipopeptide surfactin [84]. Microorganisms produce variety of phytohormones, which in turn influence the plant growth (Table 2).

Negative Root–Microflora Interactions

Antimicrobial Effects

The survival of physically vulnerable root cells under continuous attack from pathogenic microorganisms depends on “underground chemical warfare” mediated by plant secretion of phytoalexins, defense proteins, and other as yet unknown chemicals [93, 94]. *Arabidopsis*, rice, corn, soybean, and the model legume *Medicago truncatula*, which have been subject to intensive sequencing efforts, are, collectively, rich sources of antimicrobial indole,

Table 1 Physiological responses of PGPR on growth and yield parameters of crop plants

Species of PGPR	Crop	Crop parameter/response	Reference
Azospirillum brasilense REC3 (S1)	Rice	Improvement in grain yield	[61]
Azospirillum brasilense CD 4	Rice	Increased shoot growth, root growth and NPK uptake	[62]
P. *fluorescens*	Pearl millet	Growth	[63]
P. *putida* strains R-168 and DSM-291; *P. fluorescens* strains R-98 and DSM-50090; *A. brasilense* DSM-1691 and *A. lipoferum* DSM-1690	Maize	Improved seed germination, seedling growth and yield	[64]
P. putida strain R-168	Maize	Increased seed germination, growth parameters of seedlings in greenhouse and also increased grain yield of field grown crop	[65]
Azospirillum brasilense, Azospirillum irakense	Maize and wheat	Growth	[66]
R. leguminismarum (Thal-8/SK8) and *Pseudomonas* sp. strain 54RB	Wheat	Improved yield and phosphorus uptake	[67]
Cyanobacterial strains CW1, CW2 and CW3 (Anabaena sp., Calothrix sp. and Anabaena sp. respectively)	Wheat	Enhancement in grain yield, harvest index and protein content	[68]
Pseudomonas, *Azotobacter* and *Azospirillum*	Chickpea	Stimulated growth and yield	[69]
Rhizobium leguminosarum	Canola, lettuce	Direct growth promotion	[70]
Mixed inoculations with N2-fixing bacteria (*Bacillus* OSU-140 and *Bacillus* OSU-142) and a strain of phosphorus solubilizing *Bacillus* (M-13)	Sugar beet and barley	Significantly increased root and sugar yields of sugar beet, and grain yield of barley	[71]
P. putida	Tomato	Growth stimulation	[72]
P. fluorescens strains, CHA0 and Pf1	Banana	Increased growth, leaf nutrient contents and yield	[73]
85G (Escherichia fergusonii), 161G, 163G, 160G, 150G (Acinetobacter calcoaceticus) and 109G (Salmonella enterica)	Coffee	Increased plant growth	[74]

Table 2 Production of phytohormones by microorganisms and their influence on plant growth

Phytohormones detected	Microorganisms	Plants	Responses
Auxin-indole-3 acetic acid (IAA)	Rhizobacteria	Wheat	Rhizobacterial strains active in IAA production had relatively more positive effects on inoculated seedlings [85]
	Rhizobacteria	*Brassica juncea*	Significant correlation observed between auxin production by PGPR in vitro and growth promotion of inoculated seedlings [86]
	Pseudomonas putida GR12-2 an IAA-deficient mutant	Canola and mungbean	Primary roots of canola seeds treated with wild-type strain 35-50 % longer than roots from seeds treated with the IAA-deficient mutant and roots from un-inoculated seeds. Exposing mungbean cuttings to high levels of IAA by soaking in a suspension of wild-type strain stimulated formation of many adventitious roots [87]
	Azotobacter	Maize	Inoculation with strains efficient in IAA production had significant growth-promoting effects on maize seedlings [88]
	Rhizobium Azospirillum	Rice	Inoculation with diazotrophs had significant growth promoting effects on rice seedlings [89]
	Rhizobium leguminosarum (strain E11)	Rice	Growth promoting effects open inoculation on axenically grown rice seedling [90]
	Bacillus cereus	Sorghum	Significant increase in shoot and root biomass [91]
Cytokinins (CKs) and indol-acetic acid (IAA)	*Azotobacter chroococcum* Az d10, *Bacillus megaterium* PI-04, and *Bacillus mucilaginosus* B-1574	Cucumber	Stimulated seed germination and increase in the growth rate, the biomass of shoots, the number of lateral roots, and the root hair area [92]

terpenoid, benzoxazinone, and flavonoid/isoflavonoid natural products. The unexplored chemodiversity of root exudates in all these genetically tractable species is an obvious place to search for novel biologically active compounds, including antimicrobials.

