Review

Harnessing the Rhizosphere Soil Microbiome of Organically Amended Soil for Plant Productivity

Ayansina Segun Ayangbenro [1] [iD], **Chinenyenwa Fortune Chukwuneme** [1] [iD], **Modupe Stella Ayilara** [1] [iD], **Funso Raphael Kutu** [2] [iD], **Motlagomang Khantsi** [1], **Bartholomew Saanu Adeleke** [1] [iD], **Bernard R. Glick** [3] [iD] and **Olubukola Oluranti Babalola** [1,*] [iD]

1   Food Security and Safety Focus Area, Faculty of Natural and Agriculture Sciences, North-West University, Mmabatho 2735, South Africa
2   School of Agricultural Sciences, Faculty of Agriculture and Natural Sciences, Riverside, University of Mpumalanga, Mbombela 1200, South Africa
3   Department of Biology, University of Waterloo, Waterloo, ON N2L 3G1, Canada
*   Correspondence: olubukola.babalola@nwu.ac.za; Tel.: +27-1838-92568

Abstract: Soil degradation remains an ongoing process that is exacerbated by the effects of climate change. Consequently, these processes decrease soil organic matter and nutrient contents, soil biological functions, and plant productivity. The addition of organic amendments (OAs) to the soil is a widespread practice to enhance soil quality and the health of agricultural soils. One of the most significant microbial hotspots controlling the processes, dynamics, and cycling of nutrients, carbon and water in terrestrial ecosystems is the rhizosphere. Understanding the continuing transformations of OAs and the distribution of different factors (C, nutrients, and microbial activities) across and along roots is crucial in the rhizosphere. The application of OAs to soil increases soil organic matter and nutrients, water holding capacity, improves soil structure and stimulates soil microbial activity and biomass. This review evaluates the role of the rhizosphere microbial community in organically amended soils for promoting plant growth and health. The diversity of the rhizosphere microbiome and the mechanisms used in plant protection are discussed.

Keywords: soil degradation; organic amendments; soil microbiota; soilborne pathogens; plant-microbe interactions; sustainable agriculture

1. Introduction

Intensive agriculture, improper land management practices, and mining of minerals and resources from soil have resulted in soil degradation and poor soil quality, which is a major concern worldwide. Other recognized threats that lead to soil degradation are contamination, erosion, salinization, flooding, and biodiversity loss [1]. Soil degradation is an ongoing process that is currently worsened by the effects of climate change [2]. Degraded soils are characterized by depleted soil organic matter and organic carbon, with losses ranging from 25% to 75% of the original soil organic matter and organic carbon pool [3]. According to the United Nations special report on climate change and land, it is estimated that human-induced degradation affects about a fourth of the earth's ice-free land area [4].

Soil degradation is accompanied by a loss of microbiological diversity and biological functions. Recent studies have shown that climate change and anthropogenic activities are reducing soil capacity to perform fundamental processes and functions, such as primary production, nutrient cycling, litter decomposition, and organic matter mineralization [5,6], which has led to increasing concerns that reduced soil biodiversity may have a negative impact on an ecosystem's functions and services [7,8], putting in danger the agroecosystems' productivity, stability, and sustainability. The diversity of functions performed by microbes, including whether specialized groups carry them out or generally, across the community, as well as variations in soil properties that affect the bioavailability of nutrients or toxins,

make it difficult to understand the role of soil microbial communities in biodiversity and ecosystem function relationships [9]. For instance, many different microbial species are involved in the decomposition of organic matter, and community-level respiration frequently remains constant in a wide range of different communities, but only a few specialized species are capable of symbiotic N_2 fixation and xenobiotic degradation [9]. Therefore, some functions will be more affected by diversity loss than others will.

The addition of organic amendments (OAs) is a strategy commonly employed to restore degraded agricultural land. OAs can also improve soil resilience to climate change and mitigate some of their effects by counteracting CO_2 emissions [3]. An OA is any organic material applied on the soil surface or incorporated into the soil to enhance plant growth [10]. The use of OA as a soil amendment resulted in increased soil fertility, enhanced soil quality, improvement in soil water holding capacity and soil aggregation, enhancement of soil microbial activity and biomass, and an increase in crop yield [11] (Figure 1). Examples of OAs include animal manures, biosolids, biochar, compost, crop residues, sewage sludge, biofertilizers, and synthetic soil conditioners, such as polyacrylamides, polysaccharides, and polyethyleneoxide, used to improve soil fertility and health [2,10,12]. Soil OAs vary greatly in the composition of their organic matter, origin, chemical composition, and the effects of their decomposition in soil. Mineralization of the organic matter in OAs by soil microorganisms is critical for the release of nutrients into the soil. However, this slow process depends on the characteristics of organic wastes, the soil type, the prevailing environmental conditions, and the microbial communities present. While this slow process reduces the risk of nutrient leaching, it may not provide adequate nutrients for efficient plant growth [13]. In addition, higher-level application can generate high electrical conductivity, which may cause injury to plants whereas insufficient application may not provide enough nutrients for effective plant growth. Similarly, the presence of alkyl C, carbonyl C, and methoxyl C in OAs can be toxic to plant growth [14,15]. This implies that OAs must be applied more frequently or at an experimentally determined optimum rate to achieve the desired effects [16,17].
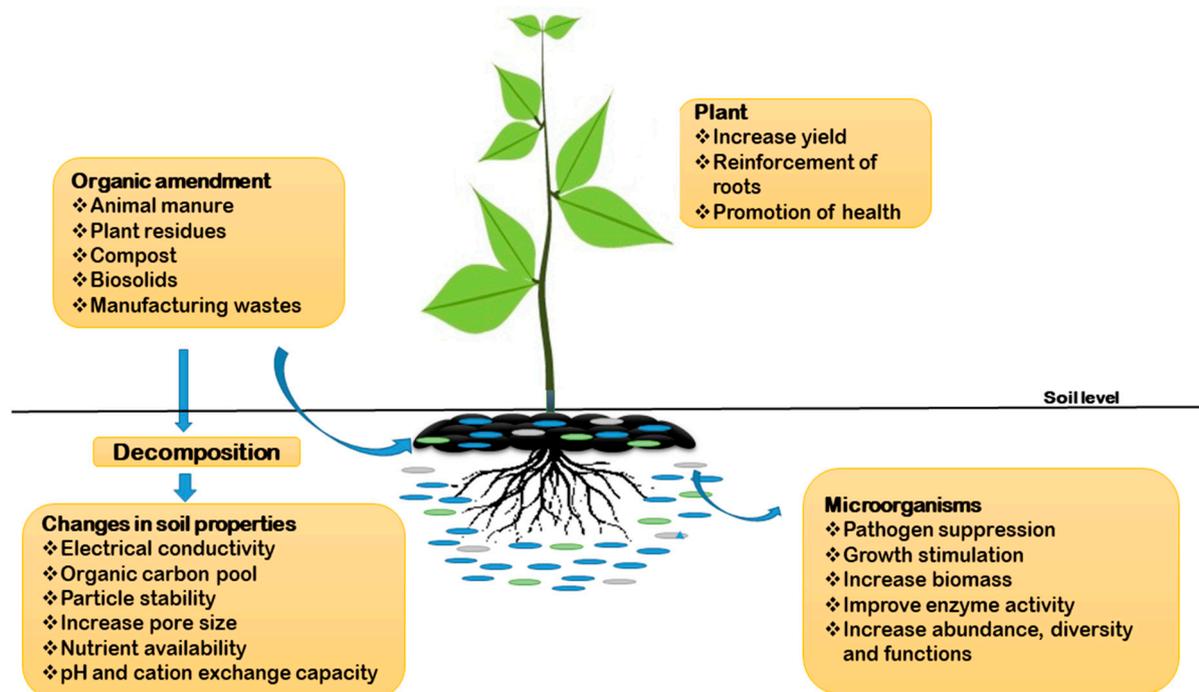

Figure 1. The impact of organic amendments on soil and plant and soil microorganisms.

Fortunately, there is increasing global interest in sustainable soil management, which is critical for environmental stability. The innovative use of OAs has recently focused on enhancing not only soil's physical and chemical properties, including nutrient availability

and carbon sequestration, but also, most importantly, the soil biological properties in agroecosystems. The use of OAs have been reported to alter the structure and function of soil microbiomes (microbial community that interacts with its environment to produce specific ecological niches. It has unique characteristics and functions [18] including the suppression of pathogens) [19,20]. Hence, the use of OAs helps reduce the reliance on agrochemicals and presents an economically attractive and ecologically sound alternative for the disposal of organic materials.

The rhizosphere, as described by Kuzyakov and Razavi [21], is the area of soil surrounding the root that is significantly impacted by root activity. It is a dynamic region that is governed by complex interactions between host plants and microorganisms that are closely associated with plant roots. The rhizosphere is characterized by intense biological activity due to the release of root exudates by the host plant, which promotes or inhibits rhizosphere organisms [22]. The microbiome of the region act as partners in plant health, fitness, and metabolic functioning, such as synthesis of phytohormones, improved nutrient uptake, defense responses, and pathogen suppression [23]. The fundamental functions carried out by this rhizosphere microbiome contribute to the cycling of nutrients and plant health. The activities of these organisms are regulated by the chemical properties of the soil, such as soil pH, organic carbon, and total nitrogen content [24], soil physical properties, plant community composition, disturbance history, and seasonal and climatic differences [25].

The addition of OAs to soil may be used to manipulate the soil microbial community composition and to regulate soil enzyme activities [26]. Many studies have demonstrated a significant alteration in the composition and diversity of soil microbial communities in plant rhizospheres following the application of OAs [3,27,28]. A study by Zhan, et al. [29] demonstrated that OA enhances the activities of many soil microbes and increases numerous synergistic interactions within the microbial community, thus improving banana growth, biomass, and health. It has also been demonstrated that soils receiving OAs, such as compost, are characterized by increased microbial richness and a shift in the structure of the soil microbial community [30]. However, the associated general taxonomic responses to OAs and the mechanisms underpinning these shifts are still poorly understood. To improve crop productivity, it is vital to understand the influence of OAs on both crops and soil microbial assemblages. The role of rhizosphere microbial assemblages of organically amended soil as a successful strategy for plant growth and health needs to be investigated given the growing use of OAs in agroecosystems. Thus, we highlight the diversity of the rhizosphere microbiome due to changes in resource availability as well as their role in plant growth and the mechanisms used in plant protection.

