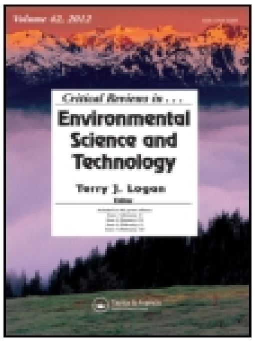

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Recycling of Solid Organic Wastes Through Vermicomposting: Microbial Community Changes Throughout the Process and Use of Vermicompost as a Soil Amendment

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Vermicomposting (i.e., the processing of organic waste by earthworms) is a low-cost rapid technique for transforming large amounts of waste into a safe and valuable product called vermicompost. The effects that earthworms have on microorganisms largely determine the rate of decomposition of organic matter during the process and, in turn, the quality of the final product. Recent studies highlight the importance of the earthworm gut as a major shaper of microbial communities. Passage of the material through the earthworm gut favors the existence of a reduced but more active microbial population in the egested material. The addition of these microbial communities to fresh organic matter has been shown to modify the level of activity and the functional diversity of microbial populations in vermicomposting systems. A review of the main changes observed in the structure and activity of microbial communities during vermicomposting is discussed, to provide further insight into the role of vermicompost as a soil amendment. The mechanisms involved and the factors that determine the suppression of pests are also addressed in this review article.

KEY WORDS: animal manures, *Eisenia andrei*, epigeic earthworms, organic matter decomposition, pest suppression

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1. INTRODUCTION

Organic waste can be used as a valuable resource for renewable energy production and as a source of nutrients in agriculture. Macro- and micronutrients present in organic waste represent a low-cost, environmentally friendly alternative to mineral fertilizers for crop growth (Moral et al., 2009). Overproduction of organic waste has led to the use of inappropriate disposal practices such as the indiscriminate and poorly timed application of the waste to agricultural soils. The potentially adverse effects of such indiscriminate applications are summarized in Table 1.

The use of appropriate management technologies, involving stabilization of the waste prior to use or disposal, could mitigate the environmental risks associated with the application of excessive amounts of organic waste. Stabilization involves the decomposition of an organic material to minimize hazards; stability is usually reflected by decreased microbial biomass and activity and by decreased concentrations of labile compounds (Bernal et al., 2009). Composting and vermicomposting are two of the best known environmentally appropriate technologies for recycling a large variety of hazardous waste and organic waste of different nature (Domínguez and Edwards, 2010a). Although Charles Darwin highlighted the important role of earthworms in the decomposition of dead plants and the release of nutrients (Darwin, 1881), more than a century passed before vermicomposting (i.e., the processing of organic waste by earthworms) was considered a viable technology.

Vermicomposting as a means of managing waste has advanced considerably in recent years, primarily because of the low cost and large amounts of organic waste that can be processed. Organic waste from sewage sludge, paper industry waste, urban residues, food and animal waste, and horticultural residues from cultivars have been successfully managed by vermicomposting to produce vermicomposts (Domínguez, 2004). Vermicompost, which

TABLE 1. Overview of the potentially adverse effects derived from the indiscriminate application of organic wastes to soils

Environmental effects	References
Overfertilization with N, P, and K	Vervoort et al. (1998)
Gaseous emissions of odors, hydrogen sulfide, ammonia and other toxic gases	Chantigny et al. (2007, 2009)
Heavy metal accumulation and concentration in soil surface and soil biota	Steinfeld et al. (2006)
Gradual increases in soil alkalinity	Chantigny et al. (2004)
Establishment of anaerobiosis and anoxic decomposition pathways	Massé et al. (2011)
Input and dispersal of human pathogens	Hutchison et al. (2005)
Groundwater pollution	Sharpley et al. (2002)

is a peat-like highly porous material with a high water holding capacity, contains nutrients that are readily taken up by plants.

2. THE VERMICOMPOSTING PROCESS

Vermicomposting is defined as a bio-oxidative process in which detritivorous earthworms interact with microorganisms and other fauna within the decomposer community, thus accelerating the stabilization of organic matter (OM) and greatly modifying its physical and biochemical properties (Domínguez, 2004). Epigeic earthworms are natural colonizers of organic waste and the following properties make them suitable for vermicomposting: high rates of consumption, digestion and assimilation of OM; tolerance to a wide range of environmental factors; short life cycle, high reproductive rates, and endurance and resistance to handling (Domínguez and Edwards, 2010b). Few epigeic earthworms display all these characteristics, and only four species have been extensively used in vermicomposting facilities: *Eisenia andrei*, *Eisenia fetida*, *Perionyx excavatus*, and *Eudrilus eugeniae* (Domínguez and Edwards, 2010b). However, other earthworm species have been successfully used for vermicomposting (Edwards and Bohlen, 1996; Gajalakshmi et al., 2001; Tripathi et al., 2004). The latter group of authors observed that the anecic earthworm *Lampito mauritii* from the semiarid region of Rajasthan was as effective as *E. fetida* in degrading a mixed bedding material comprised mainly of biogas slurry, cow dung, and wheat straw. The use of local endemic species therefore appears to be appropriate for vermicomposting, as such species are well adapted to local environmental conditions. Other earthworm species such as the endogeic earthworms *Polypheretima elongata*, *Metaphire houletti*, *Dichogaster annae*, *Pontoscolex corethrurus*, and *Amynthas asiaticus* (syn. *Pheretima asiatica*) have also been used in the field of vermicomposting. However, little is yet known about the life cycles and optimal growth conditions of these species in relation to validating their potential for vermicomposting (Domínguez and Gómez-Brandón, 2010).

