Review

Enhancing Soil Quality and Plant Health Through Suppressive Organic Amendments

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Abstract: The practice of adding organic amendments to crop soils is undergoing resurgence as an efficient way to restore soil organic matter content and to improve soil quality. The quantity and quality of the organic matter inputs affect soil physicochemical properties and soil microbiota, influencing different parameters such as microbial biomass and diversity, community structure and microbial activities or functions. The influence of organic amendments on soil quality has also effects on crop production and plant health. The enhancement of soil suppressiveness using organic amendments has been widely described, especially for soil-borne diseases. However, there is great variability in the effectiveness of suppression depending on the nature of the amendment, the crop, the pathogen, and the environmental conditions. Although the effects of organic amendments on soil properties have been widely studied, relationships between these properties and soil suppressiveness are not still well understood. Changes in soil physicochemical parameters may modulate the efficacy of suppression. However, the parameters more frequently associated to disease suppression appear to be related to soil microbiota, such as microbial biomass and activity, the abundance of specific microbial groups and some hydrolytic activities. This review focuses on the effect of organic amendments on soil microbial populations, diversity and activities; their ability to enhance plant health through disease suppression; and which of the parameters affected by the organic amendments are potentially involved in soil suppressiveness.

1. Organic Matter and Soil Quality

Soil organic matter, one of the main indicators of soil quality, is fundamental to the long-term sustainability of agroecosystems and plays a critical role in global biochemical cycles [1]. In natural soils, a range of drivers of global change is affecting the balance between organic matter inputs and outputs. In agricultural soils, land management is an additional key factor affecting this balance. Several crop management practices could help in the maintenance of soil quality, for example, crop rotation, low tillage, cover crops and external organic inputs. Among them, the direct addition of organic amendments to crop soils can improve soil quality by affecting many parameters, such as soil aeration, structure, drainage, moisture, holding capacity, nutrient availability and microbial ecology [2,3].

Organic amendments, such as animal manures and composts, were commonly used in the past for agricultural production due to their value as fertilizers and for their ability to improve plant health. The widespread availability of chemical fertilizers and pesticides led to the replacement of those organic materials by these highly effective and inexpensive synthetic agrochemicals [4]. The small amount of organic matter input to agroecosystems during the past 50 years has led to a decline in soil structure and health, which has been associated to an increase in plant diseases and other pest problems [2]. At present, however, there is an increasing interest, intensified by environmental concern, in the replacement of synthetic agrochemicals with organic amendments, which are experiencing a resurgence in popularity as efficient and environmentally benign alternatives to chemical fertilizers and pesticides [4]. The effect of the organic amendments on soil physical, chemical and biological parameters has been widely studied. The improvement of soil quality through organic amendments has a proved effect on crop production and plant health, and some of these effects have been related to the enhancement of soil suppressiveness against soil-borne pathogens [2]. This soil suppressiveness has been reliably related to soil microorganisms and its activities and for that reason, the effects of the organic amendments on soil microbiota is a key issue for understanding the role of this old management practice on disease suppression. This review focuses on the specific effect of organic amendments on soil microbial populations, diversity and activities; their ability to enhance plant health through disease suppression; and which of the parameters affected by the organic amendments are potentially involved in soil suppressiveness.

2. Organic Soil Amendments and Their Effect on Soil Quality

Soil quality is defined as the capacity of the soil to function within ecosystem boundaries to sustain biological productivity, maintain environmental quality, and promote plant and animal health [5]. There is a broad agreement in the literature that soil quality is measured by a combination of physical, chemical and biological soil characteristics (see Figure 1). The exact combination of the parameters best used to describe soil quality varies. Soil health is a newer less defined term and does generally refer to the expansion of the biological aspect of soil quality. The term "soil health" is preferred by

some authors because it portrays soil as a living, dynamic system whose functions are mediated by a diversity of living organisms that require management and conservation [3]. However, these terms are often used interchangeably in practice and they will be used synonymously throughout this paper. Soil quality cannot be measured directly, but soil properties that are sensitive to changes in management can be used as indicators. Indicators of soil quality are commonly classified in physical, chemical and biological parameters [5]. Depending on the soil management practices, the quantity and quality of the organic matter input differ. These inputs have a strong effect not only on the physicochemical properties of the soil but also on its biological components, affecting the quantity, diversity and functions of soil microbiota. In this review, we want to focus on the biological indicators of soil quality, analyzing how the addition of organic amendments could affect soil health through their effects on soil microbiota. These effects could be related to microbial biomass, microbial diversity, community structure and microbial activities [6–9].