2. Organic Amendments and Sustainable Agriculture

The use of OAs dates back to the origin of agriculture by humans and has been reported to have a positive influence on soil health and plant yield [31]. OAs may originate from suitable naturally occurring plant species, food and agricultural processing industries, disposed waste materials, or crop residues [12], and biodegradable wastes, such as sludge to improve soil fertility [25,32,33].

2.1. Sources of Organic Amendments and Their Impact on Soil Properties

The production and use of organic-based fertilizers from different sources through innovative technologies represent an important fertilization strategy for promoting increased and sustainable crop production. In addition to the various OAs sources listed in the previous section, different wastes from manufacturing industries, including distillery wastes, sugar extraction residues, and paper residues have been investigated and used over the years as soil amendments [12,34–36]. Biochar has also been successfully used and reported as a good complementary organic fertilizer material that originates from organic biomass (plant and animal biomass, such as residential plant trimmings, food processing residues, animal manures, or forestry cuttings) and contains large amounts of organic carbon. The high organic carbon content of biochar arising from pyrolysis, which involves

the heating of organic biomass at a high temperature with little or no oxygen, has been reported to be highly beneficial for soil and crop growth [12,37].

The application of OAs on agricultural soils directly enhances soil quality by modifying the physical, chemical, and biological properties of the soil. Some studies have demonstrated that applying OAs to the soil directly changes its physical properties. These improvements are due to the following: (1) reducing water and nutrient losses by increasing water holding capacity of soil; (2) enhancing nutrient cycling by stimulating existing microbial activities and populations; (3) increasing biodiversity by creating positive soil carbon budget; (4) improving soil health by suppressing soil-borne diseases; (5) increasing soil porosity and water filtration by decreasing soil bulk density; and (6) enhancing soil pH buffering capacity due to cation exchange capacity of OAs [10,25,38–40]. According to Zhang et al. [41], the application of OAs improves the stability of soil particles, increases the pore size, and decreases the density of bulk soil while positively impacting soil aeration and structure. The regulation of soil temperature can also be directly influenced by this practice as soil evapotranspiration decreases soil surface temperatures [42].

Organic amendments are used to offset the organic matter's decline to improve chemical and physical properties of arable soils. Organic amendments applied topically can increase the soil's C and N content in the top 5 cm, but they may have little to no impact below this [25]. The dry matter content of the amendment determines how much of an impact there will be. Increased carbon can improve infiltration and reduce runoff due to increased cation exchange capacity and higher resistance of soil aggregates to raindrop impact [25]. Additionally, adding OAs to soil improves its ability to store water, enhances its porosity, and reduces its bulk density [43], as well as creates greater macroporosity at the depth where OAs have been applied. Since the nature, form, and shape of OAs are crucial in the development of soil aggregates, adding OAs alone is not wholly adequate to counteract all the detrimental changes in soil chemical and physical properties [25]. Applying OAs can cause changes to the chemical properties of soil. The amount of organic C in soil can affect the surface charges needed for cation exchange capacity (CEC) and the retention of basic ions, especially magnesium and calcium, which can make the soil more acidic. Applying OAs can also lead to improved CEC. The CEC and organic C content had a direct correlation with soils with less clay [25].

Plant residues are also important soil amendments that positively influence soil structure and soil health [12,36]. The use of plant residues as soil amendment involves the addition of foliar or plant parts into the soil or growing certain crop varieties to improve soil properties. This practice is common and represents a sustainable means of replenishing the soil with important nutrients [44,45]. For example, legume crops used as covers facilitate nitrogen fixation through the help of rhizobacteria. The practice of crop rotation also preserves the soil, which makes it ready for the next crop and prevents autotoxicity [46]. Furthermore, using plant residue helps prevent wind and water erosion and increases soil water retention capacity [44]. Although, the application of plant residues as OA have been reported to produce positive effects on soils, such as the alteration of soil microbial community composition, increasing enzyme activity, and reducing soil-borne diseases. Documented evidence also focuses on species richness of pathogenic *Pythium* spp. and *Rhizoctonia solani*, following incorporation of fresh plant residues [47,48].

The addition of OAs to the soil can alter the soil pH, which can either increase or decrease depending on the type of OA and its pH [49]. Cooper et al. [16] reported a significant increase in soil pH and organic carbon compared to the control in a six-year study that included the application of compost and biochar, added separately to an agricultural field under a temperate climate. The addition of compost to the soil resulted in increased cation exchange capacity of the soil whereas biochar had no significant effect. The study also observed an increase in microbial biomass carbon, which is closely linked with an increase in pH due to the addition of compost and biochar [16]. Eventually, there was a shift toward a favorable environment for the rhizospheric microbial population to thrive and an increase in microbial biomass carbon. However, Jones et al. [50] reported that the addition

of biosolids to bauxite-processing residue sand led to a decrease in pH and acidification was more evident at the higher addition rate compared to the addition of other OAs (green waste compost, spent mushroom compost, and green waste-derived biochar).

One of the most important indicators of soil fertility and soil health is the diversity of microbial populations in soils. Amending the soil with organic materials stimulates the growth of soil microbial communities and enhances the activities of the biological components of the soil because of high organic carbon present in OAs [51,52]. The application of organic manure increases the availability of micro- and macronutrients in soil, thereby increasing the population of soil microbial communities [53]. Although microbial populations in soils may be increased by the addition of OA, the number of microbes from one OA source may vary from the other [12].

Organically amending the soil for agriculture can indirectly or directly favor the growth of certain microbial communities that contribute to changes in the biological properties of the soil [54]. Previous studies have indicated that soil biological properties, such as microbial enzymes, are good indicators of soil fertility, in addition to microbial properties, which include organic compound decomposition by hydrolytic enzymes [55]. These enzymes are involved in various ongoing decomposition processes in soil. Soil amendments enriched with available carbon may cause plants to select specific microbes, leading to changes in soil biological properties [36]. This change is caused by the induction of changes in soil structure and the amount of accessible nutrients caused by microbial activities, which can influence plant exudation, growth, and health. These changes may influence agricultural productivity by increasing crop yield and suppressing the incidence of diseases by soil-borne pathogens [36]. The increase in soil organic carbon as a result of the addition of OAs provides plants with essential nutrients and improves the microbial activity in soil [56]. It also enhances soil quality by improving soil porosity and soil density, increasing water and nutrient (N, P, K, and Mg) availability for plant use, and enhancing biological activity and cation exchange capacity [12]. These all depend on the amount of nutrients present in the OAs applied.

2.2. Impact of Organic Amendments on the Structure and Diversity of Microbial Communities in the Rhizosphere

The structure and functions of microbial communities in the plant rhizosphere are affected by a plethora of biotic and abiotic factors, some of which are soil properties [57], genotype [58], plant species [59], plant developmental stage [58], and fertilization [60]. Moreover, long-term fertilization is a critical factor that determines the properties of both the rhizosphere and bulk soils and their microbial inhabitants.

Organic materials and mineral fertilizer provide bulk soil with large amounts of nutrients. Without these additional nutrients, this soil would have otherwise been regarded as an oligotrophic environment. These nutrients both increase the activity of several dormant microbes and decrease the rhizosphere microbiome's reliance on being plant-derived [61]. Therefore, prolonged fertilization modifies both the structure and function of the soil microbial population as well as the interactions between plants and microbial communities [61]. Another significant factor influencing soil microbial communities is pH, which is significantly decreased when nitrogen fertilizers comprising urea and ammonia are applied [62]. The metabolic capabilities of microbial communities in decomposing C pools can potentially change as a result of N addition [63]. Organic fertilizers on the other hand, add a significant amount of C, other nutrients, and associated microbes to the soil, in addition to N. Previous research has demonstrated that the condition of cultivated soil determines which native microbes will be exposed to its roots and this could be activated by root exudates [57,64]. As a result, the addition of OAs to agricultural soils would modify the bulk soil microbiome. This opens the door to the possibility of modifying the native microbial communities in the rhizosphere of plants by introducing different kinds of substrates into the soil to improve microbial functions in the rhizosphere soil and increase crop yield.

Studies have suggested that fertilization shapes the composition of rhizosphere microbiomes compared to other factors, such as plant, soil properties, and rhizosphere effect [65,66]. OAs change the composition of rhizosphere soil microbiota, with an increase in prokaryotic richness and the formation of prokaryotic groups known to be associated with the breakdown of complex organic compounds, such as compost and manure [30,67,68]. Semenov et al. [65] also reported a higher abundance of nitrifiers and denitrifiers within prokaryotic communities in NPK-amended soils compared to manured soils. However, increased soil properties and nutrients were observed in manure-amended soils compared to NPK-amended soils. The authors suggested that fertilization affects soil properties, which has significant effects on microbial composition and diversity; hence, the higher total porosity and aggregation observed in manure-amended soils resulted in a more conducive environment, with optimal nutrient and water balance for bacterial communities to thrive.

On the other hand, soil protists are so responsive to environmental factors. Their mode of response to biotic and abiotic factors from fungi and bacteria also differs [69]. Among the environmental factors, the effects of nitrogen fertilizer on protists communities, particularly the phagotrophs, were more pronounced than those on bacterial and fungal communities [70,71]. This could be partially explained by higher ammonia levels caused by nitrogen fertilizers, which can inhibit protist growth by disrupting their cells [72]. In paddy soils, it was shown that phagotrophic protist communities consume bacteria, thereby altering their communities [73,74]. The studies reported that in the paddy soils, the predatory activities of phagotrophic protists influence methane cycling [75,76], fungal, as well as bacterial communities, particularly, those associated with nitrogen cycling [74,77,78], which in turn promotes the growth of rice plants [73,74,78].

