Chapter 5
Natural Mechanisms of Soil Suppressiveness Against Diseases Caused by *Fusarium*, *Rhizoctonia*, *Pythium*, and *Phytophthora*

Prashant P. Jambhulkar, Mahaveer Sharma, Dilip Lakshman, and Pratibha Sharma

5.1 Introduction

Soilborne fungal and oomycete plant pathogens are among the major factors limiting the productivity of agroecosystems and are often difficult to control with conventional strategies such as the use of resistant host cultivars and synthetic fungicides. Due to limitations in the effectiveness of fungicides and a lack of successful plant-based resistance, enhancement of soil-based natural disease suppression could be an effective option to control disease (Weller et al. 2002). This suppressive effect has been attributed to diverse microbial communities of bacteria, fungi, and protozoa and is reported to affect pathogen survival, growth in bulk and rhizosphere soil, and root infection (Barnett et al. 2006). Maintaining a high level of organic matter (OM) on the soil surface or incorporation of OM into the soil is generally associated with lower incidence and severity of root diseases. Natural disease-suppressive soils probably are the best examples in which the indigenous microflora effectively protects plants against soilborne pathogens. Soil microbes

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P.P. Jambhulkar (✉)
Agricultural Research Station (MPUAT), Banswara 327001, RJ, India
e-mail: ppjambhulkar@gmail.com

M. Sharma
ICAR-Directorate of Soybean Research, Khandwa Road, Indore 452001, India
e-mail: mahaveer620@gmail.com

D. Lakshman
Floral and Nursery Plant Research Unit and Sustainable Agricultural System Laboratory, USDA-, Beltsville, MD 20705, USA
e-mail: Dilip.Lakshman@ars.usda.gov

P. Sharma
Division of Plant Pathology, Indian Agricultural Research Institute, New Delhi 110012, India
e-mail: psharma032003@yahoo.co.in

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and disease-causing phytopathogens share the common rhizosphere and their interaction prior to crop sowing and/or in the rhizosphere, subsequently influencing both plant growth and productivity (Penton et al. 2014).

Suppressive soils to soilborne plant diseases have been described as “those in which disease development is minimal even in the presence of a virulent pathogen and susceptible plant host” (Mazzola 2007). Though some experts (Bruehl 1987) argue for limiting the use of the term disease suppressiveness to situations involving a clear biological component, there is a plethora of evidence for the role of both biotic and abiotic elements of the soil having roles in disease suppression. Physical and chemical characteristics of the soil, including pH, OM, and clay content, can operate in the suppression of plant diseases directly or indirectly through their impact on soil microbial activity. Although these abiotic characteristics of the soil can contribute to disease suppression, soil suppressiveness (SS) is often directly or indirectly a function of the activity of soil microorganisms or microbial metabolites. Another frequently quoted definition of “suppressive soil” from Baker and Cook (1974) is “soils in which the pathogen does not establish or persist, establishes but causes little or no damage, or establishes and causes disease for a while but thereafter the disease is less important, although the pathogen may persist in the soil.” However, it is difficult to precisely define the term “suppressive soil” (Hornby 1983) simply because there are many types of suppressiveness acting in the rhizosphere. The terms “pathogen suppressive” and “disease suppressive” have often been used interchangeably (Weller et al. 2002), but the former refers to the suppression of the pathogen growing saprophytically on decaying OM in the soil or surviving in the soil and is suppressed when the pathogen is growing parasitically in the host, while in latter case the term usually refers to suppression of the pathogen growing as parasite in the host (Hornby 1983). On the basis of speed with which soils become suppressive, soil suppressiveness (SS) is distinguished as induced suppression which does not show maximum effectiveness even immediately after application of inductive treatment, and in some cases monoculture (MC) is required to achieve maximum effectiveness. On the other hand, “introduced suppression” (IS) was found to be effective immediately after treatment. Hoper and Alabouvette (1996) distinguished pathogen suppression (the ability of the soil to limit the inoculum density of the pathogen and its saprophytic activity) with disease suppression (the capacity of the soil to restrict disease development) under ideal host–pathogen environmental conditions. The disease suppressiveness can be designated in soils in which disease development is minimal even in the presence of a virulent pathogen and susceptible plant host (Mazzola 2002). Suppressive soils have been described for many soilborne pathogens, including *Gaeumannomyces graminis* var. *tritici* (Andrade et al. 2011), *Fusarium oxysporum* (Alabouvette 1999), *Aphanomyces euteiches* (Persson et al. 1999), *Heterodera avenae* (Kerry 1988), *Phytophthora cinnamomi* (Keen and Vancov 2010), *P. infestans* (Andrivon 1994), *Rhizoctonia solani* (Wiseman et al. 1996), and *Plasmodiophora brassicae* (Murakami et al. 2000). Natural disease-suppressive soils are the best examples in which the activities of specific soil and rhizosphere microorganisms keep susceptible plants mostly free from infection in spite of ample exposure to/load of virulent inoculum of soilborne pathogens. For most of the disease-suppressive soils, however, the consortia of microorganisms and the mechanisms involved in pathogen control have not yet been understood. In this chapter we focus on recent progresses made toward unraveling the mechanisms of natural soil suppressiveness against four specific soilborne pathogens, viz., *Fusarium, Rhizoctonia, Pythium,* and *Phytophthora*. However, there is still a need to understand mechanisms underlying for the occurrence of disease suppression and strategies to enhance the suppressiveness through manipulating agricultural management practices eventually to create consistently suppressive soils for the management of soilborne diseases and phytopathogens.

