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Review

# Compost: Its role, mechanism and impact on reducing soil-borne plant diseases

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ABSTRACT

Soil-borne plant pathogens are responsible for causing many crop plant diseases, resulting in significant economic losses. Compost application to agricultural fields is an excellent natural approach, which can be taken to fight against plant pathogens. The application of organic waste products is also an environmentally friendly alternative to chemical use, which unfortunately is the most common approach in agriculture today. This review analyses pioneering and recent compost research, and also the mechanisms and mode of action of compost microbial communities for reducing the activity of plant pathogens in agricultural crops. In addition, an approach for improving the quality of composts through the microbial communities already present in the compost is presented. Future agricultural practices will almost definitely require integrated research strategies to help combat plant diseases.



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## 1. Introduction

Almost a century ago, Sanford (1926) started a new era of soil-borne disease investigations. In his study, he suggested that the soil-borne pathogen *Streptomyces scabies*, which causes potato scab, could be controlled by green amendments. This control was due to the action of antagonistic soil saprophytes derived from the green amendment material. Soil-borne pathogens cause great economic losses all over the world. They are also more intractable to management and control compared to pathogens that attack the above-ground portions of the plant (Bruehl, 1987). Presently, soil-borne problems are managed by using different integrated approaches, however, these approaches do not completely eliminate the pathogens from the soil. The complex nature of soil and its environment enable these pathogens to survive for long periods in the field.

Soil organisms that have the potential to be plant pathogens can be classified into five major groups: fungi, bacteria, viruses, nematodes and protozoans (Agrios, 2005). Some pathogens of the above ground parts of plants (leaves, stems) also survive in the soil at various stages in their life cycles. Therefore, a soil phase of a plant pathogen may be important, even if the organism does not infect roots. The majority of bacteria are less prone than fungi and nematodes to causing soil-borne diseases due to their inability to produce spores and thus their inability to survive in the soil for a very long period (Koike et al., 2003). In addition, bacteria also require a wound or natural opening for penetration into the plant and initiation of infection (Genin and Boucher, 2004; Nester et al., 2005). Insect damage can facilitate the entry of plant pathogens into plants (Agrios, 2005). Like bacteria, viruses also require a wound for plant infection and as viruses are transmitted by vectors, few viruses can infect plants. In soil, viruses can be transmitted by nematodes (Brown et al., 1995) or by zoosporic fungi such as *Olpidium* and *Polymyxa* (Campbell, 1996).

Fungi cause the majority of plant diseases in agricultural fields (Pernezny et al., 2011). Fungi are eukaryotic, filamentous, multicellular, and heterotrophic organisms that produce a network of hyphae (mycelium), which is able to absorb nutrients from the surrounding substrate (Alexopoulos et al., 1996). Members of the Oomycetes reportedly cause most soil-borne diseases (Fry and Niklaus, 2010). They produce swimming spores (zoospores) and contain cellulose in their cell walls. The mycelial structure of fungi helps it to spread up the root, internally or externally, or to spread to other roots in close proximity (Raaijmakers et al., 2009). This is the most effective fungal strategy for long time survival in plants.

Over the last few decades, much research investigating soil-borne pathogens and their effect on different crops and vegetables has been conducted. The fungal genera *Rhizoctonia*, *Fusarium*, *Verticillium*, *Phytophthora* and *Sclerotium* contain the major soil-borne plant pathogens known, these pathogens affecting a number of important crops including wheat, cotton, vegetables and temperate fruits (Koike et al., 2003; Noble and Coventry, 2005). To overcome such diseases, different approaches have been taken in the past. The most common method to control these diseases is the use of fungicides. Using fungicides against a pathogen can help to control disease in a very effective way, however, frequent and indiscriminate use of fungicides may also lead to atmospheric pollution and the development of fungicide resistance (Christopher et al., 2010). Therefore, an alternative to chemical control is much needed. Alternative approaches include solarisation (Katan, 1996), biofumigation (Kirkegaard et al., 2000), biological soil disinfestations (Blok et al., 2000) and application of biocontrol agents (Hoitink and Boehm, 1999; Ryckeboer, 2001) or organic amendments such as composts (Paulitz and Belanger, 2001; Bailey and Lazarovits, 2003).

In a biological control approach, microorganisms isolated from the soil can be directly used for the reduction of plant disease. A group of papers in the 1920s and early 1930s (Hartley, 1921; Henry, 1931) was published on the biological control of plant pathogens. Approximately 50 years later, books by Baker and Cook (1974) and Cook and Baker (1983) which collected and analysed available knowledge on the use of microorganisms for the biological control of plant diseases, have renewed research activity in the area, resulting in many laboratory scale studies, but few effective field trials. In recent years, biological control has become an increasingly promising alternative to chemical control in the management of soil-borne disease (Harman et al., 2004). Numerous studies have demonstrated reduced incidence of diseases in different crops after supplementing the soils with fungal or bacterial antagonists (Singh et al., 2002; Ahmed, 2011; Akrami et al., 2011). Different approaches for the biological control of pathogen borne diseases can be used, and composting is one such approach.

Composting is a controlled biological decomposition process by which organic materials are degraded through the activities of successive groups of microorganisms (Dees and Ghiorse, 2001). Composting transforms raw organic waste materials into biologically stable, humic substances that make excellent soil amendments (Adani et al., 1995). Composting has been used in farming to improve soil fertility and crop health for centuries, however the process was somewhat modernised in the nineteenth century in Europe, with the onset of what is known today as organic farming (Heckman, 2006). In composting processes, the most important step is the decomposition of organic matter, and this occurs via mostly aerobic decomposition, although some anaerobic decomposition also occurs (Cooperband, 2002).

Compost application can help reduce pathogen attacks and in addition, also improve the soil health and its nutrient levels. Most of the literature on the role of compost, its mechanism of action, its microbial structure and the possibilities to improve compost quality for disease suppression is scattered, and so far, these topics have been reviewed separately. Therefore, in this paper, we have reviewed pioneering as well as recent works in detail, and provide clear information about the role of compost in disease suppression, as well as the major factors and mechanisms contributing to compost quality.

## 2. Role of compost in disease suppression

The role of composts in disease suppression was first suggested by Hoitink et al. (1975). Inclusion of compost in the growing media as a method to suppress a wide variety of soil-borne plant pathogens like *Rhizoctonia* root rot (*Rhizoctonia solani*) on bean and cotton, *Fusarium* wilt (*F. oxysporum* f. sp. *cucumerinum*) of cucumber, *Sclerotinia* drop (*Sclerotinia sclerotium*) of lettuce etc. was studied by Lumsden et al. (1983). These studies showed the importance of composts in the biocontrol of different soil-borne plant diseases. Today, compost application is a well established commercial prac-

tice, corroborated by a large body of scientific evidence including Hoitink and Fahy (1986), Hoitink and Boehm (1999), Hoitink et al. (2001), Noble and Roberts (2004), Noble and Coventry (2005), Termorshuizen et al. (2006), Lillywhite et al. (2009) and Yu et al. (2011).

Composts can be used for improving crop production, soil health, nutrient levels, organic matter, plant growth and also for the suppression of disease caused by soil-borne plant pathogens (Chaney et al., 1980; Lumsden et al., 1983; Hoitink and Fahy, 1986; Mays and Giordano, 1989). In 1986, Hoitink and Fahy reported that various types of agricultural and forestry wastes, as well as municipal wastes could be used for compost preparation. They also reported the role of these wastes in the suppression of soil-borne plant pathogens, especially those belonging to the genera *Rhizoctonia*, *Pythium*, *Fusarium* and *Phytophthora*. The studies suggested that the fungal antagonists which are most effective for control of various soil-borne plant pathogens in bark compost-amended substrates are *Trichoderma* spp., *Gliocladium virens* and a variety of bacterial antagonists, such as *Flavobacterium balustinum*, *Pseudomonas putida*, and *Xanthomonas maltophilia*, all of which are rapid colonisers of organic matter. This study also concluded that antagonists have long-term effects only in substrates amended with mature composts and have short-term effects or are ineffective in substrates prepared with sphagnum peats as the sole organic component.