Chemical fertilizers do not only affect the diversity of soil protists, but agricultural land-use also impacts protist communities by modifying the pH, organic matter, and moisture contents of soils [79]. Phagotrophic and autotrophic protists reacted differently to changes in soil porosity and nutrients induced by biochar amendments [80]. Altogether, earlier studies demonstrated that protists are more vulnerable to environmental changes than their bacterial and fungal counterparts, especially in relation to climate, soil nutrients, soil water nutrients, and plant rhizosphere effects [69]. Furthermore, previous studies using T-RFLP and DGGE highlighted that the major drivers of protist community changes are organic and inorganic fertilizers [81], soil oxygen and water availability, and the rhizosphere effect [82,83]. However, a study using the high throughput sequencing method reported a significantly higher richness and diversity of protist community in bulk soils compared to those observed in the rhizosphere soils of the three fertilizer treatments [84]. Moreover, bio-fertilizer application to bulk soils resulted in significantly higher richness and diversity of protists, as opposed to the chemical fertilizer treatment. In the study, organic fertilizer and bio-fertilizer treatments showed higher richness and diversity in both the rhizosphere and bulk soils compared to the chemical fertilizer-treated soils, although, the differences were not significant.

Microbial communities within the plant rhizosphere play major roles in plant growth and health. For example, an increase in the community diversity of rhizosphere microbes promoted the growth of strawberry (*Fragaria* × *ananassa* Duch.) seedlings [85]. The study investigated the effects of using apple fruit fermentation (AFF) alone or in conjunction with *Bacillus licheniformis* on strawberry tissue culture seedlings in vitro. The rhizosphere of the control matrix (water treated) had the most bacterial species, whereas the rhizosphere soil treated with *B. licheniformis* alone had the least diversity. *Coprinus atramentarius*, *B. megaterium*, *B. licheniformis*, *Weissella*, and *B. subtilis* were found to be the most common bacteria in AFF. When AFF and *B. licheniformis* were combined in one treatment, the leaf area, plant height, root length, plant weight, and antioxidant enzyme activities were all significantly increased. The study concludes that treating the matrix with AFF and *B. licheniformis* increases antioxidant enzyme activity in strawberry seedlings, improves rhizosphere microbial status, and promotes plant growth [85].

The composition of microbial communities and soil enzyme activities can be manipulated through the application of OAs [86,87]. According to Zhang et al. [29], OA (a mixture of cassava residue, ground tobacco, mushroom compost, concentrated molasses, and filter mud from a sugar factory) can stimulate the activities of soil microbes and improve synergistic interactions within microbial populations in a given habitat, thus increasing plant biomass. Soils amended with organic fertilizer were reported to be dominated by specific microbial groups, known to be associated with the degradation of complex organic compounds such as manure and compost [30]. Some field studies have also reported that the application of bio-organic fertilizer over a long term can alter the rhizosphere community composition of tomato and banana plants [88,89]. The bacterial diversity and relative abundance of the plant growth-promoting bacteria *Pseudomonas*, *Burkholderia*, and *Chrysosporium* were increased in the rhizosphere of kiwifruit after the application of composted pig and sheep dung [26]. The authors concluded that long-term application of OA may improve the productivity of kiwifruit by increasing the populations of plant growth-promoting microbes and simultaneously suppressing the growth of plant pathogens. Other studies have shown that OAs, such as manure and composted plant residues, can inhibit the growth of *Fusarium* populations by promoting the growth of potential biocontrol populations in the plant rhizosphere. For example, the application of compost amendments resulted in the suppression of the population of *Fusarium* wilt-causing strains and increased the populations of beneficial fungi, bacteria, and actinomycetes in spinach [90]. In another study, the application of bio-organic fertilizers increased the abundance of *Sphingomonas* and *Gemmatimonas* and reduced the incidence of *Fusarium* wilt disease in banana plants [91].

2.3. Organic Amendment and Disease Suppressive Soils

The term "suppressive soils" refers to those where the development of disease is minimal even in the presence of a virulent pathogen and a susceptible plant host [92]. Contrarily, in non-suppressive soils, where abiotic and biotic factors encourage the pathogen, disease is easily transmitted [93]. Suppressive soils are also described as soils where a pathogen either does not persist or establish, establishes but causes little to no disease, or develops and initially causes disease but subsequently the disease declines with subsequent crops of a susceptible host despite the pathogens perhaps still persisting in the soil [94,95]. Some disease-suppressive soils are naturally occurring and reliant upon the chemical or physical characteristics of the soil, whereas in other systems, a soil's ability to slow the spread of disease evolves over time in response to particular agronomic practices [94], such as the addition of OAs, such as green manure.

The activity of disease-suppressive soils depends on a combination of "general" and "specific" suppression. General suppression is the ability of soils to restrict the growth and activity of soilborne pathogens to some extent, caused by the overall competitive and antagonistic activity of the entire soil microbiome that is in completion with the pathogen(s) [94,95]. It is a natural and inherent property of soil that is effective against a wide range of soilborne diseases. It is not transferrable from one soil to another or a field to the other with very small amounts of microbial inoculum or soil [95]. General suppression is reduced by steaming and is eliminated by soil sterilization but can be enhanced by agronomic practices that increase the diversity, population size, and activity of soil microbiomes [95].

Specific suppression is highly effective and specific species or select groups of microorganisms cause it. It can be transferred by mixing pure cultures or very small amounts, between 1–10% of suppressive soil with conducive soil [95]. Specific suppression is eliminated by pasteurization at 55–60 °C for 30 min [96] and soil fumigation with methyl bromide [95]. The key element that distinguishes specific suppression from general suppression is the ability to transfer by adding a small amount of soil or an inoculum of the responsible microbial species. Transferring 1% or 10% to a favorable soil ultimately results in a same level of suppression. It does not take much for a population of a particular

organism to get established in its niche since specific suppression is caused by a population rather than a community [95].

By selectively enriching for populations of pathogen antagonists, OAs are frequently investigated as an environmentally benign method of controlling soilborne pathogens. The most popular OAs used in this context has been composts, which have shown notable levels of efficacy, especially in controlled environments or container-based production systems. The most frequent explanation for effectiveness has been an increase in biological activity in a soil system; however, in other systems, a distinct component of the microbial community and an operational mechanism have been identified [92]. The inability to accurately duplicate compost composition, both from a substrate and microbial perspective, is a significant drawback of this method [92].

Studies have demonstrated that OAs can effectively control diseases caused by pathogens, such as *Ralstonia solanacearum* [97], *Rosellinia necatrix* [54], and *Fusarium* spp. [90,91]. Different mechanisms have been proposed to be responsible for the suppressive nature of OAs and these include increased antagonistic microbial activity, increased competition against pathogen for natural resources that causes antibiosis, parasitism, release of toxic compounds during organic matter decomposition, or the induction of systemic resistance in the host plant [93,98]. Competition for carbon by non-pathogenic *Fusarium oxysporum* [99] and competition for iron by rhizosphere bacteria through the production of siderophores [100] were demonstrated to be important processes for *Fusarium* wilt suppressive soils. The all-encompassing pathogens of wheat and barley, *F. oxysporum* and *Gaeumannomyces graminis*, were suppressed by the addition of siderophore-producing *Pseudomonas* from suppressive soils or their siderophores into conducive soils [101].

The efficacy of rhizosphere organisms can also be increased through the addition of OAs to increase their activities against pathogens. *Streptomyces*, an efficient soil saprophytes, are particularly likely to react to the incorporation of organic material into soil and are frequently the microbial agents responsible for causing amendment-induced suppression [92,95]. Klein et al. [102] studied root-associated microbial communities in connection to suppression and supplemented soils with wild rocket (*Diplotaxis tenuifolia*) to boost the general suppressiveness to *F. oxysporum* f. sp. radicis-cucumerinum. In contrast to the unamended (conducive) soil, the amended soil had a higher relative abundance of root-associated *Streptomyces*. This shift also occurred in non-inoculated controls, and the induced suppression was thought to happen regardless of the presence of the pathogen. The study discovered that 3 days after amendment, a population of *S. humidus* thought to be hostile to phytopathogenic fungi predominated root actinobacteria by observing changes in the actinobacterial community. However, suppressive soils also saw a surge in other potential antagonists [102].

2.4. Potential Negative Effects of Organic Amendment

The application of OA can be either beneficial or harmful to plant growth and soil ecosystems. The harmful agents, such as organic pollutants, heavy metals, human pathogens, and antibiotic-resistance genes, that may be present in OAs negatively influence soil health [1]. In addition, excess, inappropriate and uncontrollable use of OAs can pose hazardous effects on terrestrial and aquatic habitats [103]. For instance, soil acidification, the release of greenhouse gases, nutrient immobilization, eutrophication, and excess nutrient discharge into bodies of water result from surface run-off and create undesirable ecological disturbances [104].

Another negative impact of OAs is metal toxicity, which alters soil chemistry and health. Metal toxicity depends on the metal concentration in the soil, although this can be different from the actual values when measured [105]. The long-term persistence and non-biodegradable nature of heavy metals coupled with continuous OA application have resulted in metal accumulation in soil, thus posing potential risks of metal biomagnification and bioaccumulation along different trophic levels [106]. The biotransformation of organic pollutants in the soil through the activities of soil microbes can reduce the effect of metal

toxicity on soil microbes [107]. Hence, there is a need to investigate the ecotoxicity of organic pollutants present in OAs, relative to their continuous use for soil health sustainability and ecological safety.

One of the major concerns of using OA derived from animal waste is the presence of pathogenic microorganisms and parasites [104]. Some identifiable pathogenic bacteria from certain organic waste include *Bacillus anthracis*, *Bordetella pertussis*, *Escherichia coli*, and *Klebsiella pneumoniae* [108,109]. To avoid soil contamination and intrusion of pathogens into the food chain, there is a need to measure the safety level of OA before applying it to agricultural soils to avoid human health complications.

Cumulatively, the aforementioned-negative effect of OAs on the ecosystem threatens their usage in agriculture with the potential risk associated with environmental and human health [25]. These challenges vary depending on the type of OAs applied; therefore, the need to choose appropriate organic manure with less toxic effects to amend soils is important for enhancing microbial activities for plant growth and survival in diverse environments. To further avert this potential problem, research innovations, legislation guidelines, and policies on waste disposal in many countries are geared toward regulating a number of contaminants in organic waste beyond a set threshold.