5.2 Categories of Soil Suppressiveness

There are two mechanisms of soil suppressiveness (general and specific) according to the spectrum of microorganisms involved in the process. The "general soil-suppressive potential" is linked to abiotic and biotic substrate characteristics that are not related to the microorganism or group of antagonistic microorganisms in particular, while in "specific soil-suppressive potential," the suppression is related to the action of one or few organisms in the substrate (Termorshuizen and Jeger 2008).

5.2.1 General Soil Suppressiveness

General suppression of the crop diseases occurs when a high microbial activity is created in the soil environment/rhizosphere which inhibits the propagation of pathogen propagules. It occurs when a large number of different microorganisms compete with pathogens for nutrients and/or produce general antibiotics that reduce pathogen survival and growth. In compost there is a slow release of nutrients which supports beneficial activity of the microflora. General suppression is often enhanced by the addition of OM, certain agronomic practices, or the buildup of soil fertility (Stone et al. 2004) which consequently can increase soil microbial activity. The general suppressive potential of suppressive soil is explained by the ability of practices/materials to sustain sufficient microbial activity over time, fed by slow degradation of complex carbon compounds, particularly the polymeric carbohydrates (Hoitink et al. 1996). No one microorganism is responsible for general suppression (Alabouvette 1986; Cook and Baker 1983) and the suppressiveness is not transferable between soils. Thus, the entire soil microbial community increases nutrient withdrawal, resulting in fungistasis of fungal pathogen propagules or competition for colonization of rhizosphere zones which are rich in radical exudates. When an inoculum of a pathogen is added to pairs of raw and sterilized soil samples, the effect of general suppression becomes apparent by the greater severity of disease on a host grown in the sterilized soil as compared to the raw soil (Weller et al. 2002). The extent of production of antifungal microbial metabolites varied with the species (de Boer et al. 2003) and showed positive relationship between microbial diversity and general disease suppression of different pathogens (Garbeva et al. 2006; Postma et al. 2008; Benitez and McSpadden Gardner 2009). It may be due to synergistic interaction between microbial populations producing secondary metabolites or to greater collective efficiency in the removal of nutrients (Garbeva et al. 2011). Each pathogen is usually preferentially associated with one type of suppressive potential. *Pythium* spp. and *Phytophthora* spp. have propagules with small amounts of nutrients and depend on exogenous carbon sources for germination to affect host plants. They are described as highly sensitive to microbial nutrient competition and antibiosis and related to general suppression (Aryantha et al. 2000). The control of pathogens such as *Pythium*, *Fusarium*, and *Phytophthora* has often been related to general suppression due to OM amendments (Weller et al. 2002). Under such conditions, a broad variety of microbial species creates a competitive environment suppressive to pathogens (Serra-Wittling et al. 1996; Stone et al. 2001).