Figure 1. Parameters affecting soil quality and some of the methodologies for their assessment.
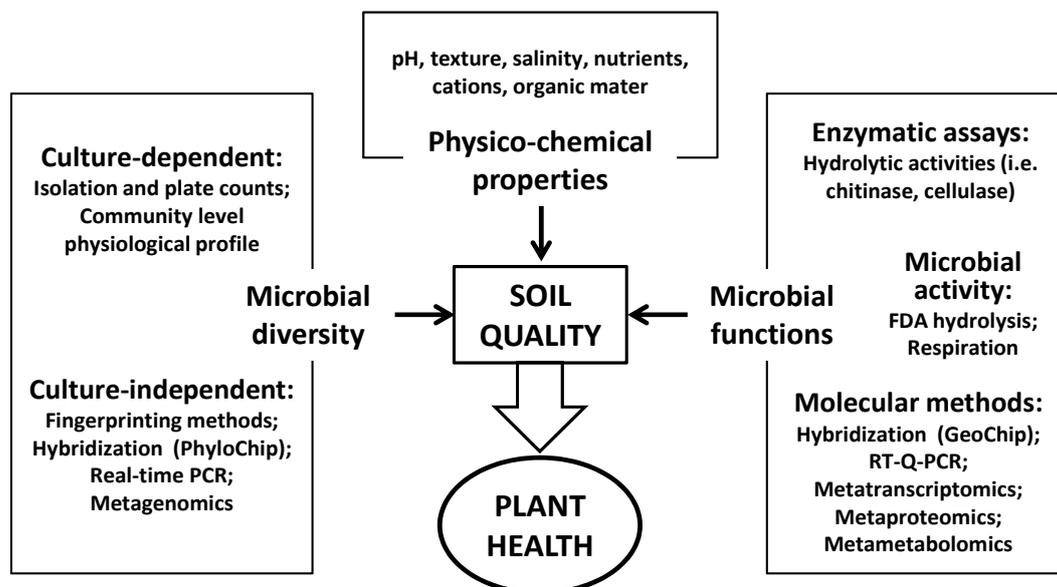
2.1. Microbial Populations and Community Composition

The enhancement of microbial biomass is one of the aims of some cultural practices such as the addition of organic amendments [10]. In fact, the addition of different types of compost to crop soils has been shown to be related to an increase in microbial biomass in comparison with unamended or equally inorganic fertilized soils [7,11,12]. Many authors have reported the enhancement of specific microbial groups, depending on the type of organic matter added as amendment. The enhancement of culturable heterotrophic bacteria has been shown to be affected by the addition of animal and vegetal commercial compost, composted almond shells and composted yard waste [6–8]. Several studies have shown enhancement in specific microbial groups, such as fluorescent pseudomonads [11,13] and endospore-forming bacteria [7,14] by amendments from both vegetal and animal origin.

Organic amendments influence not only on the abundance of soil microbial populations but also on soil bacterial diversity, as has been shown by many studies. For example, Yang *et al.* [15] and Bonilla

et al. [7] used numerical diversity indices (*i.e.*, Shannon-Weaver index) based on culture-independent fingerprinting methods to compare microbial diversity of amended and unamended soils. These studies showed that the amendment with manures, yard waste or compost enhances soil bacterial diversity, although other authors have not found any effect on soil microbial diversity when studying similar amendments by using analogous methodologies [11,16]. However, microbial diversity is a highly complex parameter and its measurement by diversity indices is usually less informative than qualitative community structure analysis. In fact, even when microbial diversity was unaffected, organic amendments have shown a strong influence on the soil microbial community composition. Pérez-Piqueres *et al.* [8] described a clear influence of different types of compost on bacterial and fungal communities composition in soils from different locations by using terminal restriction length polymorphism (T-RFLP). Many other authors have shown the influence of a wide variety of organic amendments on bacterial and fungal communities composition using whole community analysis methodologies based on the direct extraction of lipids (PLFA) and nucleic acids (T-RFLP, ARISA, ARDRA, DGGE) from the soil [7,11,12,17]. These and other methodologies used for the molecular assessment of soil microbial communities have been widely described and have been previously reviewed (see Figure 1) [18,19].