Vermicomposting systems sustain a complex food web that leads to the recycling of organic matter and release of nutrients. The main properties of these systems include biotic interactions between decomposers (i.e., bacteria and fungi) and the soil fauna, such as competition, mutualism, predation and facilitation, as well as rapid changes that occur in both functional diversity and in substrate quality (Sampedro and Domínguez, 2008). The most numerous and diverse members of this food web are microbes, although it also includes abundant protozoa and many animals of varying sizes, including nematodes, microarthropods, and large populations of earthworms (Sampedro and Domínguez, 2008). Biochemical decomposition of the organic matter is primarily accomplished by the microbes, but earthworms also influence

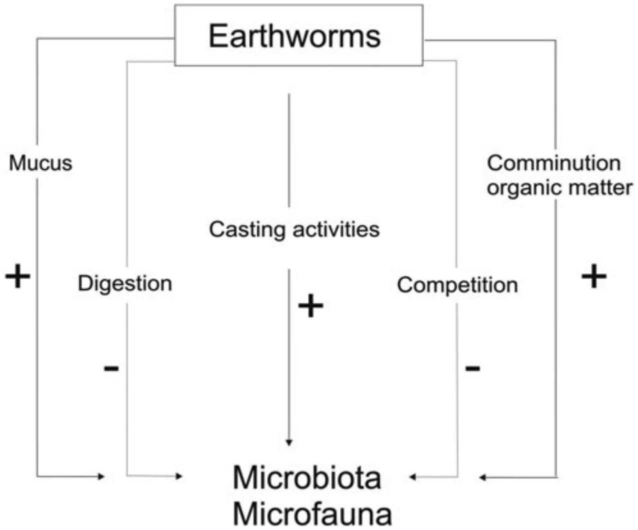

FIGURE 1. Positive (+) and negative (−) effects of earthworms on microbiota and microfauna (modified from Domínguez et al., 2010).

the process as they may affect microbial activity by grazing directly on microorganisms (Aira et al., 2009; Gómez-Brandón et al., 2011a; Monroy et al., 2009) and by increasing the surface area of organic matter available for microbial attack after comminution (Domínguez et al., 2010; Figure 1). These activities may enhance OM turnover rate and productivity of microbial communities, thereby increasing the rate of decomposition. Earthworms may also affect other fauna directly, mainly through the ingestion of microfaunal groups (protozoa and nematodes) that are present in the detritus consumed (Monroy et al., 2008), or indirectly, by modifying the availability of resources for these groups (Monroy et al., 2011; Figure 1). Furthermore, earthworms are known to excrete large amounts of casts (Figure 1), which are difficult to separate from the ingested substrate (Domínguez et al., 2010). The contact between worm-worked and unworked material may affect the decomposition rates (Aira and Domínguez, 2011) because of the presence of microbial populations in earthworm casts that are different from those contained in the material prior to ingestion (Gómez-Brandón et al., 2011a). The nutrient content of the egested materials differs from the ingested material (Aira et al., 2008), which may enable better exploitation of resources because of the presence of a pool of bioavailable compounds in the earthworm casts. Therefore, the decaying OM in vermicomposting systems is a spatially and temporally heterogeneous matrix of organic resources with contrasting qualities that result from different rates of degradation that occur during decomposition (Moore et al., 2004).

The vermicomposting process includes two different phases in relation to earthworm activity: (a) an active phase during which earthworms process the organic substrate, thereby modifying its physical state and microbial composition (Lores et al., 2006), and (b) a maturation phase, which is marked by the displacement of the earthworms toward fresher layers of undigested substrate, when microorganisms decompose the earthworm-processed substrate (Aira et al., 2007a, 2007b; Gómez-Brandón et al., 2011b; Figure 2). The length of the maturation phase is not fixed and depends on the efficiency with which the active phase of the process takes place, which in turn is determined by the species and density of earthworms (Domínguez et al., 2010), and the rate of residue application (Aira and Domínguez, 2008). Vermicompost is expected to reach optimal conditions (in terms of its biological properties that promote plant growth and suppress plant diseases) after a period of aging (Domínguez et al., 2010). However, little is known about the timing of this process or how to determine whether the optimal or mature state has passed.

Vermicomposting is a biological process. Microorganisms play a key role in the evolution of organic material and in its transformation from waste to safe organic amendments or fertilizers (vermicompost). The effects that earthworms have on the microorganisms must be established because if earthworms stimulate or depress microbiota or modify the structure and activity of microbial communities, they will have different effects on the decomposition of organic matter and its quality.