Numerous publications have shown the positive effects of compost application on the reduction of plant disease. Lewis et al. (1992) found that 3–4 years of compost treatment improved cotton stand, and also significantly reduced the inoculum density of *R. solani* in soil. Serra-Wittling et al. (1996) reported that soil amended with municipal solid waste compost significantly reduced *Fusarium* wilt in flax. Szczech (1999) also reported that the addition of vermicompost to a conductive potting medium resulted in the substrate becoming suppressive to *Fusarium* wilt of tomato caused by *F. oxysporum*. The composts produced from different types of agricultural residues proved suitable for container media and field soils (Trillas et al., 2002).

Termorshuizen et al. (2006) conducted a study with 18 commercial composts and tested these composts in 7 pathosystems i.e. *V. dahliae* on eggplant (*Solanum melongena*), *R. solani* on cauliflower (*Brassica oleracea* var. *botrytis*), *R. solani* on pine (*Pinus nigra* var. *austriaca*), *Phytophthora nicotianae* on tomato (*Lycopersicon esculantum* Mill.), *P. cinnamomi* on lupin (*Lupinus* spp.), *Cylindrocladium spatiphylli* on spathiphyllum (*Spathiphyllum wallisii* Hort. cv. *Ceres*), and *F. oxysporum* on flax (*Linum usitatissimum*). The authors found that after applying 20% of the selected compost into potting soil or sand, 54% of the tested combinations were significantly more disease suppressive, while 3% showed significant enhancement of the disease, and 43% of the tested combinations did not result in significant differences compared to the control without compost. The mean disease suppressiveness per compost ranged from 14 to 61%.

Compost based suppression of germination of *S. rolfsii* sclerotia was studied by Danon et al. (2007). Mature biosolids compost (a blend of sewage sludge and yard waste) was found suppressive for germination of the sclerotia on compost plates and also suppressed disease development in bean plants (*Phaseolus vulgaris* L.). Microscopic observations revealed that sclerotia placed on suppressive compost were attacked by mycoparasites.

*Fusarium* is a soil-borne pathogenic fungus, known to cause common root rot, stem rot and wilt diseases of plants. There are several reports in the literature on compost based suppression of *Fusarium* wilt (Serra-Wittling et al., 1996; Cotxarrera et al., 2002; Reuveni et al., 2002; Postma et al., 2003). In these studies, suppression of pathogens by the application of compost was observed to be between 20% and 90%, and microbial activity has been considered as a key factor in suppression. Increased microbial populations (Cheuk et al., 2003), and increased microbial activity (up to 50%) have been observed in composts and composted peat mixes (Cotxarrera et al., 2002). Recent study reports have shown that organic farming practices and especially compost application, may lead, with time, to some reduction of the problems caused by *F. oxysporum* f. sp. *melonis* (Yogev et al., 2011). However, reports of the deleterious effect of prolonged compost storage on disease suppression also exist.

## 3. Mechanisms for disease suppressiveness in composts

The disease suppressiveness phenomenon consists of a complex and intricate set of mechanisms. An understanding of the complexity and mechanisms behind disease suppression is critical for the maximisation of its effectiveness for crop production and soil health. Hoitink and Boehm (1999) suggested several mechanisms (listed below) which are likely to be factors in disease suppression.

### 3.1. Competition among microbial populations

In every ecosystem, microbes compete for nutrients (Chen et al., 1988) and space (Serra-Wittling et al., 1996). Pathogens which grow or move to the sources of nutrients must also compete with the beneficial microflora in the infection court on the surface of the seed or root (Hoitink and Changa, 2004). This type of competition plays a major role in general suppression and with "nutrient-dependent" pathogens such as *Pythium* and *Phytophthora* species, and involves microbial competition for nutrients and competition for infection sites and root colonisation (Diánez et al., 2005). A significant reduction of disease in compost amended soils was observed towards *F. oxysporum* f. sp. *radicis-lycopersici*, *Pyrenochaeta lycopersici*, *Pythium ultimum*, and *R. solani*, all known pathogens of tomato. These effects were associated with a marked increase in the percentage of siderophore producers within the root-zone of tomato (de Brito-Alvarez et al., 1995). Massive production of siderophores leads to reduced levels of iron which are essential for successful germination of the pathogen and penetration of the host. Fluorescent pseudomonads, well known for their siderophore production, can compete with *Fusarium* by suppression of *Fusarium* chlamydospore germination (Elad and Baker, 1985). Analyses of mutants lacking the ability to produce siderophores suggest that they contribute to suppression of certain fungal diseases (Duijff et al., 1994; Buysens et al., 1996). Thus, microbes with siderophore producing abilities can work against pathogens and can suppress their effect on crop/vegetable plants. The role of *Pseudomonas* spp. in disease suppression is well known. Recent studies also support their role as a competitor against pathogens in soil and reduce their direct effects on plant and also help in plant growth promotion (Kyselková and Moënne-Loccoz, 2012).

### 3.2. Antibiosis

Antibiosis is an antagonistic process mediated by microbes through specific or non-specific metabolites, lytic agents, enzymes, volatile compounds, or other toxic substances (Jackson, 1965; Fravel, 1988). The word antibiosis refers to an association of two organisms in which one is harmed or killed by the other. Production of antibiotics by compost microbes is thought to be a mechanism for suppressiveness against pathogens, although it has not yet been proven. Antibiotic production is very common among compost microbes, and the process can be detected by inhibition of growth of pathogenic microbes in a plate assay. Different bacterial species such as *Pseudomonas* and *Bacillus* are well known for their antibiotic production properties, and for their biocontrol of

several crop diseases. *B. cereus* UW85 produces the antibiotics zwittermicin A and kanosamine, known to be important in the biocontrol of oomycetes like *Phytophthora* (Silo-Suh et al., 1994; Milner et al., 1996). *Pseudomonas* spp., well known for their antagonistic property against *Fusarium* wilts, potato scab, apple replant disease, and take-all (Weller et al., 2002), are able to significantly reduce disease incidence and also protect plant roots from different infectious diseases (Haas and Défago, 2005).

*Trichoderma* and *Gliocladium* are also known to be capable of the production of antimicrobial compounds that can suppress disease by diverse mechanisms (Howell et al., 1993). Gliotoxin, an antibiotic produced by *Gl. virens* in composted mineral soil populated with natural microbiota, has been shown to effectively control damping-off of zinnia seedlings (*Zinnia elegans*) caused by *Py. ultimum* and *R. solani* (Lumsden et al., 1992). Recently *Zygosporium masonii* was reported as a new fungal antagonist against anthracnose disease in bell pepper caused by the pathogen *Colletotrichum capsici* (Ajith and Lakshmidevi, 2012).

### 3.3. Hyperparasitism

Hyperparasitism is a type of direct antagonism where a microorganism directly attacks a pathogen and kills it (Heydari and Pessarakli, 2010). In general, there are four major classes of hyperparasites, obligate bacterial pathogens, hypoviruses, facultative parasites, and predators. *Pasteuria penetrans*, a bacterial parasite known for its biological control activity against root-knot nematodes, is a perfect example of hyperparasitism (Pal and McSpadden Gardener, 2006). There are several examples of hyperparasitism in fungi where non-pathogenic microbes parasitise or lyse the mycelium, resting spores (oospores), hyphae or sclerotia of several pathogenic soil fungi such as *Pythium*, *Phytophthora*, *Verticillium*, *Rhizoctonia*, *Sclerotinia*, and *Sclerotium* (Diánez et al., 2005). Suppression of *R. solani* by *Trichoderma harzianum* is a common example of hyperparsitism (Chet and Baker, 1980). The frequent occurence of *T. harzianum* in composts is indicative of a compost where suppression of *R. solani* is taking place (Kuter et al., 1983). Some examples of multiple hyperparsitism also exist, where multiple hyperparasites such as *Acremonium alternatum*, *Acrodontium crateriforme*, *Ampelomyces quisqualis*, *Cladosporium oxysporum*, and *Gl. virens* together have the capacity to parasitise powdery mildew pathogens (Kiss, 2003). *Phytophthora capsici* oospores, known for their wide host range including Cucurbitaceae, Fabaceae, and Solanaceae families, are parasitised by beneficial actinomycetes and fungal species such as *Acremonium* spp., *Humicola fuscoatra* and *V. chlamydosporium* (Sutherland and Papavizas, 2008). Therefore, hyperparasites can control populations of many pathogens that play a major role in crop diseases (Fodor, 2011).