2.2. Microbial Activity and Soil Functioning

Many efforts have been made to characterize the genetic diversity present in soils. However, microbial diversity itself does not necessarily affect ecosystem functioning. For example, Wertz *et al.* [20] caused an experimental depletion of microbial diversity by dilution. After incubation, the structure, cell abundance and activity of denitrifying and nitrite-oxidizing communities were characterized. Increasing dilution led to a progressive decrease in community diversity as assessed by the number of DGGE bands, while community functioning was not impaired when cell abundance recovered after incubation. Actually, it is widely accepted that species identity and community composition, rather than richness, matters for specific microbial processes [20,21]. Furthermore, some studies have reported that phylogenetic and functional changes in the soil are not reliably correlated [22]. In fact, there is evidence of a direct effect of organic amendments on soil functions without any changes in microbial community structure [16]. Many characteristics of soil microbial communities, such as high functional redundancy and physiological versatility, could be involved in the independence from biodiversity of many ecosystem functions [21]. Phylogenetic diversity alone is therefore not sufficient for understanding how microbial communities work, and the functional diversity of the ecosystems must be considered.

Soil microbial activity is the overall quantification of soil functioning, including carbon and nitrogen biogeochemical cycles, organic matter decomposition. This microbial activity could be measured by fluorescein diacetate (FDA) hydrolysis, soil respiration or other specific activities (Figure 1). Many studies have shown that organic soil amendments increase total microbial activity, measured as soil respiration [6,8,11]. Other studies have analyzed the effect of soil amendments on particular hydrolytic activities involved in C, P and N biogeochemical cycles such as dehydrogenases, phosphatases, proteases, urease or β-glucosidase. In general, the response of these enzymes is strongly affected by the level of soil organic matter. For that reason, they usually respond positively to organic amendments in degraded or semiarid soils and they have been considered suitable indicators of soil

quality in this type of study [23–25]. However, the response of these enzymes in soils with naturally high organic matter is more complicated and depends largely on native physicochemical soil properties, the type of amendment and the application rate [9,26]. On the other hand, one enzyme activity alone cannot provide complete information on the nutrient status of a soil. Nannipieri *et al.* [27] defended that the simultaneous measurement and the multivariate analysis of several enzyme activities may describe better soil microbial activity. This approach has been widely used; for example by Tiquia *et al.* [28] who obtained an overall picture of the enzymatic activity in different types of compost, revealing differences in composts and compost maturity.

3. Organic Amendments and Their Effect on Plant Health

The beneficial effects of organic materials on different aspects of plant health have been widely reviewed by several authors [2,29,30]. Different works have shown that organic amendments to crop soils can increase plant growth and crop yield both in herbaceous and woody plants such as maize, wheat and avocado [31–33]. However, most of the studies have been focused in the ability of these organic materials to enhance natural soil suppressiveness. Suppressive soil has been described as a soil in which "the pathogen does not establish or persist, establishes but causes little or no damage, or establishes and causes disease for a while but thereafter the disease is less important" [34].

There is sufficient data to indicate that organic amendments can reduce the incidence of diseases caused by a wide range of plant pathogens including bacteria, fungi, and nematode species [2,35]. Although some authors have demonstrated the enhancement of soil suppressiveness by both composted and uncomposted amendments [14], several works have stated that composted materials are more suppressive to root rots than uncomposted ones [35]. The use of compost for the suppression of such diseases has been widely reported and reviewed [29,30]. For example, Yogev *et al.* [36] showed that composts based on plant-waste residues suppress diseases caused by different *formae speciales* of *Fusarium oxysporum*. Vegetal composts were also able to delay or decrease the symptoms of avocado root rots caused by *Phytophthora cinnamomi* [37] and *Rosellinia necatrix* [38]. In fact, compost amendments have a consistently demonstrated suppressive effect on several soil-borne diseases, such as damping-off and root rots (*Pythium ultimum*, *Rhizoctonia solani*, *Rosellinia necatrix, Phytophthora* spp.) and wilts (*Fusarium oxysporum* and *Verticillium dahliae*) in a wide range of crops [14,36,38–43] (Table 1). The use of organic amendments or mulches has been successfully incorporated into the integrated management of certain diseases, such as the avocado root rot caused by *P. cinnamomi*, in combination with genetic host resistance, fungicide applications or physical inactivation [44]. However, the suppressive capacity of different types of compost differs dramatically depending on the type of organic matter, plant host and pathogen species that are involved; and several authors have reported negative effects, such as phytotoxicity or an increased incidence of the disease, related to the use of organic amendments [45,46]. The identification of the mode of action of each amendment could be crucial for the incorporation of effective organic amendments to the integrated management of soil-borne diseases [2].