5.2.2 *Specific Soil Suppressiveness*

In contrast to general soil suppressiveness, “specific suppression occurs when the individual or selected groups of microorganisms compete with ”pathogens for nutrient and produce specific antibiotics during a certain stage in the life cycle of a pathogen to reduce its survival (Weller et al. 2002). Specific suppression is considered to be generated through the activities of one or several populations of organisms. Specific suppression is more qualitative, owing to more specific effects of individual or select group of microorganisms antagonistic to the pathogen during some stage in its life cycle (Cook and Baker 1983). Transferability is the key factor of specific suppression (Andrade et al. 1994; Westphal and Becker 1999) and the term “transferable suppression” has been used synonymously with specific suppression. Activity in suppressive soils is because of their ability to combine general and specific suppression. This combination acts as a continuum in the soil, although they may be affected differently by edaphic, climatic, and agronomic conditions. Weller et al. (2002) observed that most suppressive soils maintain their activity when brought into the greenhouse or laboratory while assessing the mechanisms of suppression under more controlled and reproducible conditions. Biotic and abiotic variables affect the structure and activity of microbial populations including pathogens and their antagonists which eventually help in disease suppression. Specific soil suppressiveness depends on microorganisms that operate as biological control agents emerged after the thermophilic phase. Many conducive soils possess properties with regard to microorganisms involved in disease suppression, while other attributes are unique to specific pathogen-suppressive soil systems. Modes of action of biocontrol agents (BCAs) include inhibition of the pathogen by antimicrobial compounds (antibiosis), competition for iron through production of siderophores, competition for sites of colonization and nutrients supplied by seeds and roots, induction of plant resistance mechanisms, inactivation of pathogen germination factors present in seed or root exudates through allelopathy, degradation of pathogenicity factors of the pathogens such as toxins, and parasitism that may involve production of extracellular cell wall-degrading enzymes such as chitinase and β-1,3-glucanase that can lyse pathogen cell walls (Keel and Défago 1997; Whipps 1997). None of the mechanisms are necessarily mutually exclusive, and frequently, several modes of action are exhibited by a single BCA. Indeed, for some BCAs, different mechanisms or combinations of mechanisms may be involved in the suppression of different plant diseases (Whipps 2001). So the organisms operative in pathogen suppression do so via diverse mechanisms including competition for nutrients, antibiosis, and induction of host resistance. Nonpathogenic *Fusarium* spp. and fluorescent *Pseudomonas* spp. also play critical roles in naturally occurring soils that are suppressive to Fusarium wilt. The suppression of take-all of wheat (*Triticum aestivum*), caused by *G. graminis* var. *tritici*, is induced in the soil after continuous wheat monoculture and is attributed in part to selection of fluorescent *Pseudomonas* spp. with capacity to produce the antibiotic 2,4-diacetylphloroglucinol (DAPG). The cultivation of orchard soils with specific wheat varieties induces suppressiveness to *Rhizoctonia* root rot of apple (*Malus domestica*) caused by *R. solani* AG 5 (Mazzola and Gu 2002). Long-standing suppression is a biological condition naturally associated with the soil and is called natural disease suppression. Its origin is not known and it appears to survive in the absence of crops in the field (Weller et al. 2002). In contrast, long-term adoption of crop management practices that supply higher levels of biologically available carbon inputs either through crop residues or addition of composts and organic manures can support higher levels of suppression. This occurs through changes to the composition and activity of the soil microbial community (Gupta et al. 2011; Postma et al. 2003). Induced suppressiveness is initiated and sustained by practice of monoculture in the presence of pathogens (Weller et al. 2002). Soils suppressive to take-all disease of wheat and barley, caused by the fungal pathogen *G. graminis* var. *tritici*, are referred to as take-all decline soils and are well-known examples of induced suppressiveness. The Fusarium wilt-suppressive soils from Châteaurenard (France) and Salinas Valley (CA, USA) are among the best examples of long-standing suppressive soils. Wheat cultivars that stimulate disease suppression enhance populations of specific fluorescent pseudomonad strains with antagonistic activity toward this pathogen.

Sterilization by autoclaving and gamma radiation can eliminate both general and specific suppression. General suppression is reduced but not eliminated by soil fumigation and usually remains after treatment at up to 70 °C moist heat (Weller et al. 2002). Pasteurization can eliminate specific suppression but this characteristic is not a prerequisite for specific suppression. Another strategy which allows confirmation of the biological basis of suppression involves transfer of suppressiveness to raw, conducive, fumigated, or sterilized soil by addition of 0.1–10 % or less (wt/wt) of the suppressive soil into the conducive soil (Weller et al. 2002).

5.3 Mechanism of Soil Suppressiveness

Mechanisms of the majority of cases of soil suppressiveness are unknown or unproven, but most explanations for suppressiveness involve microbial antagonism like antibiosis, competition, predation, and parasitism (Mazzola 2007). Investigations into the causes of disease-resistant and disease-tolerant soils sometimes revealed correlations with certain chemical and physical properties which are not an actual determinant of suppressiveness (Weller et al. 2002). Abiotic factors most frequently cited are the proportion and type of clay, acidity, and moisture: moist acid soils and dry alkaline soils tend to be unfavorable to the growth of pathogens.

While reviewing the work done on soil suppressiveness which suggests that most of the mechanisms reported to be responsible for reduction of diseases in plants involve microbiological changes in the bulk soil, the rhizosphere soil, and/or the rhizoplane, resulting in antagonism of the pathogen. However, globally, there are various schools of thoughts and opinions on the mechanism involved which largely state that different microbial antagonists are responsible for the proliferation of disease-causing pathogens. Some of the mechanisms of disease-suppressive soils are described below.

5.3.1 Organic Matter-Mediated Mechanism of Soil Suppression

The application of organic matter (OM) such as animal manure, green manure, and peat has been proposed for conventional agriculture to improve soil structure and fertility (Conklin et al. 2002; Cavigelli and Thien 2003) and to reduce disease incidence caused by soilborne pathogens (Litterick et al. 2004; Noble and Coventry 2005). Studies revealed that OM can be very effective in reducing pathogens such as species of *Fusarium* (Szczech 1999), *Phytophthora* (Szczech and Smolińska 2001), *Pythium* (McKellar and Nelson 2003; Veeken et al. 2005), *R. solani* (Diab et al. 2003), and *Sclerotinia* (Coventry et al. 2005). There are different mechanisms to explain the suppressive capacity of organic amendments: enhanced activities of antagonistic microbes (Hoitink and Boehm 1999), increased competition against pathogens for resources that cause fungistasis (Lockwood 1990), release of fungitoxic compounds during OM decomposition (Tenuta and Lazarovits 2002), or induction of systemic resistance in host plants (Pharand et al. 2002). The inconsistent disease control results obtained with OM amendments with both suppressive (disease reduction) and conducive (disease increase) effects produced skepticism in farmers about the use of these materials.