Influence of Microflora on Plant Roots

Mycorrhizae

Unlike *Arabidopsis*, more than 80 % of higher plants associate with mycorrhizal fungi, which elicit profound changes in the root morphology of host plants [95]. In particular, ectomycorrhizae suppress root elongation and induce dichotomous branching of short lateral roots, culminating in the formation of coralloid structures resulting from higher-order dichotomous branching. All of these anatomical structures are variable depending on the plant and fungal species. Once the fungus is established, root branching is suppressed, which makes the plant more dependent on the nutrients provided by the fungus [95, 96]. Whether this modification of root system architecture (RSA) is a direct consequence of symbiosis or an indirect effect of improved nutrient status of the plant is not clear. However, it appears that symbionts can trigger RSA changes by promoting lateral root initiation very early in the interaction [97]. Moreover, the maize mutant *lrt1* normally lacks lateral roots, but displays extensive lateral root development following inoculation with the mycorrhizae *Glomus mosseae* [98]. Notably, many microorganisms that interact with plants can produce plant hormone analogs. Thus, symbiotic association might employ hormone signaling pathways to regulate RSA.

Nodulation

The second most important symbiosis of plant roots is their association with N-fixing bacteria in legumes, a process termed nodulation. Nodules and lateral roots share some common features. For instance, both organs form adjacent to xylem poles, develop meristems, and break cell layers to emerge. In support of this idea, the lateral root organ-defective mutant of *Medicago truncatula* initiates both nodule and lateral root formation, but does not complete either process. Moreover, nodule formation shares common molecular processes with lateral root development [99, 100].

Agronomic Practices vis-à-vis Plant Roots and Rhizosphere Flora Interactions

In cultivated soils, the activity of soil microorganisms is an important determinant of effective nutrient cycling and plant growth. Decomposition of organic materials by soil organisms is the largest source of nutrients for plants in systems with low input of mineral fertilizers, and some agricultural practices positively affect soil microbial activity and diversity. [101, 102]. The long-term cultivation history influences the microbial community structure in agricultural fields [102]. Management practices affect soil microbial communities, which mediate many processes essential to the productivity and sustainability of soil. Hence, proper understanding of agronomic practices for enhancement of microbial activity and diversity in soil is necessary to achieve sustainable crop production.

Crop Rotations/Diversification

Crop diversification is considered as an important tool for acceleration of agricultural growth by promoting food and nutritional security, income and employment generation, poverty alleviation, judicious use of natural resources and ecological management [103]. Different crops exploit soil resources in different ways. Maximizing the diversity of cropping systems in both time and space (by rotations, intercropping, and so on) creates a mosaic of soil resources and niches, which in turn, enhances belowground biodiversity and improves the resilience of the system as a whole. Certain cropping sequences, for example, favour the build-up of various beneficial bacteria that promote plant growth, while the availability of the host crop is known to be the biggest single factor influencing the number and diversity of plant parasitic nematodes in the soil [104]. Differences in root morphology and biomass, and in patterns of root exudation and carbon allocation, can all influence the population density and activity of other members of the soil biota. Furthermore, maintaining some kind of continuous plant cover through the use of living crops or mulches moderates fluctuations in soil temperature and moisture, and further enhances stability [104].

The increased use of cereal/legume crop rotation has been advocated as a strategy to increase cereal yields. Research at multiple sites have suggested a complex interaction of chemical and biological factors, including increased mineral N, available P, elevated pH and arbuscular mycorrhizal infection, and a decrease in plant parasitic nematodes as causal mechanisms for rotation-induced increases in cereal yields [105–107]. In principle, these chemical and biological changes should be accompanied by concomitant changes in the rhizosphere microflora. However, it is unknown how cropping systems affect the composition and structure of rhizosphere microbial communities. In subsistence agricultural systems, crop yields are directly dependent on the inherent soil fertility and on microbial processes that govern the mineralization and mobilization of nutrients required for plant growth.