Table 1. Examples of proven plant disease suppression following application of organic amendments.

Pathogen	Crop	Organic amendment	Reference
Fusarium spp.	Several hosts	Vegetal composts	Yogev *et al.* 2006 [36]
Phytophthora cinnamomi	White lupin	Fresh and composted chicken manure	Aryantha *et al.* 2000 [14]
	Avocado	Sludge vermicompost	Bender *et al.* 1992 [43]
		Chipped eucalyptus trimmings	Downer *et al.* 2001 [37]
Pythium ultimum	Garden cress	Animal and vegetal composts	Pane *et al.* 2011 [41]
		Bark compost	Erhart *et al.* 1999 [40]
Rhizoctonia solani	Garden cress	Viticulture waste compost Composted cow manure	Pane *et al.* 2011 [41]
	Basil	Fresh farmyard manure	Tamm *et al.* 2010 [42]
Rosellinia necatrix	Avocado	Vegetal composts	Bonilla *et al.* 2009 [38]
Sclerotinia minor	Garden cress	Composted municipal bio-waste Composted cow manure	Pane *et al.* 2011 [41]
Sclerotium rolfsii	Tomato	Vegetal compost Poultry manure Green manure (legumes)	Bulluck and Ristaino 2002 [13]
Verticillium dahliae	Eggplant	Horse manure Municipal green waste Wood shavings	Malandraki *et al.* 2008 [39]

3.1. The Basis of Soil Suppressiveness

It has been demonstrated that the quantity and quality of the organic matter inputs affect both the physicochemical properties of the soil and the biotic factors associated to the soil microbiota, such as microbial biomass, diversity, community structure and biochemical activities [6–9]. Particular abiotic factors, such as changes in pH or nitrogen content, have been related to the control of some plant diseases [47,48]. However, the sterilization of the soil or of the amendment usually leads to a loss of suppressiveness, suggesting a direct effect of the microbiota on disease suppression [36,39]. In fact, the influence of organic mulches or amendments on the microbiota of the soil and the rhizosphere has been consistently related to the suppressiveness of the soil for several plant diseases [19,49,50]. The effect of organic amendments on soil suppressiveness has commonly been related to a *general suppression* mechanism. The input of organic matter may lead to an increase in total microbial biomass and activity in soil, causing the inhibition of the pathogen by competition for resources or through other direct forms of antagonism. No specific microorganism is responsible for general suppression, but all the microbiota cooperate for the generation of a hostile environment for disease development [35,50]. This general mechanism plays an important role in some cases of disease suppression, but because it is based on nonspecific mechanisms, it is expected to be effective against any pathogen. However, the suppression of multiple diseases by organic amendment has only been described in a few studies, and the suppressive efficiency varies greatly, depending on the pathogen. This finding suggests that the enhancement of disease suppression with amendments or compost is often disease-specific [51]. The most suitable hypothesis is that in most cases suppressive soils owe their activity to a combination of a general and a *specific suppression*. The specific suppression is superimposed over the background of general suppression and is due, at least partially, to the effects of

individual or selected groups of microorganisms that affect pathogen growth or infection through a particular biological control mechanism, such as competition, parasitism, microbial antagonism, induced plant resistance, or a combination of these mechanisms [35,50]. To determine which management practices or amendments have suppressive capability, it is important to identify the microbial populations and associated processes that could account for disease suppression [49].

3.2. Looking for Indicators of Soil Suppressiveness

Many studies have tried to relate changes in both the abiotic and biotic factors of the soil to the inhibition of different diseases, searching the basis of disease suppression [13,14,51–55]. This information has been used in several attempts in the identification of key factors involved in soil suppressiveness, looking for predictor parameters of the suppressive potential of the soils or the organic amendments [10,19,51]. However, this is a very complex issue since it is not possible to measure the suppressive potential by numerical values. Furthermore, the search for a parameter universally related to the suppression of every pathogen in every condition has been unsuccessful. This is the main reason why most research studies deal with well-known indicators of disease suppression.