The suppressive capacity of all OM types against soilborne pathogens was evaluated by Bonanomi et al. (2007) which suggested that the OM was suppressive in 45 % and nonsignificant in 35 % of the cases, while in 20 % of the cases, a significant increase of disease incidence was found. OM amendment resulted in

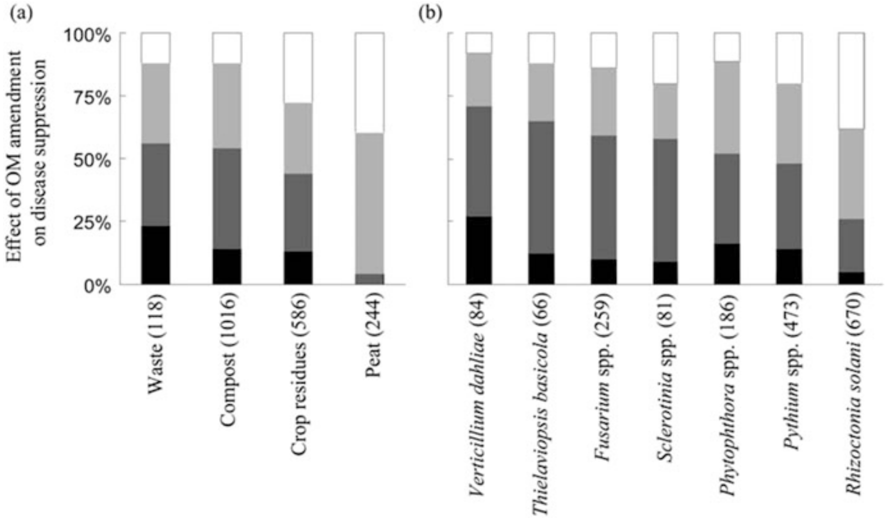

Fig. 5.1 Effect of OM amendments on disease suppression (*black* highly suppressive, *dark gray* suppressive, *gray* null, *white* conducive) in relation to different OM types (**a**) and soilborne fungal pathogens (**b**). Total percentage of suppressive cases is the sum of highly suppressive and suppressive. Only pathogens with more than 50 study cases (*numbers in brackets*) are shown (Bonanomi et al. 2007; reproduced with permission)

highly suppressive conditions (disease reduction >80 %) only in 12 % of the cases. Considering all OM types together, the suppressive capacity of the amendments varied largely with respect to different pathogens (Fig. 5.1a). Suppression was very high for both *V. dahliae* and *T. basicola* (>65 %), above 50 % of cases for *Fusarium* spp., *Sclerotinia* spp., and *Phytophthora* spp., and slightly below 50 % for *Pythium* spp. In contrast, effective control of *R. solani* was achieved only in 26 % of cases (Fig. 5.1b).

In the following paragraphs, we discuss specific mechanisms involved in OM-mediated disease suppression. Though these mechanisms are discussed individually, they act in consortia to carry out disease suppression.

5.3.1.1 Microbiostasis

Nutrient stress to soil microbial community results in repression of microbial spore germination and growth; this phenomenon is called microbiostasis or fungistasis for repression of fungal spores. Microbiostasis is an adaptive feature, as it protects the propagule from the energy losses or even death that might occur if germination occurred in the absence of a host. Microbiostasis can be overcome by inputs of external energy-rich nutrients such as root and seed exudates or organic amendments such as plant residues or manures (Lockwood 1990). Soil microbiostasis could be beneficial to microorganisms because it would be advantageous to their successful colonization in suitable habitats (Ko 2003). Germination of fungal conidia and the chlamydospores of *Fusarium* spp. is restricted because of insufficiency of energy-yielding nutrients as they require an external source of energy for germination in vitro. The competition for energy sources by the microbial community is a strong energy sink; exudation from ^{14}C-labeled fungal propagules increases in response to energy stress in the soil. However, propagules also lose energy and viability because of respiration (Hyakumachi et al. 1989). Losses in propagule energy can lead to a reduction in biological function. Addition of new energy sources to the soil system can initially destroy fungistasis, but fungistasis resumes, typically at a higher fungistatic level, after the sources have been slightly degraded (Lockwood 1990). Addition of sucrose and asparagine, or seed exudates, to compost-amended suppressive soil reduces the level of suppressiveness in a dose-dependent, linear relationship (Chen et al. 1988). In addition, compost harvested from the center, i.e., the thermophilic region, of a hardwood bark compost pile was conducive and of lower microbial activity and biomass and higher reducing sugars than the suppressive, lower-temperature outer region of the same pile. However, within days, the conducive material (incubated at room temperature) became suppressive; during the same period, the microbial activity increased and the reducing sugar content declined to levels comparable to those in the suppressive, outer-region compost (Stone et al. 2004).