Furthermore, the impact of different crop species that are used in various combinations is likely to be an important factor in determining the structure of plant beneficial microbial communities that function in nutrient cycling, the production of plant growth hormones, and suppression of root diseases.

During the colonization of plant roots by soil bacteria, microorganisms from the bulk soil undergo selective enrichment in the plant rhizosphere in response to different root exudate components. Because different plant species release different types and quantities of exudates, plants exert species-specific effects on the soil microbial community that result in broad shifts in the microflora [2]. In practice, crop rotations have been explicitly used to disrupt disease cycles [108], or in the case of legumes to fix atmospheric N_2 for the subsequent non-leguminous crop [109, 110]. When examined at the community level, crop rotations can cause changes in substrate utilization patterns, which suggest that soil bacterial communities under crop rotation have greater species diversity than under continuous cultivation with the same crop [111]. Therefore, crop rotation can cause significant shifts in rhizosphere bacterial communities.

Generally, cropping system have a significant effect on community structure ($P < 0.005$), irrespective of plant species (maize, pearl millet, sorghum, cowpea and groundnut) or sampling time [112]. Continuous cereal-soil grown plants had highly similar rhizoplane communities across crop species and sites, whereas communities from the rotation soil showed greater variability and clustered with respect to plant species. AM colonization in cereals (sorghum, pearl millet (*Pennisetum glaucum*) in rotation with legumes (cowpea, peanut) increased than in continuous cropping [107]. Nematode densities on cereals also were decreased in rotation with legumes.

Crop rotation effects on mycorrhizal functioning have repeatedly been observed. A 13 % reduction in mycorrhizal colonization after 1 year cropping with a non-mycorrhizal crop and a 40 % reduction after fallowing have been observed [113]. Lack of inoculum or inoculum insufficiency after a long bare fallow (especially in climates with an extended dry, vegetation less season) may result in low uptake of P and Zn and in plants with nutrient deficiency symptoms that have been described as long-fallow disorder. Evidence was found for increased mycorrhizal colonization of soybean if the preceding crop was maize, and increased colonization of maize if the preceding crop was bradyrhizobium-inoculated soybean in the savanna of Nigeria [114].

Tillage and Crop Residue Management

Conventional tillage immediately changes the structure of the soil microbial community, even if total microbial biomass is little affected. Under conventional tillage regimes, bacteria-based food webs predominate, and flushes of mineralization related to cultivation can lead to increased losses of nutrients and organic matter from the soil. In this way, tillage can increase the potential both for nitrate leaching and the emission of greenhouse gases such as carbon dioxide and nitrous oxide. In the long term, it can have deleterious effects on soil structure and biodiversity [104].The use of tillage techniques in seed bed preparation and land use management not only impose a physical stress on the soil structure but also on the soil microbial communities that inhabit that soil [115]. Conventional management based on agricultural practices such as straw-burning and excessive tillage increases soil erosion and compaction, which contributes to loss of soil quality [116].

In an effort to minimize such stresses, modern arable farming systems are attempting to reduce excessive cultivation in favour of limited or strategic tillage practices. Conventional tillage system involves a preliminary deep primary cultivation followed by some secondary tillage system for seedbed preparation. In contrast, conservation, or reduced tillage, can encompass any tillage practice that reduces loss of soil and water as compared to unridged or clean tillage. This can include (a) minimum tillage, considered to be the minimum amount of tillage required for seed bed preparation and plant establishment; (b) no-tillage/zero-tillage/direct drilling, which involves no seedbed preparation other than chemical preparation and soil opening for seed placement [117]; and (c) high-residue mulched beds [118].

