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Tropical Crops and Microbes

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Abstract

Sustaining crop production in order to meet the growing demand of the teeming populace in the tropics has been one of the utmost goals of Scientists nowadays since the conversion of the tropical ecosystems to other uses has posed serious threat to it. Crops that were either introduced or adopted to the tropical nations by the European conquerors are referred to as tropical crops. The ubiquitous nature of microorganisms has made the soil to be one of their habitats or reservoirs. Microorganisms belonging to bacteria, fungi, protozoa, micro-algae, and viruses inhabit the soil. In crop production, beneficial soil microbes have been used as biofertilizers, biopesticides, and phytostimulators and also increase resilience in plants. Biofertilizers obtained from effective and indigenous microorganism have been used to improve and maintain the biological, chemical, and physical properties of cropland soils, which in turn improve crop growth and yields. Plants also contribute to the population of microbes in the soil by supplying them carbon from their photosynthates. The mutual relationship between beneficial microbes and plants cannot be underestimated in improving crop growth and yields in threatened tropical ecosystem.

Keywords: soil, tropical crops, beneficial microorganisms, mutual relationship, crop production

1. Introduction

In the era of sustainable crop production, the interaction between plants and soil microbes play an important role in the transformation, solubilization, mobilization, etc. of nutrients from a limited nutrient pool and make it available for the uptake of plants in order to realize their full genetic potential. Microorganisms perform numerous metabolic functions which are essential for their own maintenance and can directly or indirectly be beneficial to the biosphere through environmental detoxification, soil health improvement, nutrient recycling, waste water treatment, etc. [1].

For more than three centuries, endophytic microorganisms which colonize and reside in plant roots have been known to be in existence. Though their value in increasing crop yields and buffering environmental conditions have become appreciated in recent decades. When describing the formation of galls on roots in 1967, Malpighi reported the symbiotic association between microorganisms and plants. His report was not seen as scientific rather borne out of curiosity. After two centuries, Hellriegel and Wilfath, showed that these galls are nodules composed of both bacterial (Rhizobiaceae) and plant cells which fix N_2 from the atmosphere, providing leguminous plants with an essential nutrient known as ammonia (NH_3) [2]. In 1882, fungi which are presently known as arbuscular mycorrhizal fungi

(AMF) were found to symbiotically improve plants' productivity by colonizing their roots [3]. In the 1920s and 30s, *Trichoderma*, the commonly known soil-inhabiting fungi were found to biologically control pathogenic fungi, thus having the potential in protecting agricultural crops [4]. In addition to protecting plants against pathogenic fungi, some strains of *Trichoderma* have been found to induce multiple benefits to plants when they colonize their roots [5]. Another group of fungi known as *Piriformospora indica* that beneficially colonizes and inhabits plant roots was discovered in the 1990s [6]. Once these microorganisms colonize and inhabit plant roots, they induce physiological changes and modify the expression of genes in the plant they reside in, thus improving plants' productivity and resilience.

2. Tropical agriculture

Geographically, the tropical region is the region of the earth that centers in the equator and limited by the tropics of cancer (23.5°N) and capricorn (23.5°S). All the parts of the earth where the sun reaches at an altitude of 90° and move between the two tropics during the average length of the year are contained in the tropical region. The sun's position makes this region not to experience notable changes in temperature (seasons), and during the wet seasons, water evaporation produces abundant rainfall in this "torrid" region due to constant daily radiation. A dry season which ranges from a month to over 6 months also occurs at different times and regions depending on the sun's position during the year and the region. A bimodal or unimodal distribution may be presented by these dry and wet (raining) seasons during the year. However, tropical ecosystems vary considerably from deserts to rainforests, and the concept of vertical geography which ranges from hot lowlands to snow-capped mountains within a few hundred kilometers can change the temperature drastically [7].