### 3.4. Systemic acquired resistance (SAR) and induced systemic resistance (ISR)

Systemic acquired resistance (SAR) and induced systemic resistance (ISR) are two forms of induced resistance to pathogenic attack. In both SAR and ISR, plant defenses are preconditioned by prior infection or treatment that results in resistance (or tolerance) against a pathogen or parasite (Vallad and Goodman, 2004). In general, SAR and ISR are defined as a state of enhanced defensive capacity developed by a plant when appropriately stimulated (Bakker et al., 2003). Great advances have been made over the past few decades to understand the physiological and biochemical basis of SAR and ISR. SAR can be induced by chemicals, pathogens, and beneficial soil microorganisms (Maurhofer et al., 1994; Pieterse et al., 1996; De Meyer and Höfte, 1997). A variety of microbes present in compost amended substrate are capable of inducing systemic resistance in plants (Wei et al., 1991; Liu et al., 1995). Interaction of the compost and pathogen infection is considered a critical factor for rapid activation of SAR-associated gene expression in cucumber plants grown in compost mix (Zhang et al., 1996). On the other hand, ISR is referred to as one of the most important mechanisms through which compost induces disease resistance to plants. Many bacterial and fungal isolates have been reported to turn on an ISR property in plants (van Loon et al., 1998). The microbial communities in composts are also known for triggering

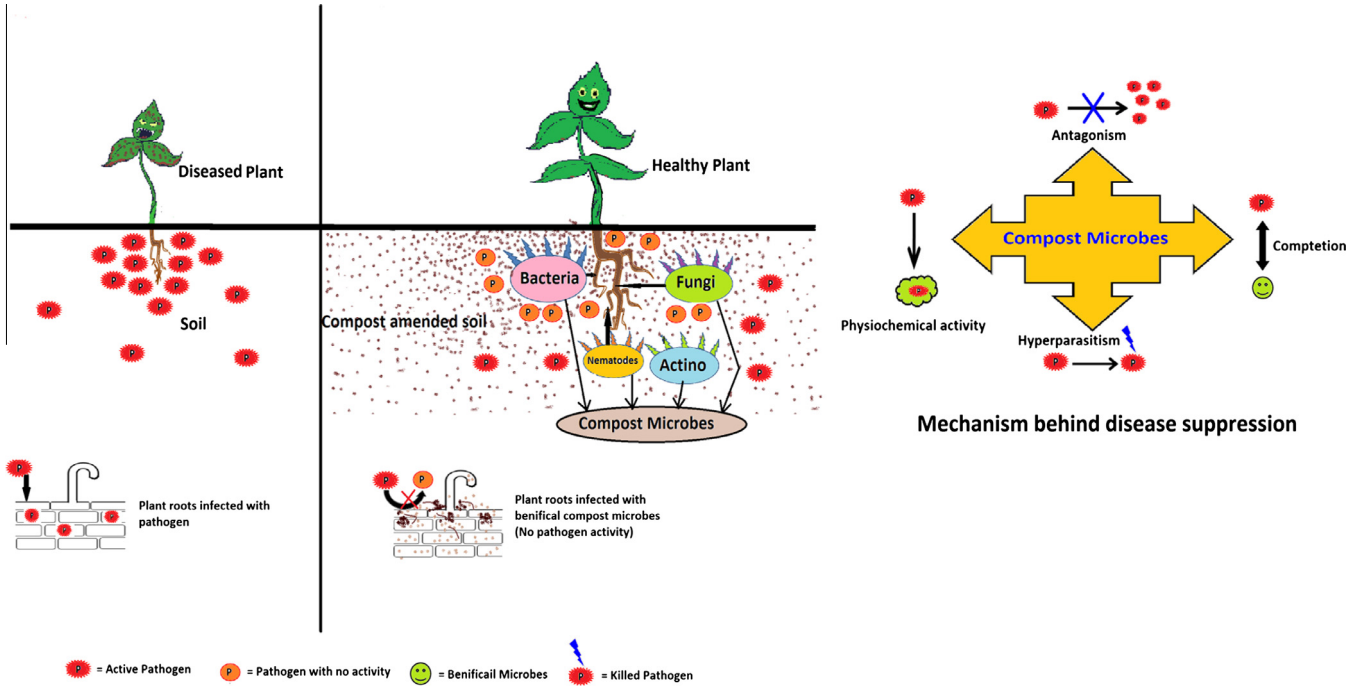



**Fig. 1.** Compost based disease suppression.

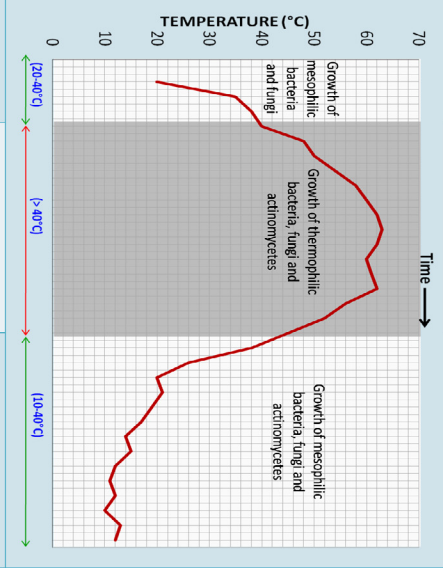
| Composting phases | Composting phases vs. Temperature | Major microbial communities during different composting phases | References |
|---|---|---|---|
| Mesophilic Phase (Early) |  | **Bacteria:** Pseudomonas, *Bacillus, Flavobacterium, Clostridium, Serratia, Enterobacter* and *Klebsiella*<br>**Fungi:** *Alternaria, Cladosporium, Mucor, Aspergillus, Humicola,* and *Penicillium* | Ghazifard et al., 2001<br>Chandna et al., 2013<br>Rawat et al., 2005 |
| Thermophilic Phase | | **Bacteria:** *Bacillus* and *Thermus*<br>**Fungi:** *Aspergillus, Mucor, Chaetomium, Humicola, Absidia, Sporotrichum, Thermoascus* and yeast.<br>**Actinomycetes:** *Streptomyces, Thermoactinomyces,* and *Thermomonospora* | Beffa et al., 1996b<br>Rawat et al., 2005<br>Makawai, 1980 |
| Cooling/ Maturation Phase (Late Mesophilic phase) | | **Bacteria:** *Bacillus, Flavobacterium, Pseudomonas* and *Cellulomonas*<br>**Fungi:** *Alternaria, Aspergillus, Bipolaris* and *Fusarium*<br>**Actinomycetes:** *Streptomyces* and *Thermopolyspora* | Ryckeboer et al., 2003<br>Ryckeboer et al., 2003<br>Corbaz et al., 1963 |



**Fig. 2.** Diagrammatic representation of the different phases of the composting process and the microbial communities involved in these phases (Epstein, 1997).

anatomical changes in plants (Pharand et al., 2002). Composted pine bark was found to be suppressive to *Pythium* root rot of cucumber and it was suggested that the resistance mechanism was systemic and related to enzymatic or hormonal activities (Zhang et al., 1996). Expression of pathogenesis-related (PR) genes in compost amended roots of tomato plants was studied and it was found that PR genes were expressed by plants even in the absence of pathogens. It was concluded that the expression of PR genes may be triggered by the microflora of the compost or could be associated with abiotic characteristics of the compost (Kavroulakis et al., 2006). A study of Sang and Kim (2011) indicated a compost mediated ISR property. The authors reported that a water extract from compost significantly reduced anthracnoses caused by *Colletotrichum coccodes* on pepper leaves and *Colletotrichum orbiculare* on cucumber leaves.

### 3.5. Ineffective pathogen proliferation

Normally, a pathogen propagule does not proliferate in the absence of a host (Lockwood, 1990). Chemical signals from the root or shoot exudates are required for host identification by the pathogen (Chen et al., 1988), but compost containing media can mimic these signals and trigger the germination of a pathogen before it comes in contact with its host. This is a probable reason behind the effectiveness of plant generated composts against soil-borne disease (Cheuk et al., 2005) and the reduction of pathogen activity level, even in the absence of plants (Yogev et al., 2006). A study of Cheuk et al. (2005) reported a significant reduction of *Fusarium* crown and root rot in tomato seedlings applied with compost amendment from several different batches, as a seed cover or plug substitute.