Preemptive metabolism of exudate from a seed that initiates germination of pathogen propagules can induce microbiostasis and thus prevent disease; this is an indirect form of biological control because the pathogen is not directly antagonized. McKellar and Nelson (2003) elegantly described this phenomenon for BCA and compost-mediated suppression of damping-off of cotton caused by *Pythium ultimum*. The BCA *Enterobacter cloacae* metabolizes plant exudates required for germination and infection. *P. ultimum* oospores and sporangia germinate, grow, and infect cotton seeds in response to long-chain fatty acids (e.g., linoleic acid) released by the seeds as they germinate. *E. cloacae* inoculated onto cotton seeds competitively metabolizes the fatty acids and prevents *P. ultimum* germination, thereby suppressing the disease. Fatty acid uptake and oxidation mutants of *E. cloacae* do not prevent germination. In addition, there is no evidence to suggest that *E. cloacae* produces compounds inhibitory to the *Pythium* propagules (e.g., antibiotics) or is directly engaged in parasitism (van Dijk and Nelson 2000). In addition, populations of linoleic acid-metabolizing bacteria and actinobacteria were higher in the seed-colonizing microbial consortium from the suppressive compost than from the consortium isolated from the conducive compost. Individual isolates were not as suppressive as the suppressive microbial consortium, and linoleic acid metabolism varied greatly among isolates. This suggests that competition for linoleic acid was a strong determinant of damping-off suppression and that suppression was generated not by single isolates but by the combined activities of the linoleic acid-degrading microbial consortium supported by the suppressive compost substrate (McKellar and Nelson 2003).

5.3.1.2 Microbial Colonization of Pathogen Propagules

Pathogen propagules incubated in compost-amended potting mixes and organic residue-amended field soils are typically colonized by higher densities of bacterial and fungal propagules and, in some cases, protozoa, than in conducive or non-amended soils (Toyota and Kimura 1993). Colonized fungal spores germinate less readily and lyse and die more rapidly than noncolonized spores (Lockwood 1990). Bacterial colonization increased the rate of lysis, reduced the germination potential, and decreased the virulence of spores of various *Cochliobolus* spp.—the causal agents of root rots of grasses (Fradkin and Patrick 1985). Adherence might be an important component of biological control in and of itself; bacterial–fungal, fungal–fungal, and fungal–nematode interactions might be mediated by specific adherence mechanisms.

5.3.1.3 Destruction of Pathogen Propagules

Microbial antagonists generate hyphal lysis and degradation of chlamydospores, oospores, conidia, sporangia, and zoospores. Sporangia of *Phytophthora* spp. were destroyed after bacterial colonization of the sporangial surface. Sporangia nearing maturity release substances attractive to both microorganisms and microfauna. *Trichoderma* spp. can stimulate oospore formation, hyphal lysis, and chlamydospore formation in *Phytophthora* spp. (Costa et al. 2000). *Pseudomonas stutzeri* and *Pimelobacter* spp. isolated from chlamydospores of *F. oxysporum* f. sp. *raphani* (incubated in a manure-amended field soil) prevented chlamydospore formation or reduced chlamydospore germination (Toyota and Kimura 1993).

5.3.1.4 Antibiosis

Antibiosis is "antagonism mediated by specific or nonspecific metabolites of microbial origin, by lytic agents, volatile compounds, or other toxic substances" (Fravel 1988). The evidence for the role of antibiotics in the biocontrol of plant diseases has been extensively reviewed by Fravel (1988). *Pseudomonas* spp. that produce the antibiotic DAPG have been implicated in suppression of take-all of wheat, Fusarium wilt of pea, cyst nematode and soft rot of potato, and *Thielaviopsis* root rot of tobacco (Weller et al. 2002). Antibiotic production has also been implicated in the suppression of damping-off (causal agent *P. ultimum*) by *Gliocladium virens* (Howell and Stipanovic 1983).

5.3.1.5 Competition for Substrate Colonization

Most plant pathogens are weak saprophytes, and competition in the soil environment for organic substrates is strong. Pathogens that grow saprophytically on plant residues can be managed by pre-colonizing plant residues with nonpathogens, termed as the *possession principle* by Leach (1938) (Cook and Baker 1983). In studies of competitive interactions in soil aggregate colonization, closely related fungal species (other *F. oxysporum* formae speciales) strongly inhibited colonization by *F. oxysporum* f. sp. *raphani*. Other fungal genera moderately inhibited colonization, and bacterial species mildly inhibited colonization. *Burkholderia cepacia*, an antibiotic-producing bacterial species, also strongly inhibited colonization (Toyota et al. 1996). *P. nunn*, a saprophytic species of *Pythium*, outcompetes *P. ultimum* for colonization of added organic substrates, resulting in nutrient deprivation and production of survival structures by *P. ultimum*. In many cases, these structures are of lower inoculum potential, resulting in a reduction in the disease potential of *P. ultimum* (Paulitz and Baker 1988).

5.3.1.6 Competition for Root Infection Sites

Potato root colonization by the nonpathogenic fungal species *F. equiseti* was found effective in suppression of *Verticillium* wilt. Root colonization by *V. dahliae* was positively related to wilt incidence and negatively related to root colonization by *F. equiseti*. Sudangrass-cropped fields had the highest soil and root inoculum of *F. equiseti* and had the lowest wilt incidence. However, it is not clear if the increased *F. equiseti* colonization directly impacts *V. dahliae* colonization and disease incidence (Davis et al. 1996). Nonpathogenic strains of *F. oxysporum* compete with pathogenic strains for colonization of the root (Benhamou and Garand 2001) and other plant tissues (Postma and Luttikholt 1996) and might thereby contribute to suppression of Fusarium wilt.