In terms of crop, tropical agriculture is usually described as those crops that were either introduced or adopted by European conquerors in the tropical nations that are under their dominion. Tropical agriculture is often dominated by crops [8]. A large number of plants use in agriculture today were originated and domesticated in the tropics, mountainous area where ecoclines often overlap [9–11]. This is due to the wide range of microclimate, temperatures and rainfalls in the mountainous tropics thereby increasing genetic diversification through selection, mutation and adaptation [12, 13]. A major reservoir of plant and animal biodiversity is the tropical ecosystems which play essential roles in global climate regulation and biogeochemical cycling [14, 15]. The exact yield potential for almost all tropical fruit crops still remains unclear. Though some industrialized crops such as banana, oil palm and citrus have very high production efficiencies, this is exceptional to the norm. For most tropical crops, the maximum recorded yields are much higher than the average yields over large area. Poor soil and water management, pests and diseases, low commodity prices, shortage of skilled and productive labor and failure of the market to provide incentive to growers are some of the reasons for the yield gap [16]. Crop production in the tropical regions is highly diversified compared to the large acre crop farming system in the temperate regions. In the tropics, food and industrial crops may be cultivated either in small holdings, plantations or in mixed gardens. Plantation crops may be large and continuous but they may be owned either by major corporations with uniform cultural practices or by a number of contiguous small farmers with varying practices [17]. Large number of pathogenic bacteria, fungi, viruses and other pests, especially insects often destroy tropical crops. The harsh winter conditions of the tropical regions do not reduce the pathogens population as in the temperate regions. The availability of plants, which serve

as hosts to the pathogens during the year, maintains the populations of a myriad of pests at a damaging level in tropical regions. The tropical ecosystems have been seriously threatened due to its conversion to other uses [18].

3. Soil

Soil is gradually formed from various parent materials, which is modified by climate, time, micro- and macro-organisms, vegetation and topography. It is a complex mixture of minerals, organic compounds and living organisms that interact continuously in response to natural, biologically, chemically and physically imposed changes [19]. In addition to root anchorage, the soil serves as a natural medium for plant growth and habitat for a wide range of microbes [20]. The growth of soil microbes and plants may be directly and indirectly influenced through a variety of interaction. These interactions may result in positive growth through mutual benefits, negative growth through antagonism, or no growth stimulation through neutral effects [21].

Cropland soil can be classified into three types and these include spermosphere, rhizosphere and bulk soil. Spermosphere is the portion of soil that surrounds germinating seeds. It has been described as the short-lived, rapidly changing and microbiologically dynamic zone of soil that surround germinating seed [22]. Rhizosphere has been described as a narrow soil zone that surrounds the roots of leguminous plant which stimulates intense bacterial activities [23]. It is a huge reservoir of microbial diversity. The release of exudates from the roots of plant into the rhizoenvironment initiates the establishment of rhizosphere. The exudates include plant mucilage, mucigel, root secretions and lysates [24]. Thus, exudates are the most vital factors that contribute towards the dynamics of rhizosphere. The rhizosphere is the most important niche that affects diverse aspects of plant life. Bulk soil is composed of soil outside the spermosphere and rhizosphere. With regard to microbial activities, it is considered to be the least dynamic. Out of the three groups of cropland soils, it occupies the largest portion of cropland soil. A large population of micro- and meso-organisms that include surviving propagules of soil inhabiting plant pathogens are harbored in the bulk soil [25].

3.1 Soil microorganisms

Microorganisms are small microscopic organisms that cannot be seen with naked eyes. They inhabit animal intestine, food, soil, water and other different environment. They belong to any of the following group of organisms: bacteria, fungi, protozoa, micro-algae and viruses [26]. The largest proportion of the earth's biodiversity has been reported to be microorganisms and they play an integral role in the processes of ecosystem thereby providing functions that eventually sustain all forms of life [27, 28].