### 3.6. Physicochemical properties of compost

Evidence also suggests that the physicochemical properties of composts, namely nutrients and organic molecules such as humic, phenolic or bioactive compounds (Hoitink et al., 1997; Siddiqui et al., 2008; Spatafora and Tringali, 2012), may protect plants against disease through improved nutritional status, direct toxicity toward the pathogen or induced systemic resistance. Among all available technologies, mass spectrometry (MS) is most commonly used for the analysis of volatile organic compounds (VOC; Font et al., 2011), the chemical composition, and the presence of antimicrobial and antioxidant compounds in composts (Shahat et al., 2011).

In conclusion, the various mechanisms involved in compost based disease suppression suggest an important role of the microbial communities present in composts.

## 4. Compost microbiology

Diverse microbial consortia exist in compost, and their physiological activities are thought to be responsible for the improvement of plant growth and health. In addition to bacteria, fungi and actinomycetes which are known to be actively involved in the composting process, invertebrates and a few protozoans also play a major role in composting (Fig. 1). The different groups of microorganisms act on compost substrates in succession (Mehta et al., 2012). The composting process entails essentially three different phases, firstly, a mesophilic or moderate-temperature phase (up to 40 °C), followed by a thermophilic or high temperature phase (over 40 °C) and finally a mesophilic curing or maturation phase (up to 40 °C; Fig. 2). Different microbial communities play an important role during the various temperature phases. The initial decomposition is carried out by mesophilic microorganisms, which are responsible for a rapid degradation of the soluble and readily degradable compounds. During this degradation process, temperatures are initially mesophilic, but start to rise. Once temperatures exceed 40 °C, thermophilic microorganisms become more active and replace mesophilic microorganisms in the composting process. The thermophilic stage is one of the most important phases in composting, and the high temperatures allow microbes to break down proteins, fats, and complex carbohydrates like cellulose and hemicellulose, the major structural molecules in plants. This phase is also important because the high temperatures in the compost pile kill weed seeds and pathogenic organisms. As the availability of major structural compounds becomes

exhausted, the compost temperature gradually decreases and mesophilic microorganisms once again take over for the final phase of "curing," or maturation of the remaining organic matter. The ambient temperature of the compost during the curing phase helps to make the remaining organic matter more stable and suitable for plant use (Epstein, 1997).

### 4.1. Bacteria

During composting, the bacterial population is mainly responsible for substrate decomposition and heat generation. Bacteria constitute the majority of microorganisms in composting piles, with eubacteria and actinomycetes usually present in greater numbers than fungi (Davis et al., 1992; Rebollido et al., 2008). At the beginning of the composting process, mesophilic bacteria predominate. They include hydrogen-oxidising, sulfur-oxidising, nitrifying, and nitrogen-fixing bacteria. Most of these bacteria can also be found in topsoil. Mesophilic bacteria observed in the initial stages of composting include Gram-negative *Escherichia*, *Klebsiella*, *Aeromonas* and *Alcaligenes* species, as well as Gram-positive *Enterococcus* and *Bacillus* species (Ghazifard et al., 2001). Their populations increase exponentially during the initial stages of composting as they take advantage of the readily available sugars and starches. Heat is produced by their metabolic activity, and if conditions are suitable, compost temperatures begin to rise. When temperatures rise above 40 °C, thermophilic species take over from the mesophilic bacteria. The microbial populations during this phase are dominated by members of the genus *Bacillus* (Epstein, 1997; Partanen et al., 2010). Finstein and Morris (1975) reported that when temperatures reach 55 °C or higher, rod-shaped bacteria disappear and spore formers (e.g. longer rods) become more common. Bacteria such as *B. schlegelii*, *Hydrogenobacter* spp., and species of the genus *Thermus* (*T. thermophilus*, *T. aquaticus*) appear to be the main active microbes in hot composts with temperatures of 65 °C and above (Beffa et al., 1996b). Several *Bacillus* species have been recorded during the thermophilic stage of the composting process including the thermotolerant *B subtilis*, *B. polymyxa*, *B. pumilus*, *B. sphaericus*, and *B. licheniformis*, as well as thermophilic species like *B. stearothermophilus*, *B. acidocaldarius*, and *B. schleglii* (Ghazifard et al., 2001). Studies on the bacterial community during the thermophilic phase of composting revealed the presence of mainly Gram-positive bacteria (86% of all tested), along with some heterotrophic Gram-negative, aerobic, thermophilic bacteria ($10^7$–$10^{10}$ cells/g dw compost) belonging to the genus *Thermus*, a non-spore-forming group of bacteria (Beffa et al., 1996a). Interestingly however, a large number of mesophilic bacteria (more than 60% in the vegetative state) can be isolated from the thermophilic stages of composting (Nakasaki et al., 1985c). A possible reason behind mesophilic bacterial survival in the high-temperature phases of composting is the formation of microcolonies (Nakasaki et al., 1985b). As the activity of thermophilic bacteria decrease, the temperatures also decrease and mesophilic bacteria again predominate and are involved in compost curing and maturation. Both Gram-positive and Gram-negative organisms (Davis et al., 1992) are involved in the later mesophilic stages of composting.

### 4.2. Fungi

Fungi are known as the most important primary lignocellulose degraders involved in degradation of complex polymeric substrates (McCarthy and Williams, 1992). Because lignin and cellulose are closely associated in lignocellulosic material, it has been postulated they are depolymerised simultaneously (Deschamps et al., 1981; Davis et al., 1992). In composting, the moisture content is critical to fungal involvement, and the high moisture levels in composts generally favor bacteria over fungi (Finstein and Morris, 1975; Nakasaki et al., 1985a). Fungi are present in higher numbers when compost temperatures are moderate, and moisture levels lower. Nonetheless, mesophilic fungi, yeasts and molds have been observed in the initial stages of the composting process, despite temperature of up to 60–68 °C (Beffa et al., 1996b). Rawat et al. (2005) observed that diverse populations of mesophilic fungi existed from the start to the end of the composting process.

During the later stages of composting where temperatures between 40 and 60 °C occur, a high diversity of thermotolerant fungi including *Thermomyces* spp., *Penicillium duponti*, *Geotrichum candidum* (Finstein and Morris, 1975; Le Goff et al., 2010), *Cladosporium*, *Aspergillus*, *Mucor*, *Rhizopus*, and *Absidia* spp. have been observed (Ghazifard et al., 2001; Rawat et al., 2005). The optimum range for the survival of thermotolerent fungi is between 45 and 50 °C (Nakasaki et al., 1985b), and the disappearance of viable fungi in composts is well advanced before temperatures reach 60 °C, and is essentially completed by 65 °C (Finstein and Morris, 1975; Nakasaki et al., 1985b). It has also been reported that a consortium of microorganisms may be necessary to degrade lignocellulosic materials, however, interactions among species are not well documented (Davis et al., 1992). At the late mesophilic stage where temperatures decrease and the activity of thermophilic fungi also decrease, mesophilic fungi again begin to recolonise. Several studies on fungal communities during the later stages of composting reported that species of *Alternaria*, *Aspergillus*, *Bipolaris*, *Fusarium*, *Mucor*, *Rhizopus*, *Peziza*, *Phoma* and *Trichoderma* dominate (Grewal et al., 1988; Ryckeboer et al., 2003).

### 4.3. Actinomycetes

Actinomycetes, considered a higher form of bacteria, are primarily strict aerobic saprophytes. They form chains or filaments and are common in many environments (Goodfellow and Williams, 1983). They can utilise a wide range of carbon sources and sporulate prolifically (McCarthy and Williams, 1992). In composting processes, actinomycetes play an important role in degrading complex organic molecules such as cellulose, lignin, chitin, and proteins (Epstein, 1997). Golueke (1972) found Actinomycetes including *Thermophilus*, *Streptomyces* and *Micromonospora* spp. to be common in compost. These microorganisms were found to be ineffective competitors when nutrient levels are high because of their slow development compared to bacteria or fungi, but become more competitive as nutrient levels decreased (Nakasaki et al., 1985a). Although actinomycetes do not compete during the initial stages of composting, their enzymes enable them to chemically break down resistant debris, such as woody stems, bark, and newspaper that are relatively unavailable to most other forms of bacteria and fungi (Epstein, 1997). To facilitate the degradation of insoluble and polymeric carbon sources, actinomycetes secrete a range of extracellular enzymes (McCarthy and Williams, 1992). Some species of actinomycetes appear during the thermophilic phases, such as *Thermoactinomycetes* and *Saccharomonospora* spp. (Goodfellow and Williams, 1983). Certain species of actinomycetes are thermotolerent and found to be increasingly active at low nutrient levels and temperatures of up to 60 °C (Nakasaki et al., 1985a). The most commonly occurring actinomycetes found in the end of the composting process form long, threadlike branched filaments that resemble grey spider webs (Epstein, 1997).