5.3.1.7 Induced Systemic Resistance

Induced resistance has recently been implicated in some suppressive soil systems. Nonpathogenic *F. oxysporum* soil isolates induced systemic resistance in watermelon to Fusarium wilt (Larkin et al. 1996). Paper mill residual compost induced resistance to Fusarium wilt of tomato, resulting in a reduction in fungal colonization of root tissues. Suppression was associated with reduced fungal colonization of the tomato roots due to an increase in physical barriers (callose-enriched, multilayered wall appositions and osmiophilic deposits) to fungal penetration (Pharand et al. 2002). Tomato plants grown in compost-amended peat without inoculation with *F. oxysporum* did not exhibit increased physical barriers. An increased level of suppression and physical protection occurred when suppressive compost was inoculated with *P. oligandrum*, a species of *Pythium* known to induce resistance in tomato crop (Pharand et al. 2002). Composted pine bark container media was suppressive to *Pythium* root rot and foliar anthracnose of cucumber (Zhang et al. 1996), whereas dark peat container media was not suppressive to either disease. Cucumber and *Arabidopsis* plants grown in the composted pine bark expressed higher levels of β-1,3-glucanase (Zhang et al. 1998) and peroxidase (Zhang et al. 1996) than those grown in peat. Split-root experiments suggested that the resistance mechanism in cucumber was systemic (Zhang et al. 1996).

5.3.2 Compost-Mediated Mechanism of Soil Suppression

Compost is an organic material subjected to aerobic biological decomposition, during which temperatures of 40–70 °C are reached as a result of microbial activity. This process allows both the sanitization of the material (from human and plant pathogens and weed seeds) and its stabilization. Composts prepared from a variety of organic wastes are naturally suppressive against diseases caused by *Fusarium, Rhizoctonia, Pythium,* and *Phytophthora*. Only 20 % of all composts are suppressive against damping-off caused by *Rhizoctonia* and less than 10 % of all composts induced systemic resistance in plants (Hoitink and Boehm 1999). Furthermore, mechanisms that confer suppressive potential to composts depend on various factors as discussed below.

5.3.2.1 Hydraulic Conductivity and Free Air and Water Accessibility

The free air capacity of composts compared with some soils and peats is higher, which not only helps to improve plant growth but also has positive effect on the severity of rotting diseases of plant roots. Tree bark composts usually have an air capacity of over 25 % and a percolation rate of more than 2.5 cm/min and they suppress root rots. This suggests the importance of air capacity in those diseases where free water is important in the asexual multiplication of fungi (Aviles et al. 2011). It is well known that the manipulation of water potential as a control strategy is significant in diseases caused by oomycetes, particularly the possibility of producing adverse conditions for as long as possible during zoospore formation (Hardy and Sivasithamparam 1991). A negative water potential inhibits zoospore release from the sporangia of several *Phytophthora* spp. (Wilcox and Mircetich 1985). Thus, in order to reduce the incidence of disease due to these root rot pathogens, the necessary components of the growth media should be chosen in the proper amounts together with the correct irrigation system and watering strategy (Ownley et al. 1990).

5.3.2.2 Effect of pH and Electrical Conductivity in Interfering Nutrient Availability to the Pathogens

The majority of *Phytophthora* root rot diseases are inhibited by a low pH. The low pH reduced sporangium formation, zoospore release, and motility. For this reason the use of *Sphagnum* moss with low pH is beneficial in reducing *Phytophthora* and *Pythium* spp. High pH values of certain composts made from agricultural and industrial wastes were found suppressive against Fusarium wilt severity in various crops. The pH of the plant growth medium as a determinant of Fusarium wilt severity is associated with the availability of macro- and micronutrients and is important for growth, sporulation, and the virulence of *F. oxysporum* (Jones et al. 1991). A high pH reduces the availability of nutrients such as phosphorus (P), magnesium, manganese, copper (Cu), zinc (Zn), and iron (Fe) in organic growth. Borrero et al. (2004) showed a significant positive correlation between Fusarium wilt severity and final availability in the growth media of Cu on the one hand and the final nutrient status in the plants of Fe, Cu, and P on the other.

The lignin/cellulose ratio of wastes affects the duration of the composting process. Substrates with high lignin and low cellulose content do not immobilize a large amount of nitrogen, but this can be amended with essential micronutrients such as calcium and magnesium in order to improve the potential for growth of the majority of crops (Aviles et al. 2011). Hardwood bark and sewage sludge decompose well and do not require the addition of micronutrients. However, a high level of chloride, in the form of ions or as salt, can neutralize the suppressive effect of compost against *Phytophthora* root rot. There are contrasting reports presented by Pane et al. (2011) which show negative correlation between the damping-off induced by *Sclerotinia minor* and the salinity of compost-amended plant growth media. It is also important to note that phytotoxicity due to manganese available in certain bark composts must be amended with calcium carbonate before use.