Soil microbial biomass is the living component of soil organic matter. Soils with high organic substances tend to have a higher microbial biomass contents as well as their activities since organic matters are the preferred energy source for microbes. The surface horizon of the soil has the highest microbial activities when compared to the deeper horizon [29]. The soil microbial biomass helps in the enzymatic transformation of soil organic matter into humus, carbon and other nutrients which are utilized by microorganisms for their own growth [30]. Soil microbial biomass and its enzymatic activities are strongly influenced by seasonal changes in soil temperature, moisture and available residue [31]. Soil enzymes may originate from animals, plants or microbes and can either exist in bound or free form within

the soil. Soil enzymes play a vital role in the biochemical functioning of soils [32] including nutrients cycling [33], soil structure maintenance [34] and decomposition of organic residue [35]. The activities of soil enzymes are controlled by many factors such as soil microbial community [36], soil physio-chemical properties [37], vegetation type [38] and ecological disturbances [39]. Prior to the utilization of complex organic matter by microorganisms as their source of energy, they produce a quite number of extra cellular enzymes in order to decompose them [40]. Soil enzymes are specific in the types of reactions they participate. For example, a starch hydrolyzing enzyme known as amylase hydrolyses α 1-4D glucosidic linkage of amylase and amylopectin and consist of α -amylase and β -amylase. α -amylase is synthesized by animals, plants and microorganisms while β -amylase is primarily synthesized by plants [41]. To a large extent, soil microbial activities is dependent on the quantity of available carbon and this is shown by dehydrogenase activity [29]. Dehydrogenase is involved in the biological oxidation of soil organic matter, and also responsible in oxidizing organic matter by transferring hydrogens and electrons from substrates to acceptors [42]. Phosphatase originate from root exudates and microorganisms, it cleaves the phosphate from organic substrates and also involved in P cycle in soil [43]. It has been evidently suggested by Ushio *et al.* [44, 45] that plant species significantly have more direct impacts on the composition of soil microbial community and their activities in addition to soil physicochemical properties. Plants' rhizosphere has been reported by Vyas and Gupta [46] to have profound effect on microbial population and activities. From the study of Islam and Borthakur [47], increase in microbial biomass and enzyme activities indicates high rate of release of nutrients by rice crops which aid microbial activities.

4. Indigenous microorganisms

Indigenous microorganisms are naturally occurring microorganisms that have adapted to the environmental conditions where they are found thus being capable of accelerating decomposition of organic materials found in that environment [48]. They contain mainly *Lactobacillus* and sometimes *Rhizobium* with a few other species [49]. Effective microorganisms are composed of mixed cultures of beneficial and naturally occurring microorganisms which are applied to the soil in order to increase the soil microbial diversity and the growth of plants [50]. This concept was first discovered by Higa [51]. It is used as a means of improving crops' efficiency in utilizing organic matter. There are three main families of over 80 different species contained in effective microorganisms [52]. In agriculture, microorganisms are of great importance because they promote decomposition, cycling and circulation of plant nutrients and reduce the need for chemical fertilizers [53]. From the study of Desire *et al.* [53] the use of biofertilizers obtained from indigenous and effective microorganisms significantly improved and maintained the chemical, physical and biological properties of the soil, and thus increased the yield of potato in terms of number and weight of tubers when compared to untreated (control) soil.

5. Endophytic microorganism

In 1886, Anton de Bary, a German Botanist and father of plant pathology coined the term endophyte and described it as microorganisms that colonize internal tissues of stem and leaves of plants. Endophytic microorganisms are microorganisms that inhabit at least a period of their life cycle in the interior parts of plants especially leaves, branches and stems, showing no apparent harm to the host [54].