The Waste Directive (EU) 2018/851, the Directive on the Landfill of Waste (1999/31/EC), the Animal Waste Directive (90/667/EEC), and the Sewage Sludge Directive (86/278/EEC) are only a few of the legislative instruments that Europe developed in an effort to mitigate these potential negative effects. Intriguingly, these laws specify threshold values for the pollutants present in organic waste and offer advice for waste disposal [1]. Accordingly, the US environmental protection agency reported that it is critical to monitor the concentrations of NH_3^+, NO_3^-, phosphate, and trace elements (Ni, Pb, and Cd) in native soil that has been amended with sewage sludge and animal manure as well as their movement into runoff and seepage water and any potential bioaccumulation in edible plants at harvest. Ten elements (As, Cd, Cr, Cu, Hg, Mo, Ni, Pb, Se, and Zn) in sewage sludge applied to soil are controlled under the USEPA Part 503 biosolids rule. In terms of trace element composition (Cu 1500, Cr 1200, Mo 75, Ni 420, Pb 300 and Zn 1400 mg kg^{-1}), the USEPA has established standards for clean sludge and said that, if these elements fall below the typical disposal requirements, sludge may be added to agricultural land [110].

3. Diversity of Microbial Communities in Rhizosphere Soils of Organically Amended Soil

The plant rhizosphere is surrounded by diverse microbial species that significantly influence the plant's growth and fitness [111]. These microbial groups include plant growth-promoting organisms, biocontrol microbial communities, nitrogen-fixing microbes, as well as the mycorrhizal fungal communities [112]. Soil microorganisms perform different functions in the soil ecosystem, including participating in the decomposition of organic matter, improving plant growth and health, bioaugmentation, bioremediation, and nutrient cycling, thereby supporting the proper functioning of the agricultural soil ecosystem by improving its productivity and sustainability [113,114]. Consequently, a balance in the diversity of rhizosphere soil microbial communities is important to maintain soil health. The microbial diversity in the rhizosphere soils varies between regions, based on biotic and environmental conditions. Understanding the forces that drive soil microbes associated with organic farming could lead to developing suitable management schemes for sustainable crop production [115]. Therefore, studying the diversity and complexity of rhizosphere microbial communities in organically amended soils is vital to promoting the sustainable use of agricultural soil and optimal functioning of the soil ecosystem.

The diversity and distribution of microbial communities in rhizosphere soils can be changed through the addition of OAs. A shift in the microbial community structure was observed when different nutrients and organic and inorganic materials were applied to agricultural soils (Table 1). The shift increased the predicted function of N metabolism, and poultry manure that is relatively high in N, primarily in the form of uric acid, can be easily

converted to ammonium ions by soil microbes [116]. The implication of this is that there is an increase in functions performed by soil microbial communities considering that poultry litter is high in organic and inorganic N. The increased N metabolism is made available for plants in usable forms thus increasing plant growth. The study reported maximum diversity in poultry-litter amended fields in contrast to the inorganic-amended fields. This shows that nutrient management (poultry-litter vs. inorganic fertilizers) may influence the microbial community structure directly by affecting chemical soil characteristics (i.e., soil pH) and nutrient cycling, and introducing its own bacteria. This indicates that the amendment drives community structure and subsequent ecosystem services across agricultural areas. In this study, Bacteroidetes, Proteobacteria, and Acidobacteria were the most predominant bacterial phyla observed [116]. The rise in Bacteroidetes contributed to the change in community makeup. Bacteroidetes and poultry litter applications have been found to be positively correlated [117], which suggests that soils treated with poultry litter may be more susceptible to opportunistic pathogens.

Table 1. Shift in soil microbial community structure due to the addition of organic amendments.

Organic Amendment	Plant	Impact on Microbial Structure	Reference
Pelletized spent mushroom substrate and biochar	*Hordeum vulgare*	The dominant phyla in the rhizosphere were Proteobacteria, Acidobacteria, Actinobacteria, Gemmatimonadetes, Chloroflexi, and Bacteroidetes. An increase in abundance of Acidobacteria, whereas a decrease in the abundances of Actinobacteria, Chloroflexi, and Bacteroidetes were observed.	Obermeier, Minarsch, Durai Raj, Rineau and Schröder [28]
Mixtures of soybean oil cake, cotton cake, and wheat straw	*Triticum aestivum* and *Zea mays*	Proteobacteria, Firmicutes, Acidobacteria, Actinobacteria, and Cyanobacteria were the most dominant. There was a six-fold increase in the abundance of Firmicutes.	Su, et al. [118]
Cow manure	*Hordeum vulgare*	There was an increase in the abundance of the phyla Zygomycota and Glomeromycota, whereas the phyla Ascomycota (order *Chaetothyriales*), Deinococcus-Thermus, and Actinobacteria decreased significantly.	Suleiman, et al. [119]
Corn straw and pig manure	*Zea mays*	The relative abundance of most Gram-negative bacteria and saprotrophic fungi increased. *Ktedonobacteria, Acidobacteria, Solibacteres,* and *Alphaproteobacteria* increased with organic amendments. The fungal communities were predominantly composed of *Hypocreales, Sordariales,* and *Eurotiales*. Organic amendments significantly increased *Sordariales* but decreased *Hypocreales.*	Wang, et al. [120]
Composted cattle manure and swine manure	rice paddy	A significant increase in Alphaproteobacteria, Betaproteobacteria, Firmicutes, and Bacteroidetes and decrease in Actinobacteria and Acidobacteria in composted cattle manure were observed, whereas a significant increase in Gammaproteobacteria, Bacteroidetes, and Gemmatimonadetes and decrease in Acidobacteria were observed in composted swine manure.	Das, et al. [121]
Cow and chicken manure compost	Watermelon	Proteobacteria, Firmicutes, Planctomycetes, Actinobacteria, Bacteroidetes, Gemmatimonadetes, Acidobacteria, Chloroflexi, Verrucomicrobia, and Nitrospirae were the dominant phyla. There was a decrease in the abundance of Proteobacteria and Verrucomicrobia, whereas Firmicutes, Planctomycetes, Actinobacteria, and Bacteroidetes increased.	Zhao, et al. [122]
Compost	*Zea mays*	There was an increase in the abundance of *Glomeromycota, Ascomycota,* and *Basidiomycota*.	Enebe and Babalola [123]
Farmyard manure and cow slurry	*Hordeum vulgare*	Glomeromycetes, Cantharellales, Saccharomycetales, Trichosporonales, Agaricales, and Onygenales were indicators of OA, whereas Paraglomerales, Eurotiales, Neocallimastigales, and Chaetothyriales were observed in the control.	Harkes, et al. [124]

According to Xue et al. [125], the structure of a microbial community in organically amended soil is impacted by the composition and quantity of the applied organic material, and the resident soil microbial community that is present before the amendment is added. In one study, the rhizosphere bacterial community was amended with three organic fertilizers

(Cattle manure, Sustane® 8-2-4, and pelleted poultry manure) and used to grow maize were profiled using 16S rRNA sequencing [126]. The authors of that study reported an average of 1549 Operational Taxonomic Units (OTUs) in the rhizosphere soil samples, composed of 45 bacterial phyla with Actinobacteria, Proteobacteria, Acidobacteria, and Bacteroidetes as the most predominant phyla present. While the number of OTUs may be viewed as a measure of how many distinct species are represented within a particular taxonomic category, the number of sequence reads from a given taxonomic category may be viewed as representing the abundance of members of that category in the soil community. The changes in the bacterial community structure between samples were most significantly linked to differences in bulk and rhizosphere soils and sampling locations, with treatments accounting for just a small percentage of the variation. This implies that bulk soil has greater OTU richness and diversity than the rhizosphere soil and the species richness and diversity were lowered by the amendments compared to the control. This contradicts the popular belief that OAs usually increase soil microbial diversity and raises the possibility that OAs may actually shorten evenness in the short-term by promoting copiotrophic species [127], which tend to grow faster in habitats rich in nutrients, notably carbon.

The impacts of the three fertilizer applications on soil chemistry and microbiology were different. The effects of pelleted poultry manure and Sustane® treatments, which resulted in considerable increases in soluble N levels, were like those of mineral N addition, except with a lower pH. Cattle manure did not increase NO_3-N, implying that N immobilization may have outweighed N release in this treatment with no changes in pH or bacterial diversity treatment. They also reported that the relative abundances of bacterial families, Cytophagaceae, Sphingobacteriaceae, Oxalobacteraceae, Micromonosporaceae, and Micrococcaceae, were the most influential in predicting the functional profiles (maize yield, nitrogen mineralization, N-acetyl-B-D-glucosaminidase, phosphatase, B-glucosidase activity, and soil respiration) of the rhizosphere community [126].

A study of the effect of swine and cattle manure on soil quality and the productivity of paddy crops using 16S rRNA amplicon sequencing was conducted by Das, Jeong, Das, and Kim [121]. They reported improved species richness and a higher diversity of alpha-Proteobacteria, beta-Proteobacteria, and Firmicutes in the presence of the composted cattle manure. The addition of cattle manure stimulates the microbial groups that have been frequently associated with the breakdown of complex organic compounds. Due to the high substrate availability in the amended soil, the growth of copiotrophs were stimulated, which in turn decreased evenness and increased species richness and diversity. Additionally, as compared to the un-amended control, some dominating species, including *Azospirillum Pleomorphomonas*, *Variovorax*, *Pseudomonas*, *Clostridium*, and *Bacillus*, which play important roles in promoting plant growth and development, and degradation of lignocellulose, showed increased activity. High levels of C and N cycling enzyme activity were detected in the amended soil compared to the control. This implies that improving soil fertility and C and N turnover was aided by the amendment. Higher C cycling enzyme activity in the treated soil compared to the control was caused by increased substrate availability and C demand for autochthonous microorganisms.