3. EARTHWORMS AND MICROORGANISMS

Earthworms in different functional groups, and even different species within the same functional group, display particular modes of food selection, ingestion, digestion, assimilation, and movement (Brown, 1995; Curry and Schmidt, 2007; McLean et al., 2006). Epigeic earthworm species may feed directly on microorganisms or litter material and inhabit the organic layer of soil. These species have been shown to strongly affect decomposition processes (Sampedro and Domínguez, 2008) and modify the fungal composition of forest soils (McLean et al., 2000). Anecic earthworms, which live in deeper zones of mineral soils, ingest moderate amounts of soil and feed on litter that they drag into their vertical burrows. Tiunov and Scheu (1999, 2000) reported that *Lumbricus terrestris* burrows are stable microhabitats, which sustain a large and active microbial community and likely play an important role in the soil system by regulating microbial-mediated chemical processes. Endogeic earthworms can transport fresh organic detritus from the soil surface into horizontal burrows while mixing it with mineral soil. In the case of tropical endogeic species, the addition of water and readily

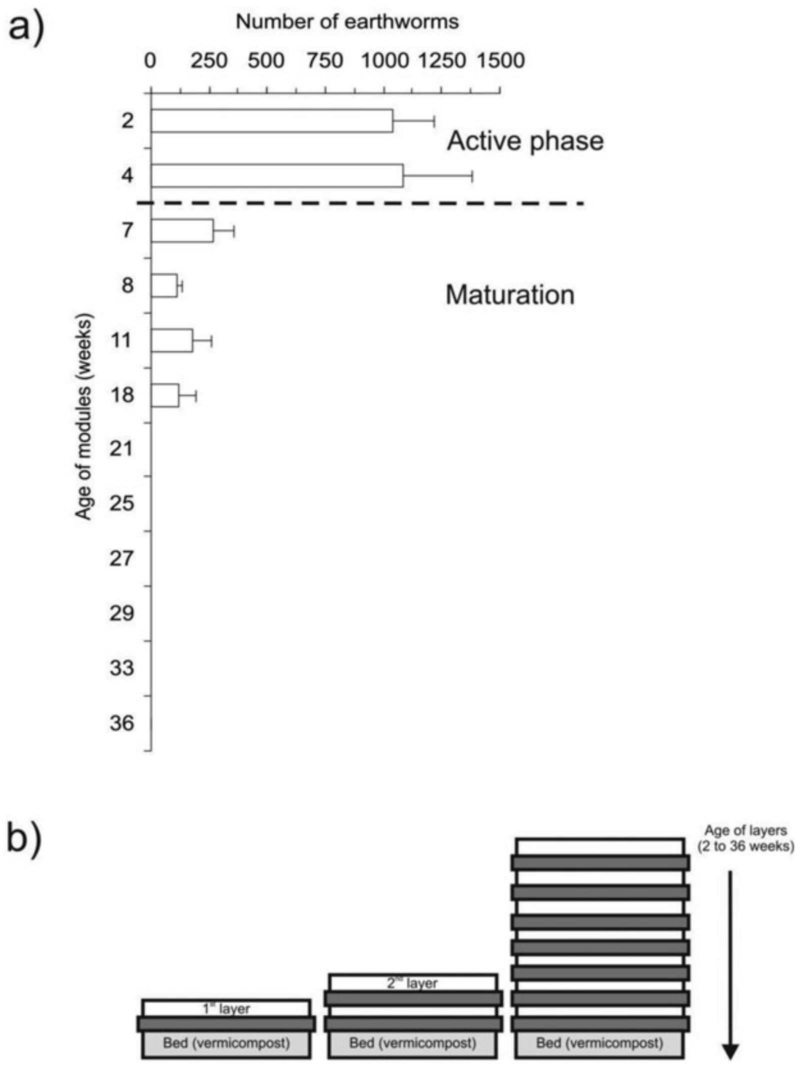

FIGURE 2. The two phases of vermicomposting that depend on the presence of earthworms in the substrate (active and maturation phase): (a) Earthworm population in vermireactors at different sampling times. Number of earthworms (means ± SE, n = 3) in each layer, from age 2–36 weeks, are shown; (b) Diagram of the setup and the procedure for adding new modules during the vermicomposting process. The earthworms moved upwards toward the new modules to which fresh waste had been added (modified from Aira et al., 2007a).

assimilable intestinal mucus to the ingested soil rapidly stimulates microbial activity (Brown, 1995; Brown et al., 2000). Moreover, mixing soluble organic carbon, in the form of low-molecular-weight mucus, with ingested OM has been found to promote the development of a microbial community that can digest cellulose and other substances that earthworms typically cannot digest (Brown and Doube, 2004; Lavelle and Martin, 1992; Lavelle et al., 1995).