5.3.2.3 Source of Nitrogen and C/N Ratio in Disease Suppression

High nitrogen levels and high ammonium to nitrate ratios increase Fusarium wilt incidence and severity. Thus, nitrate-amended composts may help to reduce Fusarium wilt diseases in ornamental (carnation, chrysanthemum) and horticultural crops (cucumber, tomato, asparagus, pea, radish, etc.) (Huber and Thompson 2007). Plants grown in bark compost immobilize mainly ammonium nitrogen and the nitrate nitrogen remains available for plant growth. However, sewage sludge compost (with a low C/N ratio) releases ammonium and consequently increases Fusarium wilt, even under colonization by BCAs capable of suppressing this wilt under other conditions (Hoitink et al. 1993). Cotxarreraa et al. (2002) used compost from vegetables and animal wastes, sewage sludge, and yard wastes and found it to reduce Fusarium wilt in tomato to a high degree. Low availability of ammonia in this compost may cause the direct effect of a high C/N ratio of other materials included in the compost, in addition to the negative effects of high pH and the reduced availability of Fe, Cu, and Zn on the pathogen.

5.3.2.4 Degree of Decomposed Compost

The degree of decomposition of compost has a strong effect on the rate of disease suppression. Immature compost could not suppress damping-off of cucumber seedlings caused by *P. aphanidermatum*. Fresh undecomposed OM mixed with *Trichoderma* does not exert biological control of *R. solani*. The synthesis of lytic enzymes involved in the parasitism of pathogens by *Trichoderma* is repressed in fresh OM due to high glucose concentrations. In mature composts, where concentration of nutrients such as glucose is low, the sclerotia of *R. solani* are killed by parasites and biological control prevails (Hoitink et al. 2001). On the other hand, the disease suppression potential of excessively stabilized compost is lost as it does not support microbial activity.

5.3.2.5 Role of Microbial Communities in Suppressive Potential of Compost

The environment around the compost plant, the system of composting used, and the composition of the raw material all affect the species richness and therefore the degree and spectrum of suppressive effect (Castano et al. 2011). The high temperature reached during the thermophilic phase of composting kills or inactivates all pathogens as well as beneficial microorganisms; thus, the composts are generally free of plant pathogens (Noble and Roberts 2004). As the temperature falls below 40 °C, mesophilic microorganisms colonize the semipasteurized compost; this is reinforced during the curing phase when there is also recolonization by surrounding antagonists, which develops the disease suppression capacity of the compost (Hoitink and Boehm 1999). Composts with high lignocellulosic substances are mostly colonized by *Trichoderma* spp. The microbial community that induced suppression of *Pythium* damping-off in cotton were populations of bacteria and actinobacteria capable of metabolizing fatty acids (linoleic acid) and thereby reducing the sporangium germination of *P. ultimum* (McKellar and Nelson 2003). Bonanomi et al. (2010) concluded that fluorescein diacetate hydrolysis, basal respiration, microbial biomass, total culturable bacteria, fluorescent pseudomonad counts, and *Trichoderma* populations gave the best predictions of disease suppression. Mechanisms involved in the phenomenon of disease suppression included competition, antibiosis, or hyperparasitism (Hoitink et al. 1993). According to Hoitink and Boehm (1999), the majority of composts suppress *Pythium* and *Phytophthora* root rot, while only 20 % of composts naturally suppress *Rhizoctonia* damping-off and very few (<10 %) induce resistance in plants. The type of organic amendment in compost has a clear positive effect on bacterial density and in particular, on the number of spore-forming bacteria, with an increase directly correlated with the dose of compost. The majority of the spore-forming bacteria isolated from the compost used in this study and selected during the composting process showed in vitro antibiotic activity against soilborne phytopathogenic fungi such as *F. oxysporum, F. solani*, and *R. solani*. Moreover, a greater decrease in damage by *Pyrenochaeta lycopersici* to tomato roots has been found in the same soil amended with compost (Zaccardelli et al. 2006, 2010). These results confirm the assumption that compost obtained from the organic fraction of municipal solid wastes produced an increase of suppressiveness against phytopathogenic fungi due to a change i,n the composition of the soil microbial community and a modification of the relationships among microorganisms—both competitive and/or antagonistic—producing a decrease in the activity of plant pathogens (Zaccardelli et al. 2013).

5.3.2.6 Arbuscular Mycorrhizal Fungi (AM Fungi) and Disease Suppression

Among beneficial soil microorganisms, the mycorrhizal fungi, particularly arbuscular mycorrhizae (AM), the most common fungal association formed almost with more than 90 % of cultivated plants, are gaining importance due to their varied benefits to plants. AM fungi offer many benefits to plants through a multiple action via absorption of nutrients, particularly P, water absorption, disease resistance, heavy metal toxicity, resistance to salt stress, etc. (Azcon-Aguilar and Barea 1996). AM fungi exert profound effects on other rhizosphere microorganisms either directly or indirectly via the host through a phenomenon termed the mycorrhizosphere effect by Linderman (1988) where most beneficial bacteria do inhabit and interact synergistically to stimulate plant growth. These interactions play a role in the suppression of fungal and nematode pathogens. Significant yield enhancement through field application of AM fungal inoculum has been recorded in a variety of crop plants (Sharma et al. 2010). Augmentation of these mycorrhizal fungi either through inoculation or through managing soil and crop management systems such as adopting conservation tillage and crop rotations (Sharma et al. 2012) can promote plants to cope up with many biotic and abiotic stresses and eventually sustain plant productivity. AM fungi protect plant roots from disease infection through several mechanisms as given below:

- One mechanism is via the changes in microbial communities that are produced as the mycorrhizosphere develops. There is strong evidence that shifts in microbial community structure and the resulting microbial changes can influence the growth and health of plants (Linderman 2000). Secilia and Bagyaraj (1987) isolated more pathogen-antagonistic actinomycetes from the rhizosphere of AM plants than from nonmycorrhizal controls, an effect that also depended on the AM fungus involved. AM fungi and other plant growth-promoting rhizobacteria (PGPR) share a common rhizosphere. AM fungi and PGPR may interact and cooperate in several ways, including their mutual establishment in the rhizosphere, improvement in plant rooting, enhancement of plant growth and nutrition, biological control of root pathogens, and improved nodulation in the case of legumes (Barea et al. 1996).