They are also capable in colonizing the roots and shoots of plants and may not remain as endophyte throughout their life cycle [55]. They include both bacteria and fungi that colonize almost every plant species [56]. Endophytic fungal appear to be symbiotically associated with almost all plants in natural ecosystem and constitute important components of plant micro-ecosystems. They have impacts on the composition of plant communities by increasing their tolerance to biotic and abiotic stress, biomass and decreasing water consumption or altering allocation of resources [57]. Endophytic microbes produce a plethora of secondary metabolites, including toxins, enzymes, anti-inflammatory, antibiotics, anticancer and antifungal compounds in order to colonize plants and also compete with other microorganisms [58]. Zhao *et al.* [59] reported that endophytic fungi produce good bioactive compound paclitaxel (taxol) and many other bioactive molecules such as terpenoids, alkaloids, steroids, lignans, phenols, quinones and lactones.

Endophytic bacteria have been detected inside the stems, leaves and inside the reproductive organs of different host plants [60]. Several endophytic bacteria produce low molecular weight compounds, phytohormones, enzymes, antimicrobial substances and siderophores which support the growth of plants and also increase their nutrient uptake. Endophytic bacteria in combination with the plants they are in association with, produce some metabolites which plants cannot produce alone [61]. *Enterobacter*, *Pseudomonas*, *Burkholderia*, *Bacillus*, *Erwinia* and *Xanthomonas* are the most commonly isolated genera of endophytic bacteria. Eleven culturable bacterial strains belonging to the genera, *Rahnella*, *Pseudomonas*, *Rhodanobacter*, *Enterobacter*, *Stenotrophomonas*, *Phyllobacterium* and *Xanthomonas* have been isolated from the stems of sweet potato. Among these isolates, *Pseudomonas*, *Enterobacter* and *Rahnella* produced higher amount of indole acetic acid (IAA) which promote plant growth, and *Rahnella sp.* which is resilient to stress like cold shock, antibiotics and UV radiation [62].

Webber [63] was probably the first researcher to report plant protection given by an endophytic fungus, *Phomopsis oblonga* which protected elm trees against *Physocnemum brevilineum*. He suggested that the endophytic fungus protected elm tree against the Dutch disease caused by *Ceratocystis ulmi* by reducing its spread and controlling the vector, *P. brevilineum*. It was reported by Claydon *et al.* [64] that endophytic fungi belonging to the family *Xylariaceae* synthesize secondary metabolites in the hosts of the genus *Fagus* which affect beetle larvae. Stress-related genes in *Oryza sativa* such as aquaporin, dehydrin and malondialdehyde have been found to be upregulated by *Trichoderma harzianum* responses. *Trichoderma harzianum* used in treating *Brassica juncea* improved oil content affected with sodium chloride was found to increase its vital nutrients uptake, improve aggregation of osmolytes and antioxidants, and also reduces its NaCl uptake [65]. Brotman *et al.* [66] reported that *T. harzianum* synthesize 1-aminocyclopropane-1-carboxylate (ACC) deaminase to ameliorate salinity stress. *Acinetobacter sp.* and *Pseudomonas sp.* have also been reported to increase indole acetic acid and ACC deaminase production in oats and barley under salinity stress [67].

Beneficial endophytic bacteria and fungi can be used as inoculant in roots and other plant tissues for many tuberous crops to enjoy the mutualist benefits confer to their original host plants. Many growth promoting endophytes can also be applied as a potential bio-fertilizers in tuber crops with minimal environmental risks [56]. Endophytic microorganisms have frequently been reported to be associated with crop plants such as *Triticum aestivum*, *Glycine max*, *Zea mays*, *Hordeum brevisubulatum* and *Hordeum bogdanii* [68]. The growth of tomato plants in a salinity stress soil have been improved by *Streptomyces sp.* strain PGPA39 by alleviating the salinity stress [69]. PsJN strain of *Burkholderia phytofirmans* have been reported to combat drought stress in maize and wheat, and also salinity stress in *Arabidopsis thaliana* [70].