3.2.1. Physicochemical Soil Properties

Several physicochemical parameters of the soil, such as soil pH, nitrogen, carbon and organic carbon content, as well as several cations and oligoelements, have been often related to disease suppression. Different studies have tried to unravel the role of the physicochemical soil properties in each particular experimental system. As an example, Tenuta and Lazarovits [48] showed that the accumulation of ammonia and nitrous acid released from nitrogenous amendments, such as meat and bone meal, suppresses the soil-borne pathogen *Verticillium dahliae*. In the study performed by Heyman *et al.* [56] the concentration of calcium in the soil was negatively correlated to the incidence of *Aphanomyce*s root rot of pea. Greenhouse bioassays with different Ca compounds showed that disease severity was directly related to water-soluble Ca in the soil, whereas it was not consistently affected by soil sterilization. Bonanomi *et al.* [51] showed that amendment's pH was in general not statistically correlated to disease suppression except for *Fusarium* species. In fact, some studies as that performed by Borrero *et al.* [54], established the beneficial effects of high soil pH on the reduction of *Fusarium* wilt of tomato. Nevertheless, even in this work, the sterilization of the amendments increased disease incidence, supporting the biological basis of disease suppression. However, there is no an universal rule linking physicochemical parameters and disease suppression and both positive and negative correlations with disease incidence, as well as many cases of no-correlation, have been reported [10]. In general, the physicochemical variables have been statistically demonstrated to be less informative predictors of the suppressive potential of organic amendments than the enzymatic and microbiological variables [51].The most feasible hypothesis is that disease suppression usually has a biological explanation and physicochemical parameters could affect growth and activities of soil microbiota, including pathogens, and therefore it could modulate disease suppression efficacy.

3.2.2. Microbial Biomass, Diversity and Community Structure

Disease suppressiveness has usually been related to a global increase in soil microbial biomass. Theoretically, a large amount of biomass creates a competitive environment deleterious to pathogens [10]. In fact, an increase in microbial biomass has been directly related to soil suppressiveness, both by direct measurement [55] and by culture-based methods [13,57]. However, this relationship is not consistent, and other studies have shown a lack of correlation between these two parameters [58]. Microbial diversity has long been considered a key factor in disease suppressiveness. Accordingly, several works have reported direct correlations between quantitative diversity indices and disease suppression [52,59]. However, other works have shown weak and highly variable correlations or have failed to identify a correlation [11,60]. Microbial diversity is a complex issue and its measurement by diversity indices is usually less informative than qualitative community structure analysis. Most data suggests that community composition is more important than richness for specific microbial processes [21]. In fact, changes in microbial community composition have been widely related to suppressive organic amendments and farming practices, regardless of the quantitative differences in diversity indices [8,53]. Indeed, the structure of soil microbial communities is of primary interest when studying soil suppressiveness.

Soil suppressiveness is commonly related to the presence of or the increase in specific microbial populations. Some of the microbial groups most frequently connected to disease suppression are total culturable bacteria [8,53], pseudomonads or fluorescent pseudomonads [13,52,57], *Trichoderma* spp. [13] and endospore-forming bacteria [14]; Bonanomi *et al.* [51] have shown a high percentage of positive correlations between abundance of these groups and soil suppressiveness. However, many studies only demonstrate correlations and subsequently, they suggest the potential implication of these microbial groups in disease suppression. Nevertheless, correlation does not imply a cause-effect relationship, so it would be necessary for a deeper analysis to reliably connect a specific microorganism or population to disease suppression. Initial studies in this field were based on the isolation and characterization of numerous culturable soil microorganisms. The isolates, including bacteria, actinomycetes and fungi, were usually screened, for example, by their ability to suppress the pathogen *in vitro* or to reduce disease symptoms when they were inoculated in a conductive soil [61,62]. The "microbe hunters" have identified and isolated many microorganisms responsible or contributing to the suppression of plant diseases. Many of these effective antagonists of soil-borne pathogens are, in fact, members of the microbial groups mentioned above. One of the best examples is the suppression of take-all disease of wheat by strains of fluorescent *Pseudomonas* spp., demonstrated by Weller *et al.* [63]. The *Pseudomonas* spp. strains were originally isolated in Washington State from wheat rhizosphere in a soil naturally suppressive to take-all and then selected by *in vitro* antibiosis to *Gaeumannomyces graminis* var. *tritici*, the causal agent of this disease. These bacteria applied to wheat seeds suppressed take-all disease in both greenhouse and field experiments [63]. On the other hand, in Western Australia, wheat take-all suppression has been attributed to *Trichoderma* spp., which comprise a major proportion of the total microbial community only in disease-suppressive soils [64]. *Trichoderma koningii*, the most frequently isolated species, has been shown to protect wheat against take-all disease in field trials in Australia, China, and the United States. However, within a region, the level of protection provided by *T. koningii* can dramatically vary between field sites depending on the