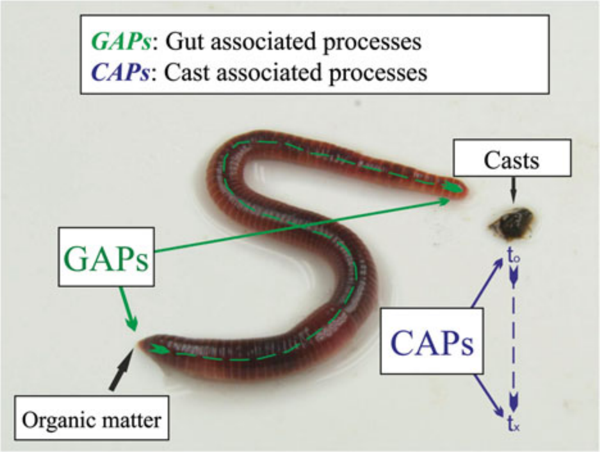

FIGURE 3. Earthworms affect the decomposition of organic matter during vermicomposting through ingestion, digestion, and assimilation in the gut and casting (*gut-associated processes*) and by *cast-associated processes,* which are more closely related with ageing processes.

Essentially, earthworms directly affect the decomposition of OM through gut-associated processes, via the effects of ingestion, digestion, and assimilation of the OM and microorganisms in the gut and by casting (Figure 3). Some bacteria are activated during passage through the gut, whereas others remain unaffected, and others are digested in the intestinal tract and thus decrease in number (Monroy et al., 2009; Pedersen and Hendriksen, 1993). Pedersen and Hendriksen (1993) reported selective reduction of the coliform *Escherichia coli* BJ18 in cattle dung during passage through the gut of several species of earthworms of the genus *Lumbricus*. Coliform reduction did not affect any other specific bacterial groups, but resulted in shifts in the microbial community composition. The selective effects on microbes of passage through the earthworm gut may be caused by competitive interactions between the ingested microbes and the endosymbiotic microbes that reside in the gut (Brown and Mitchell, 1981) or by selective suppressive activity of gut fluids against specific microbial groups (Byzov et al., 2007).

Several authors have suggested that fungi constitute a major component of the earthworm diet (Brown and Doube, 2004). Earthworms have been shown to prefer food substrates colonized by certain fungal species (Moody et al., 1995, 1996); in addition, fungi have been found to be damaged by gut passage. For instance, fungal colony forming units (CFUs) decreased from the foregut to the hindgut in the earthworm *Aporrectodea caliginosa*, indicating that endogeic gut passage caused more damage to fungal hyphae and fewer viable CFUs relative to epigeic gut passage (Krištůfek et al. 1992). Moody et al. (1996) also found that fungal spore viability (*Chaetomium globosum*) differed between two species from the same ecological category, the anecic earthworms *L. terrestris* and *A. longa*. This indicates that the relationships between earthworms and fungal populations during the passage through the gut depends on the species in question. Such species-specific effects of earthworms have also been reported in relation to actinobacteria. Although the abundance of this microbial group increased during *L. terrestris* gut passage, probably due to its longer transit time, no such increase was observed in *A. caliginosa* (Krištüfek et al., 1992). Actinobacteria are found to be dominant microorganisms in the intestinal microflora of earthworms (Jayasinghe and Parkinson, 2009). Krištüfek et al. (1993) showed that earthworm guts and casts contain active actinobacteria (in the form of cell aggregates and active cells), most of which are *Streptomyces* species, which are well known as antibiotic producers. This suggests that the ingested *Streptomyces* might inhibit the growth of other microorganisms in the earthworm gut, especially fungi, leading to a predominance of other actinobacteria and other antibiotic resistant microorganisms. Indeed, Polyanskaya et al. (1996) detected the production of the antibiotic heliomycin in the gut content of *E. fetida* fed with *Streptomyces olivocinereus*. Moreover, as observed in relation to fungi, food preference studies have shown that earthworms do not feed on actinobacteria at random (Jayasinghe and Parkinson, 2009; Polyanskaya et al., 1996).

After passage through the earthworm gut, the microorganisms (mainly fungal and protozoan spores and some resistant bacteria) are available for colonization of newly formed earthworm casts (Brown and Doube, 2004). These newly deposited casts are usually rich in ammonium-nitrogen and partially digested OM and thus provide a good substrate for microbial growth.

3.1 Effects of Epigeic Earthworms on Microorganisms During Vermicomposting

3.1.1 Short-term Effects of Epigeic Earthworms on Microbial Communities During Vermicomposting

The specific impact of epigeic earthworms on the decomposition of organic waste during the vermicomposting process is initially due to *gut-associated processes* (Aira et al., 2009; Gómez-Brandón et al., 2011a; Monroy et al., 2008; Figure 3). Specific microbial groups respond differently to the earthworm gut environment. Monroy et al. (2009) observed a 98% reduction in the density of total coliforms after passage of pig slurry through the gut of the epigeic earthworm *Eisenia fetida*. The reduction in total coliform numbers was not related to decreases in bacterial biomass C, which indicates a specific negative effect of the earthworms on this bacterial group. Such selective effects on microbial communities may alter decomposition pathways during vermicomposting, probably by modifying the composition of the microbial communities involved in decomposition. Indeed, microbes from the gut are then released in fecal material in which decomposition of egested organic matter is continued by microbes. Epigeic earthworm casts contain different microbial populations from those in the parent material (Domínguez et al., 2010), and it is expected that the inputs of those communities to fresh organic matter promote modifications similar to those observed when epigeic earthworms are present. This input is also expected to alter the activity levels of microbial communities and modify the functional diversity of microbial populations in vermicomposting systems (Aira and Domínguez, 2011).