5.1 Fungi - plants association

Fungi symbiotic relationship with plants are present in a broad range of terrestrial ecosystems which include a large proportion of plant taxa [71]. It has been established that at least 85% of plant species have been able to establish a symbiotic relationship with fungi, of which those belonging to the phylum Glomeromycota account for 70% of the association [72]. Because of the wide geographical distribution of mycorrhiza and the large proportion of plant taxa involved, mycorrhizal associations are extremely important for terrestrial ecosystem. Due to the development of specialized structures such as proteoid roots, carnivorism or parasitism on other plants, some families of plants have lost their ability to associate with mycorrhizal fungi throughout evolution [71]. For a long time, plant species belonging to the Cyperaceae family was believed not to be able to associate with the mycorrhizal fungi [71] though Bohlen [73] study has evidently shown otherwise. Plant species belonging to the Cyperaceae family are able to associate with arbuscular mycorrhizal fungi and dark septate endophytes (DSE), but the intensity of root colonization intensity may vary depending on the environment in which the samples were collected and phenological stage of the plant [72]. Mycorrhizal associations play an important role in determining the composition of plant communities, since plants that establish this type of association can obtain competitive advantages [74] or facilitate the establishment of other species [75]. van der Heijden *et al.* [76] experimental study evidently suggests the coexistence of different plants. They showed that plants inoculated with AMF grew on the average of 11.8 times more than those not inoculated, and that the distribution of phosphorus and nitrogen between plant species varied depending on the presence of AMF. They further said that AMF can redistribute resources among different species of plant thus allowing their coexistence. The final composition of AMF species varies greatly depending on the plant species cultivated in a soil [77]. The diversity of AMF was much smaller in areas dominated with the invasive species than in areas dominated by native species. Thus, the composition of plant communities and AMF are influenced by feedback interactions in each communities [78, 79].

5.1.1 Arbuscular mycorrhizal fungi (AMF)

Arbuscular mycorrhizae are formed by non-septate phycomycetous fungi belonging to the genera *Glomus*, *Acaulospora* and *Sclerocystis* in the family Endogonaceae of the order Mucorales which are not specialized in host range [80]. The arbuscular mycorrhizal (AM) symbiosis is the association between fungi of the order Glomales (Zygomycetes) and the roots of terrestrial plants [81]. Arbuscular Mycorrhizal Fungi (AMF) also known as Vesicular Arbuscular Mycorrhizal (VAM) are widespread in terrestrial ecosystems and form mutually beneficial association with nearly 80% of higher plants [82]. According to Voko *et al.* [83], the population of AMF, frequency of occurrence and distribution varied with site.

During the formation of AM symbiosis, the fungus forms a haustoria-like structure (arbuscules) that interface with the host cytoplasm by penetrating the cortical cell wall of the root [84]. They penetrate the living cells of plants without harming them and their hyphae can range far into the bulk soil establishing equally intimate contact with the microbiota of soil aggregates and micro-sites [85]. From the fixed photosynthates of the plant, it supplies carbon to the fungus while the fungus in turn assist the plant in the uptake of phosphorus and other mineral nutrients from the soil [86]. It has been demonstrated that plants can receive up to 100% of the phosphorus through mycorrhizal pathway, and 4 to 20% of plant carbon can be transferred to fungi [87].

The transference of these resources between plants and fungi have profound effect on plant nutrition, growth and ecology [88]. The activities of AMF improve crop growth and yield by increasing nutrients availability and increasing root proliferation [82] as well as altering some physiological processes in the plant that result in increased yield [89]. This might also be as a result of modification of host hormonal relations [90] and soil structure [91]. AMF can alter the pattern of gene expression, cellular programming and organ development of the host crop [92]. AMF can improve both plant growth under low fertility conditions, improve plant water balance and help in the establishment of plants in new environment [93]. AMF are useful in the cultivation of cassava in the tropics where rainfall is erratic and may seize for 2–3 months giving rise to drought-prone water deficit-stress condition [94]. AMF enhances plant resistance to drought by building up macroporous structure in soil that allows water and air to penetrate and also prevent erosion thus improving photosynthesis and reducing micropropagation stresses [95]. The mutualistic association between AMF and cassava in AMF-inoculated cassava stimulated the production of more leaf chlorophyll which increased their photosynthetic potential and enhanced growth [94].