physicochemical soil properties [65]. The combination of both biocontrol microorganisms, *T. koningii* and certain *Pseudomonas* strains, has shown to provide greater suppressive effect than *T. koningii* applied alone and much better disease control than bacterial treatments alone [66]. The identification of a specific microorganism reliably involved in disease suppression does not mean that this microorganism is solely responsible of disease control. The suppressive effect could be more likely related to a combination of parameters, both biotic and abiotic. Actually, the general suppression is not even related to a specific group of microorganisms, and many factors and populations cooperate for the inhibition of the pathogen or the development of the disease. Different organic amendments stimulate a different spectrum of microbial groups, which seems to be closely related to their effectiveness against different pathogens. This effect on soil microbial communities even varies over time, together with amendment decomposition or environmental change, so the suppressive ability of the amendment may also vary with time [51,67]. In addition, the phenomenon of disease suppression might be related to specific functions or activities of soil microorganisms rather than the simple presence or abundance of particular populations in the soil.

3.2.3. Microbial Functions and Activities

Total microbial activity has often been related to soil suppressiveness [8,40,55], suggesting an underlying mechanism of general suppression. However, recent reviews have shown great variability in the relationship between these parameters depending on the pathogen involved [50,51]. This variability agrees with the wider range of specific mechanisms that are already known to be involved in disease suppression [50]. Multiparametric analyses of the changes in the metabolic or enzymatic abilities of soil microbial communities have been successfully performed to determine the effect of organic amendments on soil functions [68], thus allowing discrimination between suppressive and conductive soils [8,41]. However, usually this type of analysis is insufficient for indicating a single mechanism as the main responsible of the biocontrol and the true cause of disease suppression remains unknown in many cases. Some authors have found consistent correlations among specific functional parameters and disease suppression [51]. Just in some cases, this correlation has been proved the actual cause of soil suppressiveness. One of the best examples is the production of antibiotic compounds. Again referring to take-all decline of wheat, the suppression of this disease by fluorescent *Pseudomonas* spp. has been related to the production of phenazines [69] and especially to the production of 2,4-diacetylphloroglucinol [70]. The abundance of antibiotic-producing *Pseudomonas* spp. in the rhizospheric soil has been reliably associated to the natural suppressiveness of the soil to take-all disease of wheat [71]. The suppression of this disease by *Trichoderma* spp. also seems to be related to antibiotics production, specifically pyrone compounds [72,73]. However, non-producing strains are able to reduce take-all, suggesting that other mechanisms of disease control must contribute to the phenomenon of disease suppression. In fact, many different mechanisms have been shown to be involved in the control of plant diseases by both bacterial isolates and Trichoderma species: production of antibiotic compounds, competition for nutrients and niches, activation of plant defenses, predation and parasitism, and hydrolytic activities, such as chitinases and glucanases. The importance and particular contribution of each mechanism in disease suppression are different for each particular disease [74,75].

Some hydrolytic activities, including those mentioned above, have been consistently related to soil suppressiveness and the biocontrol of soil-borne pathogens. The main component of fungal cell walls is chitin. Chitinolytic microorganisms have been extensively studied for their potential use in the biological control of fungal pathogens. In fact, chitinolytic activity has been related to the control of several fungal diseases by single biocontrol microorganisms [76,77], and also using compost [78]. Chae *et al.* [78] tested a chitin-compost, composed of crab shell at 30%, against late blight of pepper caused by *Phytophthora capsici*. The chitin-compost showed the ability to reduce late blight symptoms in plant assays and the compost water extract inhibited the growth of *P. capsici in vitro*, in both cases in comparison with a control-compost without crab shell. The number of chitinase-producing bacteria in the rhizosphere and the enzymatic activities chitinase and β-1,3-glucanase were largely higher in plants amended with the chitin-compost. Instead of the strategy of the microbe hunters, in this approach they are not looking for single biocontrol strains; the aim is the design of highly effective amendments, as example, the chitinolytic compost.