The shift in the structure of microbial communities in the presence of epigeic earthworms is generally accompanied by short-term decreases in bacterial populations (Gómez-Brandón et al., 2010, 2011a; Monroy et al., 2009). The latter group of authors found that the passage of organic matter through the earthworm gut affected the abundance of Gram-positive (G^+) bacteria to a greater extent than Gram-negative (G^-) bacteria, as shown by their phospholipid fatty acid (PLFA) profiles. These differences may be due to G^- bacteria with an outer membrane composed of lipopolysaccharides, which provides structural integrity, thus increasing the negative charge on the cellular membrane and protecting the bacteria from certain types of chemical attack (Vermüe et al., 1993). Other studies examining the effects of epigeic earthworms on microorganisms have also shown that G^- bacteria can survive transit through the earthworm gut (Daane et al., 1997; Hendriksen, 1995; Williams et al., 2006).

The impact of these earthworm species on fungal biomass has been shown to depend on the earthworm density (Aira et al., 2008). These authors detected a higher fungal biomass, measured as ergosterol content, at intermediate and high densities of earthworms (50 and 100 earthworms per mesocosm, respectively) in a short-term (72 hr) experiment with the earthworm *E. fetida*. This suggests that there may be a threshold density of earthworms at which fungal growth is triggered. This priming effect on fungal populations was also observed in previous short-term experiments in the presence of the epigeic earthworms *Eudrilus eugeniae* and *Lumbricus rubellus* fed with pig and horse manure, respectively (Aira et al., 2006a; Lores et al., 2006). These contrasting short-term effects on bacterial and fungal populations are expected to have implications for decomposition pathways during vermicomposting because of differences between both microbial decomposers in relation to resource requirements and exploitation (Bardgett and Wardle, 2010). This is based on the fact that fungi can immobilize large quantities of nutrients in their hyphal networks, whereas bacteria are more competitive in the use of readily decomposable compounds and have a more exploitative nutrient use strategy involving rapid use of labile substrates (Bardgett, 2005).

Recent findings reported by Gómez-Brandón et al. (2011a, 2012a) indicate that the gut of epigeic earthworms acts as a selective filter for microorganisms contained in the substrate, thus favoring the existence of a microbial community specialized in metabolizing compounds that are produced or released by the earthworms in egested materials. These authors found no differences between PLFA profiles of fresh cast samples derived from different types of manure. This suggests that the direct effects of epigeic earthworms on the microbial community composition are largely determined by factors other than the parent material (e.g., the earthworm species).

Upon completion of GAPs, the resultant earthworm casts undergo *cast-associated processes*, which are more closely related to aging processes, the presence of unworked material and physical modification of the egested material (Figure 3). During these processes, the effects of epigeic earthworms are mainly indirect and derived from the GAPs (Aira et al., 2007a, 2007b).

3.1.2 Long-term Effects of Epigeic Earthworms on Microbial Communities During Vermicomposting

To date, most studies of the effects of epigeic earthworms on microbial communities have focused on the changes that occur before and after the active phase (Aira et al., 2006a; Aira and Domínguez, 2009; Anastasi et al., 2005; Fracchia et al., 2006; Gómez-Brandón et al., 2010, 2012; Lazcano et al., 2008; Vivas et al., 2009) rather than those that occur throughout the vermicomposting process. Moreover, most of these previous studies have generally shown the actions of these earthworms in laboratory-scale systems. Recently, Gómez-Brandón et al. (2011b, 2013) evaluated the impact of the earthworm *E. fetida* on the microbial community structure and activity during vermicomposting, using continuous-feeding vertical reactors that are designed to process larger amounts of waste. Overall, a higher degree of stabilization was reached in the organic substrate after 200–250 days, as indicated by the lower values of microbial activity compared to the fresh manure. These findings highlight the continuous-feeding vermicomposting system as an environmentally sound management option for recycling animal manures, as previously reported by Fernández-Gómez et al. (2010). However, it must be considered that the functioning of this type of reactor leads to the gradual accumulation of layers and to the compaction of the substrate, thus minimizing earthworm-induced aeration, which can promote pathogen survival (Aira et al., 2011).