Compared to conventional tillage systems, reduced-tillage practices offer not only long-term benefits from soil stability, reduced soil erosion, and sustainable agriculture [119], but they can also enhance soil microbial diversity [111, 120, 121]. Thus, minimizing the mechanical upheaval associated with tillage operations tends to maximize soil microbial diversity because the disruption of food substrate at the trophic level, desiccation and soil compaction are reduced, and optimum pore volume is maintained [122]. Paradoxically, fallow periods in a crop rotation can reduce soil microbial diversity [123], an effect probably associated with food substrate depletion over time. Thus, heterogeneity in soil microbial populations tends to coincide with heterogeneity of food resources, which is often greatest in crops under conservation or zero tillage management, where the residue of the preceding year's crops adds sequentially to the variety of food substrates available for utilization. Clearly, while the act of mixing soil during tillage increases seedbed homogeneity, it simultaneously destroys the diversity of trophic microsites that occur down the soil profile together with the assemblages of soil microorganisms that occupy them. The result is a reduction in both the structural and functional diversity of the soil microbial community [124] and the efficiency of those microbially mediated processes that sustain the agricultural productivity of soil, e.g., nutrient recycling, degradation of toxic residues, maintenance of soil structure, and aggregation [125].

Tailoring amendments and cultural practices to promote beneficial soil microbes has been an underappreciated area of crop production science that offers potential for increasing agricultural productivity in a natural and sustainable manner. It is already well established that sugars and amino acids are released by decomposing plant material and can serve as carbon sources for soil microbes [126]. However, in modern crop production monocultures that rely on mineral fertilizers, carbon sources can become limited, especially where crop residues are removed from fields and soil organic matter is kept low. Consequently, the diversity of microbial activity is likely to be reduced. This is not meant to imply that soil applications of N–P-K primarily intended to provide essential nutrients to crop plants do not also benefit soil microbes. The point is that traditional fertilizer inputs are intended primarily for crop plants and not the microbes that sustain them. Even when soil organic matter is low, relatively few agriculturalists would fertilize their fields specifically to benefit soil microbes [126].

Mineral and Organic Fertilization

Plants modify their environment at several spatial scales; the global, the ecosystem, the soil horizon, and the rhizosphere. In all ecosystems, plants transform the surrounding soil making and maintaining a habitat more favourable for growth [127]. Root mediated changes to the soil are mainly associated with the ways to increase their potential for nutrient and water acquisition. Plants have evolved an array of mechanisms to increase the solubility, diffusion potential and uptake of nutrients from soil. These mechanisms are particularly important in low nutrient environments where plant demand can only be met by mobilizing nutrients from non-soluble sources.

The availability of nutrient elements can be a major constraint to plant growth in many environments of the world, especially the tropics where soils are extremely low in nutrients. Plants take up most mineral nutrients through the rhizosphere where micro-organisms interact with plant products in rhizodeposits [128]. Plant roots strongly influence C and N availability in the rhizosphere via rhizodeposition and uptake of nutrients [129]. Plant rhizodeposits consist of a complex mixture of organic acid anions, phytosiderophores, sugars, vitamins, amino acids, purines, nucleosides, inorganic ions (e.g. HCO_3^-, OH^-, H^+), gaseous molecules (CO^2, H_2), enzymes and root border cells which have major direct or indirect effects on the acquisition of mineral nutrients required for plant growth. Phenolics and aldonic acids exuded directly by roots of N_2-fixing legumes serve as major signals to Rhizobiaceae bacteria which form root nodules where N_2 is reduced to ammonia [128]. Some of the same compounds affect development of mycorrhizal fungi that are crucial for phosphate uptake. Plants growing in low-nutrient environments also employ root exudates in ways other than as symbiotic signals to soil microbes involved in nutrient procurement. Extracellular enzymes release P from organic compounds, and siderophores increase iron availability through chelation. Organic acids from root exudates can solubilize unavailable soil Ca, Fe and Al phosphates. Plants growing on nitrate generally maintain electronic neutrality by releasing an excess of anions, including hydroxyl ions. Legumes, which can grow well without nitrate through the benefits of N_2 reduction in the root nodules, must release a net excess of protons [128].