Furthermore, the bacterial community structure in bioorganic-treated soils was distinctively different from that in other treatments as reported by Zhao et al. [122]. The study compared the bacterial diversity in watermelon plants amended with bioorganic fertilizer (mixture of fermented cattle and chicken waste and beneficial microbes), composted cattle and chicken manure, and the un-amended control without watermelon. The rhizosphere's microbial populations saw significant alterations after the application of the bioorganic fertilizer to the soil, with an increase in bacterial diversity and a decrease in fungal diversity. The application of bioorganic fertilizer suppressed *Fusarium* wilt and promoted watermelon quality. Proteobacteria, Acidobacteria, Actinobacteria, Bacteroidetes, Firmicutes, Gemmatimonadetes, Planctomycetes, Chloroflexi, Nitrospirae, and Verrucomicrobia dominated the treatment and control. Proteobacteria were more prevalent than other taxa in the soil treatments, although Firmicutes were much less prevalent. Actinobacteria, Chloroflexi,

and Planctomycetes all exhibited increasing relative abundances. This implied that a new microbial population emerged from the bioorganic treated soil and induced change in the microbial structure of the rhizosphere soil of watermelon. This phenomenon is due to increased competition for substrates by the new microbial population and production of antagonistic compounds by these organisms.

Soil fungi are another group of microbes that play enormous roles in improving soil quality and fertility by acting as carbon sequesters and primary decomposers in soil [128]. Some fungal species known to be beneficial to plants include arbuscular mycorrhizal fungi (AMF) [129], *Perisporiopsis lateritia* [130], *Trichoderma* spp. [131], and ectomycorrhizal fungi [132]. The soil ecosystems depend heavily on AMF for their stability and long-term viability [133]. Soil AMF form symbiotic relationships with a vast majority of plant species [134], leading to improved growth and development of host plant. For the development, stability, and operation of plant communities, soil AMF can enhance plant nutrient uptake, disease resistance, and heavy metal tolerance [134,135]. They also improve the alkaline phosphatase (ALP) activity of the soil, which helps to promote phosphorus mobilization, a major function of "mycorrhization effect" [136] and helps to form and maintain soil aggregates with the aid of glomalin, which acts a gluing agent. Glomalin is a special glycoprotein secreted by the spores and mycelia of AM fungi. Its presence in soil is measured as glomalin-related soil protein (GRSP). Furthermore, AM fungal communities are considered as good indicators of soil fertility, owing to the fact that they are influenced by soil management practices, including fertilization and land-use intensity [137]. The diversity of AMF in soil ecosystems have been reported to be beneficial to certain C3 and C4 plants, including maize (*Zea mays* L.) and (wheat) *Triticum aestivum* plants [138]. Furthermore, many studies have shown that soil management practices, such as fertilization and tillage systems, impact AMF colonies [139–141]. It has been widely reported that conventional fertilization has a deleterious impact on AMF community diversity in agricultural ecosystems [139]. In a meta-analysis, it was reported that the diversity of AMF was negatively impacted by the addition of N fertilizers across all studies. Nevertheless, a greater negative impact of 21% was observed in the biodiversity of AMF when a high dose of N fertilizer was applied, compared to when low N additions were applied [142]. Inorganic fertilization decreases the diversity of AMF and causes a shift in favor of a few dominant species or lineages. High fertilizer input rates may drive the biological mechanisms that determine the formation of AMF communities to shift toward higher competition, as photosynthates from host plants become increasingly scarce resources [143]. However, it has been demonstrated that organic additions increase the diversity of AMF in soils. For instance, organic fertilization led to a greater diversity of AMF in grain farmlands in England, compared to inorganic fertilization [144]. When compared to conventional fertilization, organic fertilization techniques were found to increase soil AMF diversity in cereal fields, leys, and permanent pastures in southern Sweden. This had a domino effect on the generation of plant biomass [145]. According to Gottshall et al. [146], agricultural management practices that rely on organic fertilization could minimize the harmful effects of inorganic fertilization on soil AMF communities.

Aside from the studies on AMF diversity, recent studies have also reported the structural composition of other fungal communities in the rhizosphere of organically amended soils. Zhao et al. [122] reported that the fungal phyla, Ascomycota, Basidiomycota, Zygomycota, Chytridiomycota, and Glomeromycota dominated the rhizosphere soils of watermelon plants cultivated in soils amended with bioorganic fertilizer. They reported the predominance of *Rhizophlyctis*, *Basidiobolus*, *Clitopilus*, *Arthrobotrys*, *Pyrenochaetopsis*, and *Aspergillus* as the fungal genera in the samples. Nevertheless, in this study, the diversity and relativity of fungal communities in bioorganic-treated soils decreased compared with other treatments, owing to the increase in diversity of bacteria, such as Actinobacteria, which produce antifungal compounds that suppress the growth of fungal species. The structure of the fungal community in organic-amended soils was distinct from the inorganic fertilizer treatments [122].

The fungal community structure of maize roots from long-term organically and conventionally managed soils were studied using amplicon sequencing [147]. The authors reported that the fungal genera *Mortierella*, *Cryptococcus*, *Cystofilobasidium*, *Mucor*, *Helicoma*, *Exophiala*, and *Aspergillus* were more predominant across all samples. Members of the genera *Rhizopus* and *Minimedusa* seemed to be more prevalent in the conventional system, whereas *Cystofilobasgidium* tended to be more prevalent in organic soils. In terms of diversity and network structure, the rhizosphere fungal communities from conventional and organic systems were more comparable than the corresponding bulk soil communities, and community composition was influenced by management practices. The fungal communities were more taxonomically diverse in the organically managed soils, with 21 out of 30 fungal amplicon sequence variants (ASVs) differentially abundant in the organically managed soils compared to only 9 fungal ASVs in the conventionally managed soils. This highlights the impact of OA on community composition.

Through shotgun sequencing, Enebe and Babalola [123] reported that maize rhizosphere soils amended with different amounts of composted manure comprised of the fungal phyla Glomeromycota, Ascomycota, Basidiomycota, Blastocladiomycota, and Chrytridiomycota, had a greater abundance of fungal communities in composted soils than in inorganic fertilizer treated soils. This is contrary to other reports where the diversity and abundance of fungal communities decreased in the rhizosphere with the incorporation of OA in the soil. Another study reported the abundance of the fungal orders Glomeromycetes, Cantharellales, Saccharomycetales, Trichosporonales, Agaricales, and Onygenales in the rhizosphere soils of barley (*Hordeum vulgare*) plants amended with organic manure (farmyard manure and cow slurry) [124]. The unclassified class of Glomeromycetes was the strongest fungal indicator of organic farming. They have been observed to colonize the roots of vascular land plants, such as barley, forming arbuscular mycorrhiza. Arbsucular mycorrhiza fungus increases the rate of organic matter breakdown and increases the availability of nitrogen [148]. Consequently, the special type of OA used may explain the unique stimulation of Glomeromycetes.

In a shotgun metagenomic study, the microbial communities in the rhizosphere of maize soils under different fertilization systems were characterized and results revealed higher abundance of the archaeal communities, Euryarchaeota, Thaumarchaeota, *Halococcus*, *Haloferax*, and *Alphabaculovirus* in straw-amended soils [149]. In the same study, *Jd18virus* and *Betabaculovirus* were observed as the viral genera present with the highest abundances in the straw-amended samples. Alternatively, Enebe and Babalola [123] reported the predominance of the archaeal phyla, Korarchaeota and Euryarchaeota in maize rhizosphere soils treated with compost manure compared to inorganic fertilizer-treated soils. They also reported that the abundance of the viral families, Myoviridae, Podoviridae, Siphoviridae, Circoviridae, Inoviridae, and Microviridae were more pronounced in the organic-amended soils than in the chemical fertilizer-amended soils.

Survival of Rhizosphere Microbiome from OAs in Soil Conditions

Normally, soil ecosystems serve as barriers to incoming microbes. The persistence of the manure microbiome in the soil environment is closely correlated with microbial contamination by pathogens derived from the manure. The ability of the introduced microbes to survive in the soil environment is influenced by both abiotic (pH, soil type, temperature, nutrient availability, soil moisture, etc.) and biotic (interactions with predatory protists, competition for niches with native microbes, and interactions with plants and plant roots) factors [150,151]. The survival of the manure-associated microorganisms in the soil is also influenced by their own competitive saprophytic abilities [152]. For instance, the intestinal microflora of cow makes up the majority of its microbiome, and many of these bacteria may be less competitive and would not survive in the soil environment because of the differences in environmental factors between the soil and the intestines. However, some gut genera can persist for a long time in soils amended with manure. As an example, *Salmonella* has a reported survival time of more than two months, whereas *E. coli*

O157:H7 has a reported survival time of several weeks to more than six months [153,154]. In a recent investigation, manure application to soil resulted in a strong and rapid increase of taxonomic diversity, soil microbial biomass, gene abundance, and respiration activity, which decreased almost immediately (two weeks) after the treatment [152]. According to the study, almost all of the few surviving microbes were Gram-positive endospore-forming clostridia or phylogenetically related bacterial groups, suggesting that the more aerobic soil environment, as opposed to the intestinal tract, resulted in the disappearance of the oxygen-sensitive genera. Furthermore, Sun et al. [155] and Riek, et al. [156] reported that bacterial and fungal communities that are manure-specific could exist and colonize in soil after manure application, thereby introducing new immigrant taxa into soil ecosystems.

The introduction and survival of exogenous intestinal bacteria in the soil may be the reason why manure application increases soil microbial biomass and the number of observed microbial taxa, at least temporarily. OAs inhabit a wide variety of microorganisms; therefore, the transmission of exogenous species, particularly pathogenic microbes, poses a serious threat to soil and human health [157,158]. In contrast, native microbes are reportedly very resilient to change [159,160], whereas exogenous microbes are predicted to be less competitive towards their gut origin than the established soil bacterial populations. In a 389-day study into the resistance of vinasse microbiome to soil conditions and interactions with the native soil microbial community, Lourenço et al. [160] discovered that vinasse-derived bacteria vanished from soil conditions after 31 days.