The above-mentioned changes resulted in functional alterations of the system (Gómez-Brandón et al., 2011b), as shown by the greater loss of total carbon in the presence of earthworms (440 and 200 μg C day^{-1}, with and without earthworms). Accordingly, Aira et al. (2006b) found that, by enhancing fungal growth, the earthworm E. *fetida* triggered more efficient cellulose degradation and the rate of cellulolysis was two times higher than in the control without earthworms. This resulted in a 1.5-fold increase of cellulose loss after 18 weeks of vermicomposting. Together, these findings highlight the importance of epigeic earthworms in the decomposition of organic matter because of their interactions with microorganisms during the vermicomposting process. In addition to rapid carbon mineralization, epigeic earthworms have also been shown to promote a change in the functional diversity of microbial communities, thus increasing their capabilities to use more diverse carbon pools (Aira et al., 2006a, 2007a; Gómez-Brandón et al., 2010; Sen and Chandra, 2009; Sheehan et al., 2008). Gómez-Brandón et al. (2010) observed that the activity of earthworms (*E., andrei*) led to greater utilization of polymers and amino acids (rather than carbohydrates and carboxylic acids) during the vermicomposting of grape marc, and a higher substrate diversity value was reached than in the control treatment. Aira and Domínguez (2011) found that inoculation of raw organic matter (i.e., pig manure) with worm-worked material (i.e., vermicomposts from the earthworms *E., andrei*, *E. fetida*, and *Eu. eugeniae*) also modified the microbial community functioning and altered microbial community levels of activity. Such indirect effects of earthworms on organic matter decomposition were independent of the amount of worm-worked inoculated substrate, suggesting the existence of a threshold at which functioning is triggered (Aira and Domínguez, 2011). The strength of the process greatly depended on the type of vermicompost used (Aira and Domínguez, 2011), reinforcing the idea that the earthworm-microorganism interactions are greatly affected by the species of earthworm. This is consistent with the fact that specific microbial groups respond differently to the gut environment of different earthworm species (Nechitaylo et al., 2010). Monroy et al. (2008) found that the decrease in pathogenic bacteria (i.e., total coliforms) as a result of gut transit differed in four vermicomposting earthworm species (*E. fetida*, *E., andrei*, *L. rubellus*, and *Eu. eugeniae*). Such a reduction is mainly due to the combination of earthworm digestive abilities, which include fine grinding of cells and the actions of several enzymes related to the degradation of the bacterial cell wall (Edwards, 2011). Other factors determining pathogen reduction during the process include the application rate of the parent material (Monroy et al., 2009) and the pathogen considered (Aira et al., 2011; Parthasarathi et al., 2007). Monroy et al. (2009) observed significant decreases in total coliforms when pig manure was applied at low rates (20 kg m^2), whereas this did not occur at high rates of application (40 kg m^2). Aira et al. (2011) detected a decrease in the abundance of fecal *enterococci*, fecal coliforms, and *Escherichia coli* across the layers of an industrial-scale vermireactor fed with cow manure, whereas no changes were reported for total coliforms, *Enterobacteria*, or *Clostridium*.

The changes that occur in the waste during the process are mainly related to the microbiological properties and they are expected to affect the quality of vermicompost in terms of its nutrient content and pathogenic load. This is critical to guarantee safe use of the end-product as an organic amendment and benefits to both agriculture and the environment. Recent studies have demonstrated the presence of various bacteria, which are useful for different biotechnological purposes, in diverse vermicomposts (Gopalakrishnan et al., 2011; Yasir et al., 2009; Zambare et al., 2011). This reinforces the idea that the biological component (i.e., the microbial community composition) of a vermicompost largely determines its usefulness in agriculture and other applications, such as soil restoration and bioremediation. However, few studies have provided relevant information on the bacterial and fungal composition in vermicomposts (Fernández-Gómez et al., 2012; Fracchia et al., 2006; Vaz-Moreira et al., 2008; Vivas et al., 2009; Yasir et al., 2009). The latter group of authors detected the presence of *Sphingobacterium*, *Streptomyces*, Alpha-Proteobacteria, Delta-Proteobacteria, and Firmicutes in diverse vermicomposts, irrespective of the parent material used for the process, by applying a denaturing gradient gel electrophoresis (DGGE) and COMPOCHIP (i.e., a microarray targeting typical bacteria of stabilized organic materials and pathogenic bacteria).

4. INFLUENCE OF VERMICOMPOST AMENDMENTS ON THE SOIL MICROBIOTA AND ON THE SUPPRESSION OF PESTS

4.1 Influence of Vermicompost on Soil Biochemical and Microbiological Properties

Vermicompost has been found to provide manifold benefits when used as a total or partial substitute for mineral fertilizer in peat-based artificial greenhouse potting media and as a soil amendment in field studies (Lazcano and Domínguez, 2011). The advantages of vermicompost as a soil amendment include its potential to maintain soil organic matter, foster nutrient availability, suppress plant diseases, and increase soil microbial abundance and activity. Some recent findings contribute to better descriptions of whether and to what extent vermicompost amendments affect soil microbial biomass, activity and community structure. For instance, Arancon et al. (2006) observed that a single application of vermicompost to a strawberry crop resulted in a significantly greater increase in soil microbial biomass than the application of an inorganic fertilizer, regardless of dosage. In addition to increasing microbial biomass, vermicompost amendments have been shown to enhance microbial activity (Ferreras et al., 2006) and to promote the establishment of a specific microbial community in the rhizosphere of different plants supplemented with mineral fertilizers or other types of organic fertilizers such as manure (Aira et al., 2010). Inorganic fertilization often only supplies nitrogen, phosphorus and potassium, whereas organic fertilizers also supply different amounts of C and macro- and micronutrients that can influence microbial communities with different nutritional requirements (Tate, 2000). Moreover, microbial communities in vermicompost are metabolically more diverse than those in manure (Aira et al., 2007a) and may be incorporated, at least in the short term, to soils (Gómez et al., 2006). Interestingly, Aira et al. (2010) observed that the effect of the addition of vermicompost occurred despite the low dose used (25% of total fertilization) and despite the short duration of the experiment (four months). Similar results were found by Lazcano et al. (2012). Aira et al. (2010) also found significant differences in the rhizosphere microbial community of two genotypes from cultivars of maize, with the sugary endosperm mutation (*su1*) and with the shrunken endosperm mutation (*sh2*), which differ in their C storage patterns (Revilla et al., 2006). Different hybrids or plant genotypes will respond differently to vermicompost, considering that plant genotype determines important differences in nutrient uptake capacity, nutrient use efficiency and resource allocation within the plant (Kabir et al., 1998).