### 4.4. Nematodes

Nematodes are the most abundant of the invertebrate decomposers and are suggested to play an important role in compost maturity. Steel et al. (2009) reported that immediately after the thermophilic phase peak, the compost nematode population was comprised of opportunists that fed solely on bacteria (members

of *Rhabditidae*, *Panagrolaimidae* and *Diplogastridae*). Afterwards, general opportunists who fed on either bacteria (members of *Cephalobidae*), or fungi (members of *Aphelenchoididae*) could be found. During the maturation phase, the bacterial feeding predator nematodes (*Mononchoides* sp.) became dominant and finally, in the most mature stage, the fungal feeding *Anguinidae* (mainly *Ditylenchus filimus*) dominated.

### 4.5. Protozoa

Protozoa make up only a small proportion of microbial biomass in compost. They are found in water droplets in compost and feed on bacteria and fungi (Epstein, 1997). In composting processes, Protozoa play an important role in the decomposition of organic matter, in disease suppression and in nutrient cycling. Protozoa feed on bacteria which have high nitrogen contents, thus these organisms can have a significant effect on the nitrogen cycle in compost (Hoorman and Islam, 2010). Therefore, it is essential to understand the diversity and distribution of these microbial components in compost ecosystems.

## 5. Methods for studying microbial diversity

There are two different approaches for studying compost microbial diversity: culture based methods and molecular methods.

### 5.1. Culture based methods to study microbial diversity

Culture based techniques for the investigation of microorganisms in compost traditionally has involved isolation of microorganisms using growth media such as Luria–Bertani medium, Nutrient agar, and Tryptic soy agar (Kirk et al., 2004). Recent advances in techniques and knowledge have allowed developments in cultivation procedures. Zengler et al. (2005) developed a technique for the large scale cultivation of microbes from different sources, involving the encapsulation of cells in gel microdroplets under low nutrient flux conditions. Most environmental samples comprise a large population of currently uncultured organisms, some of which could be cultivable given the opportunity to grow in the correct growth media. Oliver et al. (2005) reported unculturable organisms as "viable but nonculturable" (VBNC). These VBNC organisms are viable in their natural conditions but do not grow under laboratory conditions. It is estimated that these VBNC organisms could represent completely novel groups and may be abundant or very active but remain untapped by standard culture methods (Rastogi and Sani, 2011). The major limitation of culture-based techniques is that >99% of the microorganisms in any environment observed through a microscope are not cultivable by standard culturing techniques (Hugenholtz, 2002). In fact, only four major phyla of bacteria i.e. Proteobacteria, Firmicutes, Bacteroidetes, and Actinobacteria, are easily cultivable under laboratory conditions (Schloss and Handelsman, 2004). Compost microbial ecology is very complex and because of the inherent limitations of culture-based methods, the development of effective methods for studying the diversity, distribution, and behavior of microorganisms in compost ecosystems is essential (Amann et al., 1995; Torsvik et al., 1998).

### 5.2. Molecular methods: An alternative to culture based methods

Molecular approaches enable the investigation of microbial communities which are not able to be detected by traditional cultural methods, and can be used to detect specific microorganisms that play an important role in various ecological systems. The first step in any molecular study is the extraction of high quality nucleic acid from an environmental sample. Considerable efforts and a variety of different DNA-based techniques have been applied to the study of compost microbial populations (Cahyani et al., 2003; Schloss et al., 2003; Franke-Whittle et al., 2005, 2009; Hultman et al., 2010; Fritz et al., 2012). Broadly speaking, molecular techniques can be classified into two major categories: partial community analysis approaches (Table 1) and whole community analysis approaches, depending on their ability to reveal microbial diversity structure and function (Rastogi and Sani, 2011).

In comparison to PCR-based molecular approaches that target a single gene, whole community analysis approaches offer a more comprehensive view of the genetic diversity of an environmental sample. These techniques, which include DNA–DNA hybridisation, guanine-plus-cytosine (G + C) fractionation,whole genome sequencing and metagenomics, attempt to analyse all the genetic information present in DNA extracted from an environmental sample or a pure culture. DNA–DNA hybridisation allows genome-wide comparison between organisms. Although DNA–DNA hybridisation techniques were originally developed for pure culture comparisons, the method can also be used in whole microbial community analysis (Goris et al., 2007; Rastogi and Sani, 2011).

The G + C content of DNA from bacteria belonging to different phylogenetic groups differ, and fractionation of total community DNA can be achieved using density-gradient centrifugation based on the G + C content (Nüsslein and Tiedje, 1999; Rastogi and Sani, 2011). Analysis of the different fractions of DNA can be used to indicate the relative abundance of various taxa of microorganisms in a sample. This technique can be combined with other molecular techniques such as DGGE/ARDRA to better assess total community diversity (Rastogi and Sani, 2011).

Whole-genome sequencing has resulted in unprecedented insights into microbial processes at the molecular level (Huson et al., 2007). Metagenomics, or community genomics, is the study of all microbial genomes present in an environmental sample. The technique is based on the theory that the entire genetic composition of microorganisms in an environmental sample can be sequenced and analysed in the same way as the genome of a pure bacterial culture is sequenced and analysed (Riesenfeld et al., 2004). Metagenomic investigations have been conducted in numerous environments, including compost (Dougherty et al., 2012; Yeh et al., 2013).

Partial community analysis includes nucleic acid approaches where the polymerase chain reaction (PCR) is used to amplify total DNA/RNA extracted from an environmental sample. Analysis of 16S rDNA genes from bacterial communities as well as 18S rRNA genes and internal transcribed spacer (ITS) regions from fungal communities have been widely used for the analysis of microbial communities. Partial community analysis approaches are listed in Table 1, and include genetic fingerprinting (Muyzer, 1999), clone library methods (De Santis et al., 2007), fluorescence *in situ* hybridisation (FISH; Amann et al., 1995), DNA microarrays (Gentry et al., 2006), quantitative PCR (Q-PCR) or real-time PCR (Bustin et al., 2005; Smith and Osborn, 2009), DNA/RNA stable isotope probing (Peng et al., 2013) and microbial lipid analysis (Larkin et al., 2011).

Among these molecular approaches, genetic fingerprinting by denaturing gradient gel electrophoresis (DGGE), DNA sequencing of PCR amplified genes and Q-PCR are the most commonly and widely used tools for the determination of the degree of diversity and for the detection of different compost microorganisms, bypassing the need for isolation and cultivation (Muyzer, 1999; Dees and Ghiorse, 2001; Green et al., 2004; Partanen et al., 2010). Although these molecular tools have significantly advanced microbial ecology studies, there are limitations with such approaches. Due to the requirement of extracted DNA for PCR amplification and subsequent community analysis, these studies are subject to various flaws, namely, biases in DNA extraction efficiency, PCR amplification biases (Farrelly et al., 1995; Suzuki and Giovannoni, 1996; Polz