5.1.2 Dark septate endophytes and crop plants

Dark Septate Endophytes (DSEs) are another important group of soil micro-organism that have the capacity to associate with the roots of several plant species [96]. They sometimes colonize roots containing AMF [96]. The increasing severity of environmental conditions increase the importance of DSE. The associations of plants with DSE in high-stress environment is more frequent than their associations with AMF [97]. AMF and DSE have appeared to have similar and complimentary roles in various terrestrial ecosystem [98]. Grunig *et al.* [99] said that since DSEs can alter the performance of colonized plants, they can also play a vital role in determining the composition of plant communities. In the study of Barrow and Osuna [100], some plants colonized by DSE were more advantageous in the absorption of phosphorus from the soil and production of biomass when compared to those not inoculated. Though DSE is advantageous to plants, its colonization of roots can be of disadvantage to plants, such as decreases in the production of biomass [99]. Thus, the interaction of DSEs with plants seems to vary from mutualism to parasitism and may alter the competitive relations between plants [99].

5.2 Beneficial soil bacteria and crop production

Apart from fungi, there are several groups of soil bacteria that are important to plant growth. Some bacteria have the ability to fix atmospheric nitrogen and form symbiotic relationship with plants [101]. In tropical soils, phosphate-solubilizing microorganisms indirectly provide phosphorus for plants by solubilizing phosphorus precipitated with iron, aluminum and calcium thus making it important for plant growth and development [102].

5.2.1 Root colonization by bacteria

Root colonization is the microbial attachment to and proliferation on roots. It is an essential factor in the beneficial interactions used for biofertilization, microbiological control, phytoremediation and phytostimulation as well as in plant pathogenesis of soil borne microbes [103]. PGPR may colonize the rhizosphere, root surface, or even superficial intercellular spaces [104].

Howie *et al.* [105] hypothesized two phase processes in which bacterium can attach itself to the plant and soil. In the phase I, bacteria on the seed are attached to the emerging root tip where they are passively transported into the soil. During root growth, some bacteria cells remain associated with the tip while others are left behind on the older parts of the root and the rhizosphere. In phase II, bacteria deposited along the root zone multiply and form microcolonies in nutrient-rich microsites, where they compete with indigenous microflora in order to avoid displacement. Both phases occur simultaneous on different root parts [106]. Root colonization can be influenced by both biotic (such as genetic traits of the host plant and the colonizing organism) and abiotic (such as soil humidity, growth substrate, soil and rhizosphere pH and temperature) factors. Changes in plant physical and chemical composition in the rhizosphere can strongly influence root colonization and competence [107]. Root exudates and mucilage-derived nutrients attract beneficial and neutral bacteria as well as harmful bacteria allowing them to colonize and reproduce in the rhizosphere [108].

5.2.2 Plant growth promoting rhizobacteria (PGPR)

In developing a sustainable crop production system, the use of plant growth promoting rhizosphere has played a potential role [109] though its mechanisms of enhancing plant growth and yields have not been fully understood [110]. PGPR play an important role in plant growth through different mechanisms [111]. The relationship of PGPR differs with different host plants. Rhizospheric and endophytic relationships are the two major classes of PGPR relationships. PGPRs that colonize root surfaces or superficial intercellular spaces of the host plant forming root nodules are known to have Rhizospheric relationships. A microbe belonging to the genus *Azospirillum* is the dominant species in the rhizosphere [112]. PGPRs that inhabit and grow within the apoplastic spaces of the host plants are known to have endophytic relationships [107]. Some researchers have shown that inoculation of plants with PGPR help in increasing their nutrient contents [113, 114] and resistivity to pathogens [115, 116]. PGPR colonize plant by interacting with the host plant thus enhancing its nutrient uptake by fixing nitrogen biologically, increasing the availability of nutrients in the rhizosphere, inducing increases in the root surface area, enhancing other beneficial symbioses of the host, and combining the modes of action [107]. PGPR help to solubilize mineral phosphates and other nutrients, stabilize soil aggregates, improve soil structure and organic matter content, and increase plant resistivity to stress. It retains more soil organic nitrogen and other nutrients in the plant–soil system, thereby reducing their need for nitrogen and phosphorus fertilizer and enhancing the release of nutrients.