Fertilization is one of the major factors controlling the population densities and activity of soil organisms. Application of inorganic and organic fertilizers can indirectly but positively affect soil microbes and animals by increasing plant growth and stimulating root exudation, both of which lead to a greater input of organic substrates. Community structure and body size of soil organisms are also affected by fertilization [130]. Most fertilizers can inhibit local microbial activity, especially when they are applied in high concentrations. Some nitrogenous fertilizers can produce biocidal levels of ammonia. Furthermore, high levels of inorganic fertilizer, particularly in tropical soils, tend to reduce populations of mycorrhizal fungi [104]. Some species may even disappear under such circumstances. For example, root nodulation in legumes by *rhizobium* is highly influenced by N supply in soil. It is a strongly suppressive effect of combined N (especially NO_3^-) which legumes will utilize as a N source in preference to forming the N-fixing symbiosis [131]. Nitrate inhibition of nodulation has been one of the clearest and most intensively studied examples of the nutritional control of plant development. Unlike other factors that inhibit nodulation (such as pH, temperature or toxicity), NO_3^- does so in a very specific way without interfering with plant growth [131]. However, the sensitivity of nodulation to NO_3^- is strongly dependent on the plant species and genotype [131].

Farmyard manure (FYM) and mineral fertilizers (NPK) have been reported to have significant effects on the size of microbial biomass and activities [132]. The application of fertilizers can also cause shifts in the soil microbial community structure, as indicated by changes in soil phospholipid fatty acid profiles [123]. There is much interest in understanding the factors which influence and regulate their activities and structure under different conditions and locations during decades or even centuries. The German long-term field experiments provide information on important functional and structural soil microbial properties as influenced by organic and mineral fertilization [133]. Responses to the fertilizer treatments over decades differed at the four sites and led to alterations of the soil ecosystems. Development of functional diversity confirmed that fertilization stimulate microbial biomass and enzyme activities in the investigated soils. The increase of microbial biomass and enzyme activities was higher in FYM than in NPK fertilized soils [133].

Inoculation of Legumes by Rhizobia

Legume inoculation with root-nodule bacteria is an established and successful practice. When a new legume is introduced into a region, some soil will contain appropriate rhizobia, and inoculation is usually needed. Under soil conditions of low nitrogen, yield increases following inoculation which can exceed 50 %, with clear differences evident between inoculated and uninoculated plants. With rare exceptions [134], re-inoculation in subsequent years will not be needed, and over time even uninoculated soils will tend to accumulate rhizobia, limiting inoculation response. A consequence, as shown for soybean in Thailand, is that there will be greater interest in inoculation and inoculant technologies in the newer areas of production than in regions where the crop has been grown for some time [135]. Where inoculation is needed, the inoculant must supply adequate number of rhizobia and use inoculant-quality strains having the following characteristics [136]: the ability to form highly effective nodules with all commonly used cultivars and species for which it is recommended; be competitive in nodule formation and persistent in the soil; the ability to tolerate soil environmental stresses such as acid soil pH and temperature; display good growth in simple, inexpensive culture media; be genetically stable and not be subject to mutation; and the ability to survive well on the seed prior to seed germination.

Inoculant strains are required to survive in stressful soils in sufficient numbers to provide a population able to nodulate under environmental constraints such as pH, temperature and competition from less effective indigenous and naturalized strains. This last problem of competition is significant in many areas, not the least in soils of the tropics and sub-tropics. Several research programs around the world are addressing the problems of stress tolerance in root-nodule bacteria. Improvements in the understanding of the molecular and physiological mechanisms of stress-sensitivity in both symbionts will be important if legume nitrogen fixation and productivity are increased. In addition, there will be a clear benefit to legume production from increasing the survival of the inoculant root-nodule bacteria on seed, or when delivered directly into soil. Enhanced formulations, granular inoculants, and seed coating techniques that protect the bacteria from environmental stress or physically separate them from toxic chemicals, such as fungicides applied to seed, offer new research directions [137].

Addition of Organic Matter

Organic matter can help modify soil structure and is of fundamental importance to many soil functions, including carbon cycling, sequestration and nutrient storage. Incorporation of rich and varied sources of organic matter not only supplies plant nutrients, but also helps to increase below-ground biodiversity by providing an array of substrates capable of supporting diverse soil organisms. Increased biodiversity in turn contributes to the ability of the soil to suppress plant pests and diseases. Suitable sources of organic matter include animal wastes, green manures, crop residues, and composted vegetation. It is important to note, however, that the effects of organic amendments can vary not only with the nature of the material added, but also with soil pH [104].