**Table 1**
Partial community level analysis approaches used in compost studies.

| Method | Method based on | Advantages | Disadvantages | Phylogenetic identification | Throughput | References |
|---|---|---|---|---|---|---|
| DGGE/TGGE | Sequence differences | Sequence information from excised DGGE bands | Limited sensitivity, gel to gel variability, partial 16S rRNA gene sequences | Yes | High | Ueno et al. (2001), Ros et al. (2006), Székely et al. (2009), Bonito et al. (2010) |
| ARDRA | Sequence differences in community DNA | Detection of structural changes in relatively simple microbial communities | More labor- and time-intensive than other molecular methods | No | High | Dees and Ghiorse (2001), Singh et al. (2012) |
| TRFLP | Restriction site differences | High sensitivity | Overestimation of diversity due to non-specific or incomplete digestion Multiple separate restriction digests for higher resolution | Possible | High | Tiquia (2005), Pérez-Piqueres et al. (2006), Tatti et al. (2012) |
| SSCP | Conformational differences | High sensitivity | Formation of more than one stable conformation resulting in the presence of extra bands | Yes | High | Thummes et al. (2007), Macedo et al. (2007), Fracchia et al. (2006) |
| ARISA | Differences in intergenic spacer region length | High sensitivity, simple technique | Shorter amplicons are over-represented >1 intergenic space region in a genome | No | High | Schloss et al. (2003) |
| RAPD | Random amplification of genomic DNA | No knowledge of DNA sequence of targeted genome needed | High quality DNA needed, resolving power lower than other methods | No | High | Zhang et al. (2002) |
| Clone library methods | Sequence differences | Accurate phylogenetic identification of clone sequences | Time demanding cloning process, and data analysis | Yes | Low | Blanc et al. (1999), Danon et al. (2008), Sundberg et al. (2011) |
| FISH | Hybridisation of rRNA with flourescently labeled probes | Quantiative, visualisation of probed cells | Autoflouresence, necessity of metabolically active target cells | Yes | Low | Iverson and Maier (2009), Hiraishi et al. (2003) |
| DNA microarrays | Hybridisation between complementary DNA strands | Parallel detection of 16S rRNA genes | High cost, quantification not possible | Yes | High | Franke-Whittle et al. (2005, 2009), Danon et al. (2008), Hultman et al. (2008), Sundberg et al. (2011), Fritz et al. (2012) |
| Quantitative PCR | Amplification and detection of PCR products in real-time | Simple, reproducible, sensitive, and quantitative | Optimisation can be time consuming, variation in rRNA copy number in different microorganisms | Yes | High | Wery et al. (2008), Innerebner et al. (2006), Yamada et al. (2007) |
| DNA/RNA Stable isotope probing | Incorporation and metabolism by microorganisms of rare stable isotope or radioisotope | Concurrent examination of metabolic function and taxonomic identity | Not as sensitive as PFLA-SIP, biased incubation conditions | Yes | Low | Peng et al. (2013) |
| Microbial lipid analysis | Signature fatty acids present in different organisms that can be used to differentiate major taxonomic groups | Culture independent, relatively easy and fast, inexpensive | Low sensitivity, underestimation of diversity, linking PLFA to microbial communities difficult | Possible in some cases | High | Larkin et al. (2011), Verdenelli et al. (2012) |

*Note:* DGGE/TGGE – denaturing gradient gel electrophoresis/temperature gradient gel electrophoresis; ARDRA – amplifed rDNA restriction analysis; TRFLP – terminal restriction fragment length polymorphism analysis; SSCP – single strand conformation polymorphism; ARISA – automated ribosomal intergenic spacer analysis; RAPD – random amplified polymorphic DNA; FISH – fluorescence *in situ* hybridisation.

and Cavanaugh, 1998), and the potential formation of PCR artifacts (Wang and Wang, 1997). Thus, studies using PCR-amplified templates can reflect a biased microbial community composition. Nonetheless, the use of PCR to amplify target DNA greatly increases the detection sensitivity of microorganisms in any environmental sample in comparison to non-PCR based methods.

### 5.2.1. Genetic fingerprinting–Denaturing Gradient Gel Electrophoresis (DGGE)

Fingerprinting techniques result in the generation of different patterns, reflective of the microbial diversity in a particular environmental sample. Included in this group of techniques are DGGE/TGGE – denaturing and temperature gradient gel electrophoresis (Muyzer et al., 1993), ARDRA – amplifed rDNA restriction analysis (Singh et al., 2012), TRFLP – terminal-restriction fragment length polymorphism analysis (Liu et al., 1997), SSCP – single strand conformation polymorphism (Fracchia et al., 2006), RAPD – random amplified polymorphic DNA (Zhang et al., 2002), and ARISA – automated ribosomal intergenic spacer analysis (Schloss et al., 2003; Nocker et al., 2007).

DGGE is an electrophoretic fingerprinting method used to identify single base differences in DNA segments. Separation techniques on which DGGE is based were first described by Fischer and Lerman (1983).

DGGE of PCR-amplified 16S rDNA fragments has been used to investigate microbial communities in many different environmental samples, including soils, composts and aquatic environments (Kowalchuk et al., 1999; Ueno et al., 2001; Schäfer and Muyzer, 2001; Székely et al., 2009). DNA from individual DGGE bands can be excised, re-amplified and subjected to sequence analysis. The excision and sequencing of DGGE bands provides information regarding the communities of the environmental sample investigated Székely et al. (2009).

Fungal communities have been also investigated with PCR–DGGE in the rhizospheres of marram grass (Kowalchuk et al., 1997), wheat (Smit et al., 1999), vanilla beans (Roling et al., 2001), wood (Vainio and Hantula, 2000), soil (van Elsas et al., 2000; Pennanen et al., 2001), and corn silage (May and VanderGheynst, 2001). PCR-DGGE analysis in fungi has been performed most often using primer sets targeting the 18S rDNA and 28S rDNA (Marshall et al., 2003). Fungal communities in the different stages of a composting process were assessed using DGGE by the analysis of DNA sequences from rDNA clone libraries in a study by Bonito et al. (2010).

DGGE represents a powerful tool for monitoring microbial communities (Bull et al., 2000), providing a cultivation-independent option for the analysis of complex microbial communities (Muyzer et al., 1993), and is a very useful tool in characterising composts (Székely et al., 2009; Fernández-Gómez et al., 2012).

*5.2.2. Clone library approach*

The construction of clone libraries from phylogenetic marker genes such as the 16S rRNA or 18S rRNA, was, prior to the onset of pyrosequencing technology, the most frequently used means of assessing microbial community composition and diversity from different environmental samples (Leigh et al., 2010). The sequence analysis of clone libraries has provided an unparalleled level of phylogenetic resolution due to the long read lengths generated by Sanger sequencing technology. Clone library analysis has been conducted to investigate the microbial communities in numerous compost studies, including those by Blanc et al. (1999), Danon et al. (2008), Hultman et al. (2008), Partanen et al. (2010) and Sundberg et al. (2011). As with all PCR-based systems for community analysis, clone libraries are subject to PCR amplification biases, which can affect the results of cloning. Nonetheless, cloning approaches have allowed great advances into the knowledge of microbial communities in composts.

*5.2.3. Fluorescence in situ hybridisation (FISH)*

Fluorescence *in situ* hybridisation (FISH) of whole cells using 16S rRNA targeted oligonucleotide probes is a powerful technique which can be used to evaluate the phylogenetic identity, morphology, number, and spatial arrangements of microorganisms in different environmental samples (Hugenholtz et al., 2002). The probes used can be designed to specifically target narrow to broad phylogenetic groups by virtue of the variable evolutionary conservation within the 16S rRNA molecule. FISH has been used to investigate the microbial ecology of many different environmental samples, including composts. The relationship between compost amendment, plant biomass produced, and bacterial root colonisation was measured by FISH in a study by Iverson and Maier (2009). In another study, the microbial community changes during the start-up operation of flowerpot-using fed-batch reactors for the composting of household biowaste was studied using rRNA-targeted FISH (Hiraishi et al., 2003). Although there are a number of problems associated with FISH such as poor cell permeability, ribosome accessibility and content and sample autofluorescence, the method allows the visualisation of different microorganisms in their *in situ* environment to be studied.

*5.2.4. DNA microarrays*

Nucleic acid microarrays provide a powerful tool for the parallel detection of 16S rRNA genes (or other genes of interest), thus allowing the identification of microorganisms from different environments (Guschin et al., 1997; Small et al., 2001; Loy et al., 2002; Franke-Whittle et al., 2005, 2009). DNA microarrays are based on the hybridisation of two complementary strands of nucleic acids, and offer the possibility to analyse an entire array of microorganisms concerning their presence or absence in a particular sample, in a single experiment. As with all molecular techniques, the application of microarrays for routine diagnostic work in microbial ecology and other fields is hindered by a lack of standardisation and insufficient evaluation of newly developed arrays (Loy and Bodrossy, 2006). Also, issues relating to the potentially low levels of target microorganisms in environmental samples have hampered the application of such diagnostic arrays (Cook and Sayler, 2003). In the case of the compost environment and compost production, microarray technology offers a tremendous potential for process monitoring, the detection of pathogens, and the detection of beneficial microbial populations.