In addition to increasing plant nutrient contents, PGPR capable of producing phytohormones produce hormones such as cytokinins, ethylene, gibberellins, auxins and abscisic acid. Some of the bacterial genera belonging to the PGPR produce indole-3-acetic acid (IAA), a compound belonging to auxins which promote plant growth. Some PGPR function as a sink for 1-aminocyclopropane-1-carboxylate (ACC), the immediate precursor of ethylene in higher plants, by hydrolyzing it into α -ketobutyrate and ammonia, thereby promoting root growth by lowering indigenous ethylene levels in the micro-rhizo environment [117]. In different ecosystems, bacteria can also play a core role in the composition of plant communities by specifically acting on certain plant species and also participating in key environmental processes. In addition to increasing plant nutrient content, it is capable of increasing the population of other beneficial microorganisms and controlling the population of harmful ones in the rhizosphere [111].

5.2.3 Biological nitrogen fixation (BNF)

The process of fixing nitrogen biologically by soil microbes is an economically attractive and ecologically sound method to reduce external nitrogen input and enhance the quality and quantity of internal resources [118]. Soil microbe can be considered as a living component of soil organic matter because the biomass comprises all soil organisms with a volume approximately less than $5 \times 10^3 \mu\text{m}^3$ apart from plant tissue [119]. This process accounts for 65% of nitrogen that are currently used in agriculture, and will continuously be of importance in the sustenance of crop production systems in the future [120]. In most terrestrial ecosystems, BNF is their largest source of new nitrogen [121]. The rates of BNF in tropical forests (15 to 36 kg N/ha/yr) are higher than/similar to their temperate counterparts (7–27 kg N/ha/yr), which are subjected to strong nitrogen limitation [122]. In the tropics, diazotrophs could have been favored because they receive enough quantity of nitrogen to maintain higher extracellular phosphatase activity, which is prerequisite for overcoming phosphorus limitation and also they have optimum temperature for their activities [123]. Important biochemical reactions of BNF occur mainly through symbiotic relationship of N_2 -fixing microbes (especially bacteria) with legumes that convert atmospheric nitrogen (N_2) into ammonia (NH_3) [124].

Symbiotic and non-symbiotic microorganisms in the soil rhizosphere can assist in fixing atmospheric nitrogen in crops and non-crop plants. Over the years, it has been accepted generally that legumes (and the non-legumes genus *Parasponia*) are exclusively nodulated by member of the *Rhizobiaceae* Family in the α -proteobacteria, which includes the genera *Bradyrhizobium*, *Sinorhizobium*, *Azorhizobium*, *Mesorhizobium* and *Rhizobium* [125]. Recently, other species of α -proteobacteria such as *Methylobacterium*, *Blastobacter denitrificans*, *Devosia* have been reported to nodulate *Crotalaria*, *Aeschynomene indica* and *Neptunia natans*, respectively [126–128]. *Ralstonia taiwanensis* and *Burkholderia spp.* belonging to the β -proteobacteria have been found in the nodules of some tropical legumes [129, 130].