Soil enzymes act as biological catalysts of specific reactions that depend on a variety of factors, such as the presence or absence of inhibitors, amendment type, and crop type, and they can be considered as early indicators of biological changes (Bandick and Dick, 1999). The activities of several enzymes have been shown to increase after the addition to soils of vermicompost at rates equivalent to mineral fertilizers (Arancon et al., 2006, Ferreras et al., 2006; Lazcano et al., 2012; Marinari et al., 2000; Saha et al., 2000). Soil microorganisms degrade organic matter via the production of a variety of extracellular enzymes, and an input of organic matter is expected to be accompanied by a higher enzymatic activity. Moreover, the added material may contain intra- and extracellular enzymes and may also stimulate microbial activity in soil (Goyal et al., 1999). Stabilization of enzyme activities in the humic matrix may contribute to a higher hydrolase enzyme activity (Nannipieri et al., 2003). Immobilized enzymes may act as stable catalysts for the detection of potential substrates, making the continuous synthesis and secretion of extracellular enzymes by microorganisms unnecessary (Burns, 1982).

4.2 Influence of Vermicompost on Plant Pathogens, Plant-Parasitic Nematodes, and Arthropod Pests

There is a large body of scientific evidence for the positive effects of vermicomposts on the suppression of plant diseases (Arancon et al., 2007a; Edwards et al., 2006; Nakamura, 1996; Nakasone et al., 1999; Orlikowski, 1999; Sahni et al., 2007; Szczech, 1999; Szczech and Smolinska, 2001; Yasir et al., 2009; Zaller, 2006). Nakasone et al. (1999) found that aqueous extracts of vermicompost were capable of reducing the growth of pathogenic fungi such as *Botrytis cinerea*, *Sclerotinia sclerotiorum*, *Corticium rolfsii*, *Rhizoctonia solani*, and *Fusarium oxysporum*. The addition of solid vermicompost to tomato seeds also significantly reduced the infection caused by *Fusarium lycopersici* (Szczech, 1999). However, Szczech and Smolinska (2001) did not observe any significant suppressive effects of a sewage sludge vermicompost on *Phytophthora nicotianae* in comparison with peat. Edwards et al. (2006)

observed that the suppressive effect exerted by several types of vermicompost on several plant pathogens such as *Pythium*, *Rhizoctonia*, *Verticillium*, and *Plectosporium*, disappeared after sterilization of the vermicompost. This suggests that disease suppression may be related to the presence of biological suppressive agents in vermicompost. The use of vermicompost extracts as foliar sprays in different crop plants also reduced the incidence of fungal diseases such as *Phytophthora infestans* (Zaller, 2006), *Erysiphe pisi*, and *Erysiphe cichoracearum* (Singh et al., 2003). Yasir et al. (2009) reported inhibition of spore germination in *Fusarium moniliforme* in aqueous extracts of vermicompost produced from paper sludge and dairy sludge. Nevertheless, a more detailed understanding of the mechanisms involved and the main factors influencing these suppressing effects is still required.

Vermicomposts may also have significant effects on both the incidence and abundance of plant-parasitic nematodes in soil. Swathi et al. (1998) found that the addition of vermicompost to soil at a rate of 1 kg m^{-2} significantly inhibited the incidence of the parasite nematode *Meloidogyne incognita* in tobacco plants. Similar reductions in the degree of plant infestation by *Meloidogyne incognita* were observed by Morra et al. (1998). Ribeiro et al. (1998) reported a decrease in the egg mass of *Meloidogyne javanica* after application of vermicompost to the growth medium. Arancon et al. (2003) observed a significant reduction in the abundance of plant-parasitic nematodes in soil plots amended with two types of vermicompost, in comparison with those with inorganic fertilizers. Thoden et al. (2011) emphasized that only those amendments capable of producing high concentrations of nematicidal substances and/or forming anaerobic conditions (e.g., slurries) can directly reduce plant-parasitic nematodes. Furthermore, several field studies have shown that the addition of vermicompost to soil significantly reduced the incidence of the psyllid *Heteropsylla cubana* (Biradar et al., 1998), the sucking insect *Aproaerema modicella* (Ramesh, 2000) and spider mites (Rao, 2002). Arancon et al. (2007) found that mealy bug attacks (*Pseudococcus* sp.) on cucumbers and tomatoes was suppressed by application of a solid food waste vermicompost. Edwards et al. (2007, 2010) observed a significant degree of suppression of aboveground foliar arthropod pests after the application of soil drenches from vermicompost aqueous extracts. A plausible explanation for this suppressive effect is the unpalatability of the plants to pests derived from the uptake of soluble phenolic compounds from the vermicompost aqueous extracts into the plant tissues.