The COMPOCHIP microarray is a 16S rRNA-gene based microarray. It includes 414 oligonucleotide probes specific for human, animal and plant pathogenic bacteria, as well as probes targeting plant growth promoting organisms and composting degrading bacteria (Franke-Whittle et al., 2005, 2009). The array has been used in several studies to investigate the microbial communities of different types of compost (Danon et al., 2008; Sundberg et al., 2011).

A method based on a ligation detection reaction (LDR; Busti et al., 2002; Castiglioni et al., 2004) was adapted for the development of a microarray specific to compost by Hultman et al. (2008). The microarray was designed to target composting fungi, and was first optimised with pure cultures and clones, after which real environmental samples were used. A comparison of fungal diversity obtained by cloning and sequencing and with the microarray, indicated that the results of the LDR microarray test appeared to give reliable results. The LDR microarray has a detection limit of 0.04% (target DNA/total DNA), a sensitivity level similar to that of quantitative-PCR (Hultman et al., 2008).

*5.2.5. Real-time PCR*

Real-time PCR allows a reproducible and sensitive detection and quantitation of specific microbial populations, and numerous different real-time PCR technologies exist (Monis and Giglio, 2006). Despite the high level of detection sensitivity attainable by real-time PCR, the method is not appropriate for studies requiring the enumeration of large numbers of target species in any particular sample. Quantitative PCR methods are subject to all of the biases associated with PCR, and real-time PCR based on the analysis of rRNA genes are also subject to a quantitative uncertainty of the numbers of rRNA genes (rrn operons) per genome. Nevertheless, the technology has been successfully applied to composting environments, and allows an accurate quantification of various targets of interest (Innerebner et al., 2006; Yamada et al., 2007; Wery et al., 2008). In a study by Innerebner et al. (2006), the diversity and community composition of ammonia oxidisers in soil from a long-term crop rotation field experiment (>10 years) where four major types of compost (from organic waste, cattle manure, green waste and sewage sludge) was investigated.

In conclusion, the use of molecular tools has allowed a greater knowledge of the microbial communities present in different soils, composts and plants to be obtained, and will hopefully help in the identification of key microbes involved in disease suppression and plant growth promotion in future studies.

## 6. Key compost microbes and their role in disease suppression

Microbes that are involved in controlling different plant diseases can be classified as competitive saprophytes, facultative plant symbionts or facultative hyperparasites. These microbes can generally survive on dead plant material, but they are also able to colonise and express biocontrol activities while growing on plant tissues (Pal and McSpadden Gardener, 2006). The composting process, where raw materials are degraded and converted into humus like structure, provides an ideal environment for the

development of these microbes. The large and less decomposed particles of organic matter in compost do not seem to contribute directly to disease control, but as they decrease in size through decomposition, their effectiveness increases. There are several reports on beneficial microbes in compost, which compete with pathogens and thus, suppress their activity. Microbial communities present in compost amended container media function as biocontrol agents against disease caused by *Pythium* and *Phytopthora* spp. (Hardy and Sivasithamparam, 1991; Boehm et al., 1993). A significant reduction in cucumber wilt (up to 61%), caused by *F. oxysporum* f. sp. *cucumerinum*; was also recorded in *in vivo* and *in vitro* conditions after inoculation with the bioagent *B. subtilis* SQR 9 (Cao et al., 2011).

*Trichoderma* spp., well known for the control of different plant diseases, is often used commercially for plant disease reduction (Verma et al., 2007). *T. asperellum* strain T34, isolated from *Fusarium*-suppressive compost (Trillas and Cotxarrera, 2003), has been reported to control *Fusarium* wilt in tomato and carnation plants (Cotxarrera et al., 2002; Sant et al., 2010) and *R. solani* in cucumber plants (Trillas et al., 2006). Competitive strategies of *Trichoderma* spp. include mycoparasitism, antibiosis, and nutrient/space competition. In addition, *Trichoderma* spp. can inhibit or degrade pectinases and other enzymes that are essential for plant-pathogenic fungi and may also control disease development by inducing resistance or promoting growth of the plant host (Harman et al., 2004; Verma et al., 2007). *Trichoderma* spp. are also considered as avirulent plant symbionts where they can colonise root surfaces and penetrate into the epidermis and a few cells below the epidermis (Harman et al., 2004). *Trichoderma* spp. (T34) have also been reported to be able to reduce foliar pathogens numbers when applied to the roots of host plants (Segarra et al., 2007, 2009).

Non-pathogenic strains of *F. oxysporum* are also well known for their biocontrol activity of pathogenic *Fusarium* diseases (Louvet et al., 1976). Protective strains of *F. oxysporum* occur naturally in almost all agricultural soils including different composts (Alabouvette et al., 2001; Cotxarrera et al., 2002) and live their life partly inside plant tissue as endophytes, without harming plant tissue (Ito et al., 2005). Non-pathogenic *F. oxysporum* have been shown to control *Fusarium* wilt in many crops, including asparagus, banana, basil, carnation, chickpea, cucumber, cyclamen, gladiolus, melon, tomato, spinach and watermelon (Rouxel et al., 1979; Magie, 1980; Garibaldi et al., 1986; Mandeel and Baker, 1991; Katzube et al., 1994; Minuto et al., 1995; Larkin et al., 1996; Fuchs et al., 1997; Hervas et al., 1997; Larkin and Fravel, 1999; Elmer, 2004; Forsyth et al., 2006). In contrast to other biocontrol agents (BCAs) such as *Trichoderma* spp., protective strains of *F. oxysporum* are mostly effective against pathogenic *F. oxysporum*. The advantage of non-pathogenic *F. oxysporum* in the control of the same and closely related pathogens is that both require similar environmental conditions, thus creating a competition between them when both are present (Larkin and Fravel, 2002). No parasitism, hyphal interference or toxin production was observed between pathogenic and non-pathogenic strains of *F. oxysporum*. The reason hypothesised for this suppression is competition with the pathogen for infection site and nutrients (Freeman et al., 2002). Only a few papers have reported on the efficacy of non-pathogenic strains of *F. oxysporum* against *Py. ultimum* (Benhamou et al., 2002), *Ph. capsici* (Silvar et al., 2009) and *V. dahliae* (Pantelides et al., 2009). Moreover, some endophytic strains of non-pathogenic *F. oxysporum* have been shown to reduce damage caused by *Meloidogyne incognita* in tomato roots (Dababat and Sikora, 2007).

Besides the above mentioned fungal bioagents, some bacteria commonly present in compost including *Pseudomonas*, *Bacillus*, *Burkholderia*, *Lysobacter*, *Pantoea*, and *Streptomyces*, are well known for their disease suppressiveness and plant growth promoting activity (PGPR; Castano et al., 2011). Sporulating Gram-positive bacteria like *Bacillus* species have been used successfully in plant disease control (Kloepper et al., 2004). *B. cepacia* has shown great potential to be used as an effective biocontrol agent of *Fusarium* dry rot of stored potatoes (Recep et al., 2009). *Bacillus* strains under *in vitro* conditions showed antagonism against different species of *Sclerotinia* and *Fusarium* (Principe et al., 2007). Antagonist *Bacillus* strains produce bioactive compounds belonging to the cyclic lipopeptides group with high stability attributable to their structure (Souto et al., 2004). *B. subtilis* produces several kinds of antibiotics, such as bacillomycin (Peypoux et al., 1980), iturin (Peypoux et al., 1978), mycosubtilin (Peypoux et al., 1986) and bacilysin (Loeffler et al., 1986). However, the bacteria require a suitable substrate for bioactive compound production in soil. Investigation into the control of *St. scabies* in potato by *B. subtilis* revealed that more antibiotic was produced when the bacteria were grown on a water extract of soybean. This shows the importance of the carrier for the production of the secondary metabolite from bacteria (Weinhold and Bowman, 1968). Tomato plants inoculated with *B. subtilis* showed biocontrol activity against damping off and root rot disease and gave high yields of tomato (Morsy, 2005; Zaghloul et al., 2007). A possible explanation for growth promotion and pathogen resistance by *B. subtilis* is that the microbes compete with other microorganisms that would otherwise adversely affect the plant and activate the host defense system. By doing so, the plant is poised to resist potential pathogens. It also makes certain nutrients (e.g. phosphorus and nitrogen) more readily available to the plant (Nagorska et al., 2007). Shanmugam and Kanoujia (2011) hypothesised that activation of the host defense system could be one mechanism for enhanced tomato growth. *B. subtilis* strains isolated from cow dung have also been reported for their antimicrobial activity against *F. oxysporum* and *Botryodiplodia theobromae* on postharvest rotting fungi of yam tubers (Ray et al., 2000; Naskar et al., 2003).