Generally, PGPR are classified as biofertilizers, biopesticides and phyto-stimulators [131]. The biofertilizers help to promote plant growth by supplying nutrients to the host, and these include *Allorhizobium spp.*, *Pseudomonas fluorescens*, *Rhizobium spp.* and *Trichoderma spp.* (e.g. *T. asperellum* and *T. hamatum*) [132]. The symbiotic association of Rhizobacteria with soil introduces $50\text{--}70 \times 10^6$ tons of nitrogen into agricultural soils thus reducing the use of inorganic fertilizers [133]. The phytostimulators produce phytohormones such as indole acetic acid, gibberellin and cytokinins which alter root architecture and promote plant development [134] and these include *Bacillus*, *Azospirillum*, *Azotobacter*, *Enterobacter*, *Pantoea*, *Pseudomonas*, *Streptomyces* and *Rhizobium spp.* The biopesticides inhibit the proliferation of pathogen and help in plant growth, and these include *Pseudomonas spp.*, *Streptomyces spp.* and *Bacillus spp.* (e.g. *B. subtilis*) [135]. In addition to these three groups, there are other PGPRs that induce tolerance in plants to abiotic stress. Those in this group include *Paenibacillus polymyxa*, *Achromobacter piechaudii* and *Rhizobium tropici* [136].

The nitrogen fixed by symbiotic *Rhizobia* in legumes can be beneficial to associated non-leguminous crops through direct transfer of biologically fixed nitrogen to cereals growing in intercrops [137] or to subsequent crops rotated with symbiotic leguminous crops [138]. In many low input grassland systems, the grasses depend on the nitrogen fixed by their legume counterparts for their nitrogen nutrition and protein synthesis, which is much needed for forage quality in livestock production [117]. *Rhizobium* and *Bradyrhizobium* species of *Rhizobia* produce molecules such

as auxins, abscisic acids, riboflavin, cytokinins, vitamins and lipochitooligosaccharides that promote plant growth in addition to fixing atmospheric nitrogen [139]. Other PGPR traits of *Rhizobia* and *Bradyrhizobia* assist in the production of phytohormones [140], release of siderophore [141], solubilization of inorganic phosphorus [142] and also act as antagonist against plant pathogenic microbes [143]. In the study of Kennedy *et al.* [144], a several number of non-symbiotic PGPR significantly increase the vegetative growth and grain yield of C₃ and C₄ plants such as rice, maize, wheat, cotton and sugarcane due to their interactions. The application of *Azotobacter* increased the yield of rice, cotton and wheat [145, 146]. In a field trial experimental study, Tran Van *et al.* [147] used *Burkholderia vietnamiensis* to inoculate rice and found out that it significantly increased the grain yields up to 8 t/ha. It has been reported that the species belonging to genus *Burkholderia* can produce substances that are antagonistic to nematodes [148].

5.2.4 Phosphorus-solubilizing bacteria

Strains of bacteria belonging to the genera of *Pseudomonas*, *Rhizobium*, *Agrobacterium*, *Flavobacterium*, *Bacillus*, *Burkholderia*, *Aerobacter*, *Achromobacter*, *Erwinia* and *Micrococcus* have been found to have the ability to solubilize insoluble inorganic phosphate compounds such as rock phosphate, dicalcium phosphate, tricalcium phosphate and hydroxyl apatite [149, 150]. Tricalcium phosphate and hydroxyl apatite have been reported to be more degradable substrates than rock phosphate while the most powerful phosphate solubilizers are strains belonging to the genera *Pseudomonas*, *Bacillus* and *Rhizobium* [151].

6. Conclusion

The soil is a good reservoir or habitat for microorganisms which might be beneficial to both plants and animals. Soil microbes help in aerating the soil by increasing the pore sizes thus increasing the rate of percolation. The relevance of soil microorganisms to crop growth and productivity cannot be overemphasize. They enhance crop growth and productivity both in stress, low fertile and fertile soil by facilitating transformation, solubilization and mobilization of nutrients, and altering the physiological processes of plants.

In order to increase agricultural production in terms of cropping in the tropics without polluting or degrading the environment, most especially cropland soils, the use of biofertilizers and biopesticides composed of beneficial microbes should be encouraged among peasant and large scale farmers instead of synthetic fertilizers. Since they do not only improve the soil fertility but also assist the roots of plants in the absorption and uptake of nutrients from the soil.

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