4. Future Perspectives

Molecular methods based on nucleic acid sequences have been a key stone for unraveling both genetic and functional diversity of soils in the last decades. The overcoming of culture-based methods led to the actual understanding of microbial diversity. In fact, the vast majority of the studies estimating soil microbial diversity and analyzing microbial community structure compiled in this review are based on the analysis of ribosomal RNA sequences. Functional diversity has also been addressed by molecular analyses of functional genes involved in biogeochemical cycles and antibiotic or enzyme production [18,79]. Most of these works were based on fingerprinting methods and the construction and screening of clone libraries. Several types of DNA microarrays have been developed and evaluated for microbial community analysis. Community genome arrays as the PhyloChip, a high-density 16S rDNA microarray, are considered effective tools for the analysis of complex microbial communities. A combined approach of PhyloChip-based metagenomics and culture-dependent functional analyses has been recently used for the analysis of the rhizosphere microbiome in suppressive soils [80]. In this study, Mendes *et al.* have identified key bacterial taxa belonging to Proteobacteria, Firmicutes, and Actinobacteria, consistently associated with the suppression of *Rhizoctonia* root rot in sugar beet. Especially interesting types of microarrays are the functional gene arrays, such as the GeoChip [81]. This array contains more than 24,000 probes from all of the known genes involved in various biogeochemical, ecological and environmental processes and it can be used to assess functional gene diversity and expression in large numbers of soil samples. Although they are still considered an effective and economical tool for the analysis of complex microbial communities, DNA microarrays are being rapidly superseded by next-generation sequencing approaches. The fast improvement of these next-generation or high-throughput sequencing technologies, as well as sequence analysis bioinformatics tools, is boosting knowledge of natural ecosystems functioning. Sequencing of metagenomic DNA provides at the same time phylogenetic and functional gene information about microbial communities. Alternatively, one can directly extract and sequence RNA to determine which microbes are active and which genes are transcribed [82]. Metagenomic studies, recently based on shotgun sequencing of environmental DNA, are being carried out with suppressive soils. Indeed, there

is a trans-European project on disease-suppressive soils denoted METACONTROL [83]. However, the next-generation sequencing techniques have lately arrived to the study of organic amendments to crop soils. Few examples are available and most of them are not based on shotgun metagenomic and they are restricted to tag-encoded amplicon sequencing of bacterial and fungal ribosomal RNA [84,85]. It is expected that with the development of such techniques and their application to suppressive amendment studies, more of its secrets will be revealed.

5. Conclusions

Despite the increasing amount of information regarding suppressive organic amendments, some challenges remain. The variability in the response of different parameters to soil organic amendments and their variable relationship with disease suppression both suggest that the organisms or activities involved in the suppressive effect may differ depending on the particular pathosystem and the nature of the amendments used [50]. The ultimate effect on pathogen activity, expressed as plant disease, will depend on the particular effects on biotic and abiotic soil parameters and the complex and dynamic interactions among all members of the system [67]. The composition, diversity, functions and activities of soil microbial communities seem to be of considerable importance in disease suppression. Of course, the plant also plays a significant role in this phenomenon and the induction of plant defense mechanisms could be an important component of compost suppressiveness [86].

In conclusion, the use of organic amendments or composts for the suppression of plant pathogens could be a promising and environmentally benign alternative to chemical pesticides. The introduction of this practice in the integrated control of plant diseases could also help in maintenance of soil organic matter, thereby improving soil quality [4]. However, despite the numerous positive reports, its practical application is still limited. The main reason for this is the lack of reliable prediction and quality control tools for evaluation of the level and specificity of the suppression effect. Unfortunately, a single chemical, physical or biological parameter does not predict suppression, and thus quality control is dependent on bioassays designed for a specific pathogen or disease. Deeper understanding of microbial ecology processes could also provide directions for possible manipulations of the community leading to a reproducible suppressive amendment. Combining measures of microbial structural diversity with functional traits should be explored in relation to soil and root health in agricultural systems. In this sense, shotgun metagenomic based on high-throughput sequencing technologies will be crucial to answer the main questions in this field. This strategy not only reveals "who is there" (richness) but also answers questions such as "how many are there" (abundance) as well as "what are they doing there" (function). Investigating structural and functional diversity in amended and suppressive soils will give a much more detailed picture of the interactions among microorganisms, soil, and plants, helping in the identification of microorganisms or processes relevant to disease suppression [82,87].

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