The genus *Pseudomonas*, ubiquitous in soil and compost environments, contains endophytic bacteria known for their PGPR and antagonistic properties towards different pathogens (Gray and Smith, 2005; Ryckeboer et al., 2003; Gibello et al., 2011). The endophytic nature of *P. fluorescens* means that the bacterium competes with pathogens, stimulates plant growth and reduces the incidence of plant disease (Kloepper and Schroth, 1978). Several fluorescent pseudomonad species such as *P. fluorescens* (Sakthivel and Gnanamanickam, 1987), *P. putida* (de Freitas and Germida, 1991), *P. chlororaphis* (Chin-A-Woeng et al., 1998) and *P. aeruginosa* (Anjaiah et al., 2003) have been used to suppress pathogens as well as to promote growth and yields in many crop plants. Studies on the efficacy of *P. fluorescens* for controlling *Fusarium* wilt reported that *P. fluorescens* produces antifungal compounds. This property, along with siderophore production and nutrient competition, leads to control of *Fusarium* wilt disease in several plant types (Cook and Baker, 1983; Chen et al., 1995). Fishal et al. (2010) reported the ability of the endophytic bacteria *Pseudomonas* sp. (UPMP3) and *Burkholderia* sp. (UPMB3) to control *F. oxysporum* f. sp. *cubense* race 4 (FocR4) under glasshouse conditions. A 51% reduction of *Fusarium* wilt disease severity in banana plants after inoculating with *Pseudomonas* sp. (UPMP3) was reported. Later studies on the biocontrol property of *P. fluorescens*, suggested that *P. fluorescens* produces a broad spectrum antibiotic 2,4-diacetylphloroglucinol (Keel et al., 1996) that inhibits the mycelial growth of *F. oxysporum* (Schouten et al., 2004). Bolwerk et al. (2003) studied the antagonistic activity of *P. fluorescens* against *F. oxysporum* on tomato roots, and hypothesised that tomato plants produce root exudates that are utilised by bacteria and prevent pathogens from colonising.

The presence of beneficial microbes like *Bacillus* spp., *Enterobacter* spp., *Pseudomonas* spp., *Streptomyces* spp., *Trichoderma* spp. and *Gliocladium* spp. in compost indicates a disease suppressiveness

property of that compost (Hoitink and Grebus, 1994). The levels of nutrients and plant disease suppressiveness are thought to be increased in composts by the addition of these beneficial microbes.

## 7. Enrichment of improved disease suppressive properties and enhanced degradation processes in compost

The disease suppressiveness property of composted biowastes has been well reported (Schüler et al., 1989; Tuitert et al., 1998; Erhart et al., 1999; Lievens et al., 2001), however, the degree of disease suppression for biowaste composts is largely unpredictable. Blok et al. (2002) reported that disease suppressiveness of commercial biowaste composts towards *Py. ultimum*, *P. cinnamomi* and *R. solani* differed considerably, ranging from slightly conducive to highly disease suppressive. Therefore, specific disease suppression of composts can only be guaranteed when composts are colonised by specific antagonists during composting (Hoitink et al., 2001).

In order to enhance degradation processes and the degree of composting humification, complex microorganisms (*B. casei*, *Lactobacillus buchneri* and *Candida rugopelliculosa*) and ligno-cellulolytic (*Trichoderma* and White-rot fungi) microorganisms were respectively inoculated in the composting process in a study by Wei et al. (2007). It was found that inoculations with microbes led to a greater degree of aromatisation of humic acids than in the control process with no microbes. This indicated that inoculation with microbes in composting can improve the degree of humification and maturation processes (Wei et al., 2007).

The effect of inoculation of *Azotobacter* and phosphate solubilising microorganisms during composting was studied by Kapoor et al. (1983). It was observed that inoculation of *Azotobacter* into already decomposed material resulted in an increased nitrogen content, but inoculation of *Azotobacter* at the start of composting did not increase nitrogen content.

The addition of microbes isolated from different composts and biofertilisers could be used in an approach for preparing a multifunctional biofertiliser. Adding thermo-tolerant, phosphate-solubilising microbes including bacteria, actinomycetes, and fungi can shorten the period of maturity, improve the quality, increase the soluble phosphorus content, and enhance the populations of phosphate-solubilising and proteolytic microbes in biofertilisers (Chang and Yang, 2009). Application of microbes such as *Agrobacterium*, *Bacillus*, *Enterobacter*, *Pseudomonas*, *Aspergillus*, *Trichoderma* and *Glomus* to the roots of plants, to soils, and in fertilisers has been shown to release soluble phosphorus, promote plant growth, and protect plants from pathogen infection (Rodriguez and Fraga, 1999; Rudresh et al., 2005; Zayed and Abdel-Motaal, 2005a,b; Biswas and Narayanasamy, 2006; Ouahmane et al., 2007). In addition, cellulolytic organisms including the fungal species, *Trichoderma*, *Humicola*, *Penicillium*, and *Aspergillus* (Gautam et al., 2009) and a wide variety of Gram-positive and Gram-negative species including *Clostridium thermocellum*, *Streptomyces* spp., *Ruminococcus* spp., *Pseudomonas* spp., *Cellulomonas* spp., *Bacillus* spp., *Serratia*, *Proteus*, *Staphylococcus* spp., and *B. subtilis* (Wood and Bhat, 1988; Gautam et al., 2010) play an important role in the degradation of cellulosic material in composts and in municipal solid wastes which are composed of 40–50% cellulose (Rani and Nand, 2000; Gautam et al., 2010). Various biological studies have been carried out to identify the major microbiological agents responsible for biodegradation. Presently, concerns exist regarding the degradation of organic wastes into valuable resources by the application of potential degrading microbes. Few microbes that are capable of secreting a complex of cellulase enzymes which have practical application in the enzymatic hydrolysis of cellulose as well as in the biodegradation of organic municipal solid waste (Gautam et al., 2012) are known. However, the application of these microbes to compost could increase the degradation process and also the efficacy of compost towards the control of different soil-borne plant pathogens.

Studies on compost enrichment through microbes also suggest the role of *B. smithii* F18 in converting agricultural and animal wastes into biofertiliser. Mixed cultures of *B. smithii* F18 and other functional microbes can convert agricultural, animal and food wastes, vegetable and fruit market wastes, and poultry and livestock wastes into multi-functional biofertilisers for bioresource recycling and sustainable agriculture applications. Therefore, inoculating beneficial microbes into agricultural and animal wastes is a useful approach for preparing multi-functional biofertilisers (Chang and Yang, 2009). The inoculation of these functionally active and pathogen suppressing microbes into less effective composts could improve the quality of composts for their disease suppressiveness and plant growth promoting properties.

## 8. Conclusion and perspectives

The reduction of organic waste products through composting yields a nutritionally rich product, which can be used to help fight plant disease, reducing the need for the application of chemicals. Successful biocontrol of plant disease requires an intricate array of interactions. Understanding these interactions at the molecular and ecological levels will make possible the rational development of biocontrol for agriculture (Mehta et al., 2012).

The microbial communities present in compost are considered to be one of the major driving forces for plant pathogen suppressiveness of composts (Schönfeld et al., 2003; Joshi et al., 2009). The high population density of fluorescent pseudomonads, actinomycetes and heterotrophic fungi in growing media amended with adequately mature composts has been shown to be responsible for suppression of various pathogens (Mehta et al., 2012). Studies on compost enrichment with beneficial microbes, such as *Trichoderma*, and non-pathogenic strains of *F. oxysporum* and *V. biguttatum* have shown increased disease suppressiveness of compost (Postma et al., 2003; Trillas et al., 2006). However, there are still uncultured, and thus unknown, potentially disease suppressive microbes present in composts that when isolated, will allow an expansion of our current knowledge on the disease suppressive property of composts.

Therefore, a better understanding of the microbial interactions that enhance or detract from disease biocontrol will determine the long-term success of biocontrol. In particular, attention needs to be paid to non-culturable members of the root associated and soil communities, because these microorganisms may be numerically and functionally significant in these environments, but have not yet been studied.

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