4. Mechanisms Used by Microbes in Organically Amended Soil in Promoting Plant Health

The ability of microbes found in soils amended with crop residues, compost, and manure for plant growth promotion and fitness relies on direct and indirect mechanisms to boost plant performance in nutrient-limiting and stressed environments [161]. Often, the immense contributions of soil microbes to high productivity are based on biocontrol efficacy in the reduction and control of pathogens [114]. The diversification of OAs in enhancing soil health and microbial functions has received a boost in recent times, as OAs for soil treatment support microbial populations, plant growth, and disease suppressiveness [114].

The nutrients supplied by OAs facilitate microbial activities in the control of soil pathogens and boost plant immunity and soil health in crop management systems (Figure 2). Regardless of the valuable attributes of OAs, the inability to predict their behavior and their inconsistency can limit their full exploration, acceptability, and incorporation into large-scale agricultural production. Hence, understanding the various mechanisms used by soil microbes in organically amended soil provides more information on their antagonism and mutualism in developing new and effective biological products.

An understanding of mechanisms employed by microbes in organically amended soils to improve plant development in terms of rooting, growth, and improved yield is only studied to a limited extent; however, these microbes may exhibit multiple functional traits, which influence plant health, directly or indirectly. Harnessing microbial products from OA soils to improve plant establishment and soil rehabilitation under semi-arid conditions has been reported as an essential strategy for recovering degraded soils and improving the nutrient content of *Lavandula dentataas* [162]. In addition, the selection of copious soil microbes can be critical; however, their singularly or combined effects with organic residues can often explain their effective use to revegetate and rehabilitate nutrient-deficient soils under different ecological conditions [163].

The direct mechanisms involve bacterial modulation of phytohormones, siderophores, phosphate solubilization, and nitrogen fixation, whereas the indirect mechanisms include antibiotic production, hydrogen cyanide synthesis, the induction of systemic resistance, synthesis of fungal cell wall degrading enzymes, metabolite secretion, and exopolysaccharide production [164,165].
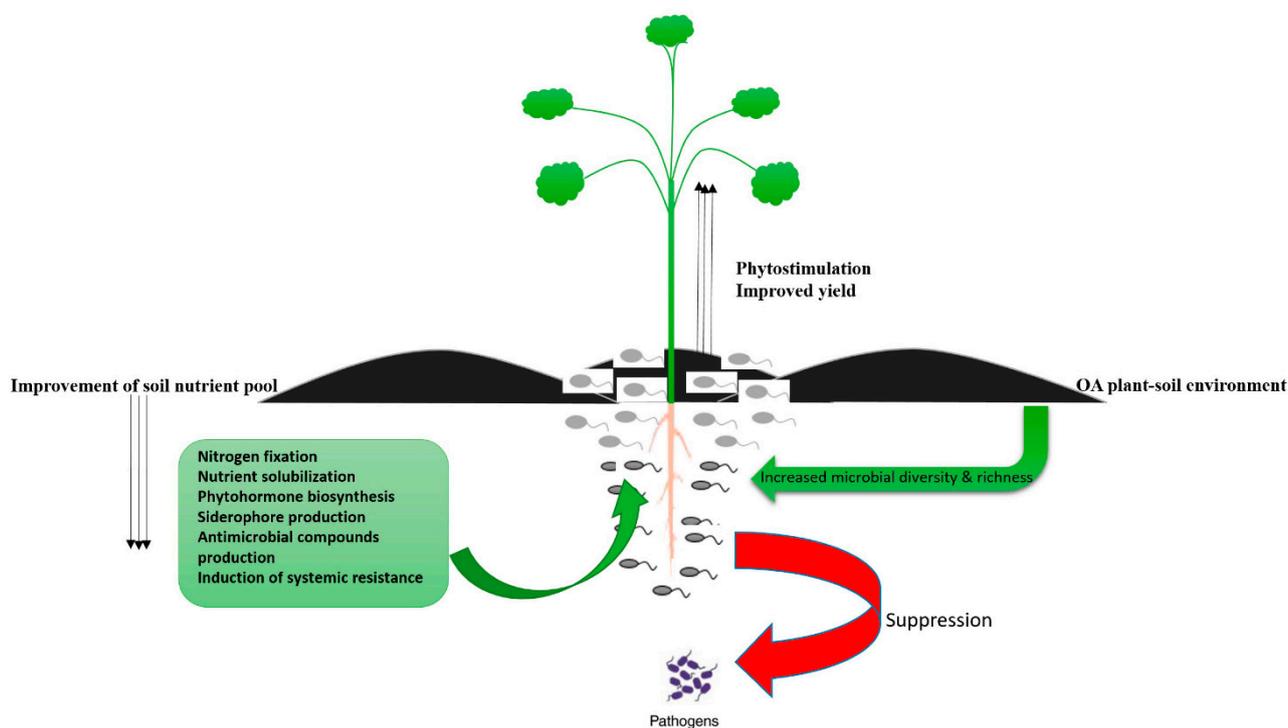
Figure 2. Mechanism of action of microorganisms in enhancing plant health.

4.1. Direct Mechanism

4.1.1. Synthesis of Plant Growth Hormones

The phytohormone production by soil microbes is directly linked to their innate attributes in promoting plant growth, health, and stability. Different microbes found in organically amended soil, for example, rhizobacteria, produce plant growth hormones, such as indole acetic acid (IAA), gibberellin, cytokinins, auxins, and ethylene [166]. IAA is a natural biomolecule produced by plants and its associated microbes [167]. The ability of rhizosphere microbes inhabiting root zones to produce IAA contributes to rooting development and overall plant performance, although excess IAA may be inhibitory to plant growth [168].

The primary functions of IAA in contributing to plant health include the control of vegetative growth, lateral and adventitious root development, cell division, differentiation, and elongation [169]. Furthermore, IAA mediates plant stimuli, the initiation of lateral root development, enhances the rate of seed germination, enhances photosynthetic pigmentation and metabolite secretion, controls plant responses to gravity, and builds plant resistance to soil stressors [170]. The increase in plant root number and development facilitates nutrient absorption by plants from the soil.

The production of IAA by the dominant bacterial genera *Pseudomonas* and *Bacillus* in amended soil has been documented [171]. In addition, cytokinins and gibberellins are important plant growth hormones synthesized by soil microbes, and their effects contribute to plant growth promotion. Similarly, ethylene functions to enhance plant growth in diverse ways including promoting leaf abscission and fruiting, inhibiting root elongation, initiating root development, and affecting the synthesis of other hormones [164,172]. Typically, high ethylene production negatively affects plant responses, whereas low ethylene synthesis may enhance crop performance.

4.1.2. Ability to Fix Atmospheric Nitrogen

Nitrogen (N) accounts for ~78% of the total atmospheric air. Due to the importance of N in crop productivity, its bioavailability through the process of biological nitrogen fixation (BNF) including the action of nitrogenase from N-fixing microorganisms is crucial

to crop production [173]. The symbiotic mechanisms involve a direct mutual relationship between rhizobia and plant roots and foster soil-microbe interactions [174]. Nodules in the roots of leguminous plants harbor rhizobacteria with plant benefits, including active BNF. There are diverse groups of symbiotic or non-symbiotic microbes that fix nitrogen in the soil. An investigation by Deng et al. [175] on the bacteria genera, *Mycobacterium*, *Caulobacter*, *Novosphingobium*, *Bacillus*, *Flavobacterium*, and *Pseudomonas* isolated from organic amended soils suggests that many species belonging to these genera are nitrogen fixers. Typical examples of the most dominant diazotroph in a biochar-amended soil include *Geobacter*, *Azospirillum*, *Dechloromonas*, *Azotobacter*, *Burkholderia*, *Sinobacterium*, and *Bradyrhizobium* [176]. The nitrogenase genes present in nitrogen fixers are central to their inability to supply nitrogen to plants for improved performance.

4.1.3. Ability to Solubilize Mineral Elements, Phosphorus, and Potassium

Potassium is the third most abundant macronutrient in soil and a key element in plant nutrition [177]. The lack of available potassium in the soil has often resulted in poor plant growth and root development and low crop yield, thus necessitating the need to sustain potassium levels in soils for better plant performance. Fortunately, the organic acid production tendencies of soil microbes enable them to solubilize complex forms of potassium into a simpler form for easy absorption by plants [178].

In recent years, scientists have successfully employed potassium-solubilizing microbes to increase crop yields [179]. The plant growth-promoting potassium-solubilizing bacterial genera, such as *Enterobacter*, associated with organically amended soil with a known activity optimum of 668 µL/mL, have been reported by Walpola and Hettiarachchi [180].

Phosphorus is a key molecule and is required for photosynthesis, respiration, signal transduction, energy transfer, and synthesis of macromolecules. About 98% of phosphate found in soil is insoluble or immobilized. However, soil microbes are actively involved in the biotransformation of immobilized phosphorus into soluble monobasic and dibasic forms, thus making it available for microbial and plant usage [181]. Nevertheless, organic P is made available by specific enzymes and inorganic P is made available by organic acids. The plant growth-promoting phosphate-solubilizing bacterial genera, such as *Bacillus*, associated with organically amended soil with known activity of 3.5–142 µL/mL, have been reported [182].

4.1.4. Ability to Produce Siderophores

Soil amendment with composts or organic wastes typically enhances microbial proliferation in the rhizosphere, contributing to root development for increased nutrient absorption and decreased inhibition by plant pathogens in part as a consequence of the production of iron-chelating siderophores [183]. Siderophores help in the electron transport chain in living cells [184]. Siderophore-like substances such as catecholate, phenolate, and hydroxymate produced by soil microbes can cause inhibition of the growth of plant pathogens [185]. In an iron-deficient soil, the presence of siderophore-producing bacteria can facilitate nitrogen fixation since iron and molybdenum serve as necessary cofactors for diazotrophs in the synthesis of the enzyme nitrogenase. The most effective metabolites produced by soil microbes in the control of certain plant pathogens include salicylic acid, pyochelin, and pyrrolnitrin [186]. Pyoverdine, identified as salicylic acid, and pyochelin produced by *P. flourescens* CHA0, and *P. aeruginosa* PA01, isolated from iron-deficient soils, have been recognized to have a similar function as siderophores, participating in bacterial iron metabolism and control of fungal pathogens. Examples of siderophore-producing bacteria from organically-fertilized soil include *Pantoea*, *Azospirillum*, *Enterobacter*, *Rhizobium*, and *Bukholderia* [187].