Green manuring is an arable-farming practice in which undecomposed green material is incorporated into soil in order to increase its immediate productivity [138]. This material may either be obtained from quick-growing green manure crops grown in situ or harvested elsewhere, and brought into soil. Green manure crops can be leguminous as well as non-leguminous [139]. Green manuring is known to have a significant positive influence on different soil properties [140–142] and eventually on crop production. Green manuring promotes colonization by mycorrhizae on the roots of succeeding crops. They may also suppress plant pests such as nematodes [143]. A fast increase in growth of soil microorganisms occurs after a young, particularly lush green manure crop or green twigs are incorporated into the soil. The microbes start multiplying to attack the freshly incorporated plant material in the soil. During the microbial breakdown process, nutrients held within the plant tissues in complex forms are released and made available to the succeeding crop. Factors influencing the microbial activity to break down complex organic matter include soil temperature, soil moisture, and carbon to nitrogen (C:N) ratio of the plant material. The C:N ratio of plant tissue reflects the kind and age of the plants from which it was originated. The optimum C:N ratio for rapid decomposition of organic matter lies between 15:1 and 25:1. As plants get older, fibrous plant material increases and protein (nitrogen) content decreases [144].

Green manuring may also drive long-term increase of soil organic matter and microbial biomass [145–148]. Combinations of inorganic fertilizer and organic amendments (wheat straw, animal manure, or sesbania green manuring) generally increased soil organic C, total N, microbial biomass C, and enzyme activity more than inorganic fertilizer alone in the top 15 cm of soil [145, 146]. In some widely spaced crops, like sugarcane, green manures can be grown and incorporated into the soil. Also, the cane trash can be mulched on to the soil. In a field study it was found that soil microbial biomass C and dehydrogenase activity at the end were at a maximum with trash burning + green manure (GM) mulch and trash removal + GM mulch treatments [149]. Compared to trash removal and trash burning, counts of bacteria in soil after sugarcane ratoon and wheat crops were significantly more only with different GM treatments; however, all GM and trash application treatments recorded significantly higher counts of fungi and actinomycetes. Application of sugarcane trash and GM increased the soil microbial biomass carbon measured at 75 days after ratooning [149].

Mulching

A mulch is defined as any form of covering applied to the soil surface. By this broad definition, it includes crop residues, weeds, GMs, and other plant material cut and carried in from elsewhere, as well as artificial materials such as paper and plastic. The organic mulches, which are more relevant to resource-poor farmers in developing countries, are quite common in the traditional farming systems of the humid tropics. Besides reducing soil erosion and improving nutrient cycling, mulching can also help suppress weeds, pests, and diseases. Herbicide use or time spent weeding by hand may be significantly reduced by mulching, and notable successes have been achieved by using mulches to suppress soil-borne plant pathogens [104].

In Kenya, for example, black rot of cabbage caused by the bacterium *Xanthamonas campestris* was controlled by a grass mulch applied immediately after transplanting [104]. In such cases, it is thought that the effect of the mulch is due to a combination of its role as a physical barrier (reducing rain splash of the pathogen onto the crop), together with its ability to change the microclimate at the soil surface and enhance the activity of beneficial soil microorganisms capable of suppressing pathogens. Mulching has also been used to divert termites from crops, and in various parts of Africa, mulching with the weed *Tithonia diversifolia* has been shown to reduce nematode damage and improve crop growth. In Uganda, mulching of banana plantations appeared to reduce number of the nematode *Radopholus similis*, possibly because the mulch reduced soil temperatures, thereby slowing nematode feeding and reproduction. Conversely, the presence of crop residues on the soil surface may enhance the biological control of insect pests by entomopathogenic nematodes. It has been shown, for example, that such residues increase the persistence of *Steinernema carpocapsae*, probably by protecting it from desiccation or ultraviolet light [104].

Conclusion

Soil flora resources are indispensable for establishing sustainable agriculture. Abuse and unscientific use of microbial resources seem to hamper the wholesome popularization of them. One needs to understand the utility and limit of their effects in agriculture scientifically. Very few data have been generated on the effect of agronomic practices on soil microflora. It is important that the accurate, scientific evidence of the fate of microbial resources as well as their effect on plant growth are understood well. The knowledge of soil microflora can be successfully utilized in managing the field crops through suitable and appropriate agronomic practices.

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