Overall, suppression of plant disease by vermicomposts may be general or specific, depending on the existence of a single suppressive agent or the joint action of several agents (Figure 4). General suppressive effects are more common following the addition of vermicompost, as a broad range of organisms may act as biocontrol agents (Gunadi et al., 2002; Arancon et al., 2006). The proposed mechanisms include competition, antibiosis, and parasitism (Figure 4). Disease suppression may also be accompanied by an

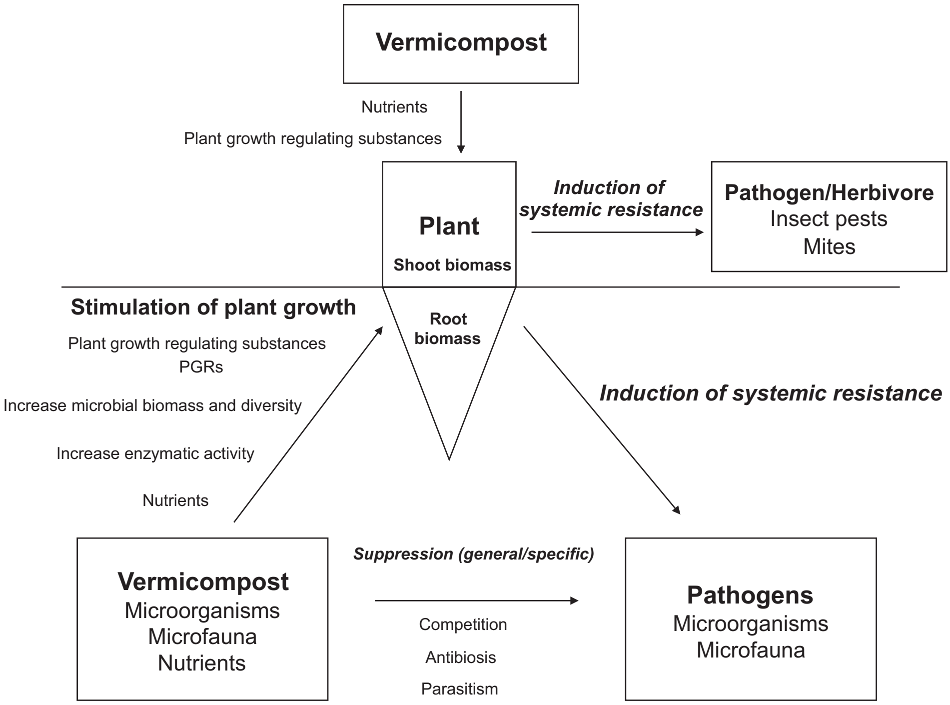

FIGURE 4. Diagram of the main mechanisms by which vermicompost may directly or indirectly influence disease suppression.

increase in the production of defense substances (i.e., phenolic compounds) by the plant (Singh et al., 2003), which suggests the induction of plant systemic resistance by vermicompost (Figure 4). Moreover, vermicompost may directly affect plant growth via the supply of nutrients (Chaoui et al., 2003; Figure 4) and/or through enhancement of plant growth regulating substances (Figure 4), as shown by Tomati et al. (1990), Grappelli et al. (1987), and Tomati and Galli (1995).

5. CONCLUSIONS AND OUTLOOK

Detailed knowledge of the diverse biological processes involved in the recycling and recovery of waste components is of increasing importance for more sustainable production and consumption systems. Composting has become one of the best-known environmentally sound waste-treatment processes under aerobic conditions. Continuous-feeding vermicomposting systems appear to be equally applicable to rapid large-scale organic waste processing (Domínguez and Edwards, 2010a). However, there is a need for further studies to evaluate the efficiency of such systems to process a wider range of residues from different sources. The rate of application of the residue and the earthworm species used are expected to influence the system functioning. Further investigation is required to test the quality of the end products under field conditions. One of the main problems associated with the vermicomposting process is the presence of human pathogens, the levels of which will restrict use of vermicompost as an organic fertilizer or its disposal by landfill (Domínguez and Edwards, 2010a). Unlike composting, vermicomposting is a mesophilic process, so that substrates do not undergo a thermal stabilization process that eliminates pathogens. However, it has been shown that vermicomposting may reduce the levels of several pathogens in different types of waste (Aira et al., 2011; Edwards, 2011). Ultimately, vermicomposting and composting are not necessarily mutually exclusive and could be used sequentially to take advantage of the unique and valuable features of each (Lazcano et al., 2008).

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