4.1.5. Lowering Plant Ethylene Levels

Ethylene plays an important role in plant growth promotion. The synthesis of ethylene by plants under environmental stress increased as a consequence of plants responses to

stress, which contributes to a decrease in biomass yield [188]. The regulation of ethylene in plants is linked to the abilities of microbes to synthesize the enzyme 1-aminocyclopropane-1-carboxylic (ACC) acid, an immediate precursor to ethylene production [189]. Furthermore, the conversion of methionine by some bacterial ethylene-forming enzymes yields hydrogen cyanide, ethylene, and carbon dioxide [190]. The expression of the enzyme ACC deaminase by microorganisms enables those microbes to degrade ACC into ammonia and α-ketobutyrate and thereby lower the level of ethylene in the plant. When ACC deaminase activity lowers ACC and ethylene levels in plants, the plant is significantly protected against a wide range of both abiotic and biotic stresses [188]. It has been postulated that the root formation in plants growing in stressful or normal environments can be mediated by ethylene produced by soil microbes [191].

Ethylene functions in overall root development in plants, senescence, ripening, stress signaling, and nodulation [192]. Exogenous application of ethylene has played a major role in the ripening of fruit, wilting of flowers, and senescence of leaves. Similarly, ethylene production during plant growth has been reported to trigger plant biological processes, such as xylem formation, flowering, induction of fruit ripening, and wilting of flowers [193]. Studies have demonstrated the effective use of microbes with ACC deaminase activity from organically amended soils are effective in the control of diverse phytopathogens [114]. Similarly, plant resistance to stress arising from drought, high salinity and temperature, polyaromatic hydrocarbons, radiation, light intensity, and heavy metals has been attributed to microbial ACC deaminase activity in soil [194]. Nevertheless, the expression of ACC deaminase in soil microbes could facilitate indole acetic acid activity and reduce ethylene levels and auxin signal transduction, thus enabling bacterial auxin to enhance plant growth [195]. Many bacterial genera from organically amended soil exhibiting ACC deaminase have been identified. These include *Alcaligenes*, *Bacillus*, *Ochrobacterium*, *Bradyrhizobium*, *Pseudomonas*, *Enterobacter*, *Achromobacter*, *Leclercia*, *Aneurinibacillus*, and *Paenibacillus* [164,196–198].

4.2. Indirect Mechanisms

4.2.1. Antibiosis

Primarily, the biocontrol activities of soil microorganisms are connected to their ability to produce antibiotics that inhibit plant pathogens [199]. Many soil microbes naturally produce these compounds. Diverse metabolic compounds from microbes found in organically amended soil with a high-spectrum of activity against plant pathogens have been studied [114]. Antibiotic resistance by some microbial strains is a major challenge of antibiotic use, thus reducing antibiotic potency against plant pathogens for adequate plant protection [200]. Nevertheless, microbial strains with the ability to synthesize multiple antibiotics can subvert antibiotic resistance in the control of plant pathogens in ensuring plant growth and health. In addition, hydrogen cyanide produced by some biocontrol strains acts synergistically with antibiotics to inhibit the proliferation of many fungal phytopathogens.

The biocontrol activity of the siderophores 2, 4-diacetylphloroglucinol (2, 4-DAPG,) and pyrrolnitrin (PRN) produced by *Pseudomonas* spp. and other rhizosphere microbes inhabiting organically amended soil enhance plant suppressive mechanisms against pathogenic microbes, such as *Gaeumanomyces graminis* var. Tritici, *Caenorhabditis elegansi*, and *Pratylenchus penetrans* [183,201]. Studies have also revealed the biocontrol effects of lipopeptides and polyketides produced by *Bacillus amyloliquefaciens* against soil pathogens [202]. The use of *B. amyloliquefaciens* isolated from bioorganic fertilized soil for control of *Fusarium* wilt in crops, such as cucumber, banana, and watermelon has been documented [203,204]. Other identifiable bacterial strains isolated from amended soil with disease suppression mechanisms are summarized in Table 2.

Table 2. Biocontrol mechanisms employed by some bacteria in organic amended soil.

Bacteria	Mechanisms	Effects	References
Acintobacter spp.	Possible production of antibiotics	Suppression of *Pythium* spp. causing damping-off of seedlings in cucumber	Yu et al. [205]
Aeromonas media	Possible production of antibiotics	Control of *Pythium ultimum* that causes damping-off disease in cress	Oberhaensli et al. [206]
Bacillus amyloliquefaciens JDF35	Nitrogen fixation, phosphate solubilization, and enzyme synthesis	Control of *Fusarium oxysporum* that causes *Fusarium* wilt in watermelon	Zhao, Wang, Liang, Huang, Chen, and Nie [203]
Bacillus amyloliquefaciens, B. licheniformis, B. subtilis	Enzyme synthesis, production of secondary metabolites, indole acetic acid, and 1-aminoclopropane-1-carboxylate (ACC) deaminase activity	Control of *Fusarium oxysporum* that causes *Fusarium* wilt in cucumber and *Verticillium dahliae* that cause *Verticillium* wilt in tomato	Tsolakidou et al. [207,208]
Burkholderia spp.	Possible production of secondary metabolites	Control of *Rosellinia necatrix* that cause white root rot in avocado	[204]
Chryseobacterium spp.	Synthesis of secondary metabolites, ACC deaminase activity, and indole acetic acid	Control of *Vericillium dahlia,* and *Fusarium oxysporum* that cause *Verticillium-Fusarium* wilt in tomato	Tsolakidou, Stringlis, Fanega-Sleziak, Papageorgiou, Tsalakou, and Pantelides [207]
Enterobacter spp.	Possible production of antibiotics	Control of *Pythium* spp., *Fusarium oxysporum,* and *Verticillium daliae* wilt in plants	Chin et al. [209]
Lechevlieria spp.	Production of antibiotics	Control of *Phytophtoria cinnamomi, Sclerotinia sclerotiorum, Agrobacterium tumefaciens, Pythium debaryanum, Thanatephorus cucumeri* that cause stem rot in tomato	Cuesta et al. [210]
Ochrobacterium spp.	Production of secondary metabolites, IAA, and ACC deaminase activity	*Verticillium dahlia* and *Fusarium oxysporum* control of wilt in tomato	Tsolakidou, Stringlis, Fanega-Sleziak, Papageorgiou, Tsalakou, and Pantelides [207]
Paenibacillus polymyxa	Enzyme synthesis, and ACC deaminase activity	Control of *Fusarium* wilt caused by *Fusarium oxysporum* in cucumber	Du, Shi, Yuan, Sun, Shu, and Guo [208]
Pseudomonas spp.	-	Control of *Rhizoctonia solani, Sclerotinia minor* and *Rosellinia necatrix* white root rot in cress and avocado	Scotti et al. [211]
Stenotrophomonas maltophilia	Secondary metabolites production, IAA, and ACC deaminase activities	Control of *Verticillium dahlia* and *Fusarium oxysporum* that cause wilting in tomato	Tsolakidou, Stringlis, Fanega-Sleziak, Papageorgiou, Tsalakou, and Pantelides [207]
Streptomyces lusitarus, S. aureoverticillatus, S. griseoruber, S. albogriseolus, S. variegatus	ACC deaminase activity, and antibiotic production	Suppresses activity of *Phytophtoria cinnamomi, Sclerotinia sclerotiorum, Agrobacterium tumefaciens, Pythium debaryanum,* and *Thanatephorus cucumeris* in plants	[204], Cuesta, García-de-la-Fuente, Abad, and Fornes [210]

4.2.2. Enzyme Production

Some enzymes produced by soil microorganisms' function in the biotransformation of recalcitrant polymers in soil into organic matter supports plant growth. Some of these enzymes degrade eukaryotic cell walls, and the cell components released can inhibit their pathogenicity [212]. These enzymes include cellulases, chitinases, hemicellulases, amylases, proteases, pectinases, and lipases. Enzyme production by plant and soil microbes helps boost plant immunity to withstand environmental stresses, hyperparasitic activity, and attack pathogens by secreting cell wall hydrolases.

The microbial composition in organically amended soils and their enzyme activities, precisely, can reflect the conditions of the soil. Soil microbe-producing extracellular enzymes can stand as an indicator in the biodegradation and biotransformation of organic matter in the soil [213,214]. Notable enzymes, such as β-glucosidase, cellobiohydrolase, N-acetylglucosaminidase, phosphatases, and xylosidase, screened from agriculturally relevant microbes from organic amended soils compared to their activities in soil fertilization with a large reserve of safety for the soil environment has been reported [215]. The enzymes catalyzed the biogeochemical transformations of C, N, and P in soil and are frequently used to measure soil microbial activity and substrate mineralization [215]. Dehydrogenase was used as a biomarker of soil quality and was found to be higher in organically managed soil due to the presence of biodegradable and easily mineralizable organic substrates [216]. Similarly, β-glucosidase and acid phosphatase were found to be higher in organically amended soil. The high β-glucosidase activity suggested an enrichment in recent cellulolytic organic materials, which serves as a substrate for these enzymes [216]. Since fungi are the primary producers of the enzyme N-acetyl-glucosaminidase, the tendency for its activity to rise in response to crop residue amendment may reflect an expansion or activation of the fungal biomass, which is influenced by the type of the organic matter added, such as straw [217]. Saprotrophic fungi break down straw and other materials high in lignin and cellulose [217].

4.2.3. Induced Systemic Resistance (ISR)

Induced systemic resistance is an indirect mechanism employed by rhizosphere microbes to stimulate a plant's defense against pathogens. In addition, plant defensive mechanisms in response to environmental stressors (systemic acquired resistance) can stimulate a plant's innate potential in maintaining plant physiology against biotic stress [218]. Diseases caused by microorganisms and those caused by insect pests have been reported to be easily controlled by certain metabolic compounds, such as 3-hydroxy-2-butanone, which triggers the appropriate plant response [219].

Induction responses by ethylene production are achieved by dependent pathways, whereas salicylate and jasmonate secretion in plants through independent pathways can help stimulate plant defense against plant pathogens [166]. The ability of soil microbes to secrete certain metabolites, such as siderophores, homoserine, acetoin, and lactones instigates the induction of systemic resistance in plants. Some examples of soil microbes that induce systemic resistance to plant pathogens include *Pseudomonas* and *Bacillus*, and their activities are known to be affected by OAs. *Bacillus* spp. can induce resistance in plants because of their genetic and phenotypic properties, thus making this genus a suitable candidate for biological control agents [220], although the link between microbes in the organically amended soil and their resistance to most plant pathogens is not well documented.

4.2.4. Exopolysaccharide Production

Exopolysaccharide (EPS) are carbohydrate polymers found on the surfaces of many microorganisms, especially bacteria [221]. Some groups of bacteria produce extracellular, intracellular, and structural polysaccharides with diverse functions in the production of signal molecules that instigate plant-microbe interactions and protect plants from drought stress [222]. EPS serves as an important pre-requisite in the establishment of microbial biomass in the rhizosphere. Functionally, EPS-producers help stabilize absorbable phosphorus in soils, making nutrients available for plant growth, at the same time EPS protects

plants from attack by pathogens. EPS-producing microbes protect plants against a range of stresses, including drought, desiccation, pathogen invasion, and salinity [223].

5. Discussion

Considering the environmental implications, such as soil degradation and accumulation of pollutants due to the effect of chemical fertilizer application, it is imperative to manage agricultural soils for sustainable productivity by promoting beneficial microorganisms in the rhizosphere and provide a basis for reducing the application of chemical fertilizers. Healthy soils are essential for sustainable crop production. The soils in which crops are cultivated have a significant impact on both the quantity and nutritional value of the crops. Because they typically lack access to industrial inputs, subsistence farmers heavily rely on soil biota and the ecosystem services they provide to sustain productivity. Soil biota is important, much like it is in minimal-input agriculture systems. One of the important functions played by soil organisms in the process of nutrient cycling is the transformation of nutrients into forms that are more or less available to plants.

In most of the literature reviewed, an increase in microbial diversity and richness in the rhizosphere compared to the control was reported. This is due to the greater availability of organic C substrates and nutrients for mineralization [51,52]. In this case, the rhizosphere acts as a crucial interface for interactions, signaling, and resource and energy exchange between plants and soil microorganisms [224]. This finding highlights how these organisms are typically suited to carbon-rich environments (common in the rhizosphere) for high metabolic activity, quick growth, and propagation. These findings suggest that OAs broaden niches by supplying more fresh organic materials, which reduces competition and creates favorable co-occurrence patterns with keystone copiotrophic taxa [120]. The rhizosphere also regulates the activities of soil C and N dynamics. Cellulolysis, xylanolysis, ligninolysis, ureolysis, and chitinolysis were among the organic compound decomposition and transformation processes that were often more intensive in the rhizosphere, suggesting the greater number and activity of organisms that break down these materials [38].

Similarly, organic modifications affected the composition of bacterial communities by increasing the relative abundance of most Gram-negative bacteria. This is because the majority of these Gram-negative bacteria are copiotrophs, which are often more prevalent in nutrient-rich environments [120,127]. The abundances of these Gram-negative bacteria are more likely to rise when new organic materials are added. When compared to Gram-positive bacteria, gram-negative bacteria often exhibit quick growth rates but poor soil organic carbon usage efficiency [225]. As a result, OAs boost the rates of soil organic carbon mineralization with a greater abundance of Gram-negative bacteria. However, OAs dramatically enhance biomass and fungal abundance while a reduction in fungal diversity was observed and hindered the detection of numerous fungi taxa from the rhizosphere soil. This is due to their large bodies and the development of hyphal networks across aggregations such as backbones [120].

These trends are varied, as application of OAs could result in increased, decreased, or unaffected diversity, thereby making generalizing the effect on microbial diversity difficult in some instances. Similarly, depending on the environmental conditions, these effects can be exceedingly varied, and in some cases, the application may not bring about the desired effects. The performance of OAs and the interpretation of the results of tests using them may be influenced by a variety of circumstances, such as tropical and temperate regions and prevailing environmental conditions (temperature, soil water content, etc.). This showed that the effect of OAs on microbial diversity in the rhizosphere is not fully understood but evidence suggests that the incorporation of OAs favored copiotrophic taxa [127]. A wider variety of possible substrates for microbial growth and respiration is offered by the addition of OAs. For instance, oyster shells used as OA contains glycosaminoglycan and aspartic proteinases, which encourage microbial growth [226,227]. Thus, a suitable organic substrate is needed to stimulate the microbial activities in the rhizosphere to enhance plant

growth. Similarly, the efficacy of OAs depends significantly on the type and amount of nutrients in the amendment as well as the duration and method of storage.

Plants are constantly challenged by microbial communities, including commensals, pathogens, and symbionts, especially in the rhizosphere. Because their ability to reproduce and function depends on the availability of organic material from the plant host, plant pathogens are more abundant in the rhizosphere [38]. Despite the fact that the rhizosphere is a dynamic environment and the microbiome varies quickly over time and location, mounting data suggests that plants can manipulate the rhizosphere microbiome to their advantage and effectively make use of the microbial functional repertoire [228].

The suppressive effect is likely caused by an increase in pathogen-antagonistic organisms, since the organic fertilizers may act as an alternative C source for the antagonists. In comparison to conventional farming, Banerjee et al. [229] found that organic farming had stronger network connectivity and keystone microbial species abundance, which may be related to increased soil suppressiveness. Because of this, phytopathogen antagonistic activity is dependent on specific ecological conditions that may or may not occur. Additionally, the antagonistic impact can occur at a latency that can only be seen by collecting numerous samples over time rather than simultaneously [66]. The complex rhizosphere community interacts with pathogens and determines the course of infection in the rhizosphere, which serves as both the site where soilborne pathogens attack plants and the battleground where they do so [230]. The quantity and quality of organic carbon, as well as the results of microbial interactions in the rhizosphere, all influence the number and diversity of harmful and helpful organisms. According to reports, soil microbial diversity offers a defense against soilborne pathogens and prevents the establishment of soil pathogens. The decline in pathogenic organisms demonstrated that the addition of OAs has the ability to improve soil health, reduce crop morbidity, and enable soil function [120]. Overall, the improvement in the diversity and richness of soil bacteria following the application of soil amendments may help to reduce pathogens. The suppressive power of OAs include mechanisms such as release of toxic compounds during organic matter decomposition, increased antagonistic microbial activity, increased pathogen competition for resources, and induction of systemic resistance in the host plants [98]. The activities of suppressive biocontrol organisms are reported to be responsible for disease suppression and these include the production of siderophore, pyrrolnitrin, lipopetides, polyketides, volatile compounds (methyl 2-methylpentanoate, murolool, sesquiterpenes 2-methylfuran, 2-furaldehyde), etc.

To examine the microbial (mostly bacterial) community composition of soils suppressive or favorable for particular plant diseases, a number of "omics"-based studies need to be combined to unravel the mechanisms of action. Poudel et al. [231] underlined the significance of creating microbial networks to ascertain microbial community structure and assemblage for disease management. To focus in on particular microbial consortia, network analysis of differences in relative abundance between bacterial and/or fungal communities in suppressive and conducive soils might be quite helpful. However, in order to identify the precise microbiological characteristics involved in suppressiveness and to differentiate between cause and effect, these descriptive studies must be used in conjunction with other methods [93], such as metatranscriptomics, metabolomics, and metaproteome. The combination of these approaches will help to understand the complexity of the unique microorganisms and mechanisms driving disease suppressiveness.

There are uncertainties concerning the effectiveness and possible negative effects of OAs that prevent its widespread use. For instance, the effectiveness of OAs modification varies and, in other circumstances, can actually increase disease severity [232]. These effects are linked to either increase inoculum of pathogens or the release of toxic compounds that harm biocontrol organisms or plant roots and make them susceptible to pathogen attack [98]. The varied outcomes with both suppressive (disease reduction) and conducive (disease growth) has raised some doubts about their use. A reliable way to forecast how various OM amendments may affect soilborne pathogens is also not yet available, despite substantial study in this area.

However, depending on the environmental conditions, these effects can be exceedingly varied, and in some cases, the amendment application may not bring about the desired effects. The performance of OAs and the interpretation of the results of tests using them may be influenced by a variety of circumstances, such as application rates, controlled conditions versus field applications, and type and nature of OAs, and performance of different crops based on the parts of the plant that are measured.

6. Conclusions and Future Perspective

The changes in land uses combined with inappropriate land management practices have intensified soil degradation with their associated effects on agroecosystems. To restore soil health and functioning and increase crop production, best soil management practices that include the use of OAs can positively influence the composition and structure of the soil microbial community. There are many different types of OAs and sources from which to obtain OAs. Numerous parameters, including their composition, stability, maturity, frequency and rate of use, soil type, cropping style, climatic conditions, etc., can have a favorable or negative impact on the functioning of the soil ecosystem. Therefore, in order to determine the potentialities and limitations of any particular OA for soil and crop health, a thorough characterization of both the OA and the agroecosystem itself must be carried out prior to its application. Anaerobic digestion and composting are recognized as effective methods for reducing some of the possible negative effects that OAs may have on the soil ecosystem and the environment as a whole. Some emerging contaminants, such as antibiotics resistance genes, are raising a lot of concern since they constitute a severe risk to the environment and human health.

Organic amendments affect soil organisms involved in cycling of nutrients and the interactions between plants and organisms in the rhizosphere. Various forms of OAs applied to soil can modify the conditions, facilitating microbial-mediated processes to improve soil health, nutrient use efficiency, and plant growth. However, the role of microorganisms from organically amended soils in plant growth and health is less documented. Nevertheless, evidence abounds of the plant growth-promoting potential of these organisms and underpins their role in sustainable crop production. Future studies should continue to explore the interactions between different OAs and soil microbial communities, simultaneously targeting their functions to advance an understanding of appropriate soil management practices that enhance plant health and growth.

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