- Many authors suggested that the ability of AM-colonized plants to protect from root pathogens can be ascribed to an increased nutritional status in the host plant due to presence of the AMF. However, the effectiveness of AM fungi to suppress the) disease is dependent on the AM fungus involved and the substrate and the host plant (Whipps 2004). AM-mediated P-nutritional plants are more tolerant because these plants with a high phosphorus status are less sensitive to pathogen damage. Recently, Li et al. (2007) also found that AM fungi-associated bacteria (AMB) from the genus *Paenibacillus* have biocontrol ability against *Pythium*, which causes damping-off of cucumber. The possible antagonistic mechanisms of AMB against plant pathogens have been suggested to be the same as those of PGPR, i.e., competition for nutrients such as Fe, production of antibiotics, or production of fungal cell wall-degrading enzymes (Compant et al. 2005). Bharadwaj et al. (2008) suggested that some AMB could contribute to the often described ability of AM fungi to inhibit pathogens, acquire mineral nutrients, and modify plant root growth.
- Non-nutritional mechanisms are also important because mycorrhizal and nonmycorrhizal plants with the same internal phosphorus concentration may still be differentially affected by pathogens (Cardoso and Kuyper 2006). Such non-nutritional mechanisms include activation of plant defense systems, changes in exudation patterns and concomitant changes in mycorrhizosphere populations, increased lignifications of cell walls, and competition for space for colonization and infection sites. The mycorrhizal fungi protect plant roots from diseases by providing a physical barrier to the invading pathogen. A few examples of physical exclusion have been reported (Ingham 1991). However, some studies have shown that nematodes can penetrate the fungal mat (Maronek 1981), but still, disease development was affected adversely. Activation of plant defense mechanisms, including the development of systemic resistance, has also been proposed by Pozo et al. (2002). Among the compounds involved in plant defense (Bowles 1990) studied in relationship to AM formation are phytoalexins, enzymes of the phenylpropanoid pathway, chitinases, β-1,3-glucanases, peroxidases, pathogenesis-related (PR) proteins, callose, hydroxyproline- rich glycoproteins (HRGP), and phenolics (Gianinazzi-Pearson et al. 1994).
- By providing antagonistic chemicals and plant root exudates, AM fungi can produce a variety of antibiotics and other toxins that act against pathogenic organisms. Meyer and Linderman (1986) found that the number of sporangia and zoospores formed by cultures of *Phytophthora cinnamomi* was reduced by the application of extracts of rhizosphere soil from AM plants. Furthermore, Caron (1989) reported a reduction) in *Fusarium* populations in the soil surrounding mycorrhizal tomato roots as compared with the soil of nonmycorrhizal controls.

5.4 Soil Suppression of Soilborne Pathogens

5.4.1 Mechanism of Soil Suppressiveness Against Fusarium spp.

Fusarium wilt is caused by pathogenic *F. oxysporum*, a soilborne fungus, and it attacks many plant species. *Fusarium* spp. have good competitive saprophytic abilities and populations can increase after organic amendments. However, similar to *Pythium* spp., many *Fusarium* spp. are poor competitors and cannot colonize organic substrates previously colonized by other organisms. Natural suppressiveness of soils to Fusarium wilt was first recognized in the nineteenth century by Atkinson et al. (1975) and was later described for other soils around the globe (Peng et al. 1999; Dominguez et al. 2001). The suppressiveness is specific only to Fusarium wilts and not effective against diseases caused by nonvascular *Fusarium* species including *F. roseum* and *F. solani*, *F. subglutinans*, or other soilborne pathogens (Deacon and Berry 1993; Fravel et al. 2003). Such soils share many of the same biological and physical properties and several abiotic features including soil pH, OM content, and clay content, which play roles in disease suppression (Amir and Alabouvette 1993; Hoper and Alabouvette 1996). As early as 1970, Smith observed and reported that entities responsible for suppressiveness may be pleomorphic bacteria closely adhering to the stunted and lysed germ tube of chlamydospores of Fusarium wilt pathogen. But they were absent or few in number in steamed (54 °C) conducive soil. Soil pH also plays a significant role in soil suppressiveness and host susceptibility to Fusarium wilt pathogens (Barea et al. 1998). In clay loam soil at pH 8.0, the soil was suppressive; at 7.0, disease incidence significantly increased; and at pH 6.0, disease incidence was significantly higher than at pH 8.0 and 7.0. These factors pointed toward the presence of bacteria in sandy loam soil which is suppressive against Fusarium wilt pathogen as bacteria prefer alkaline soils.

Long-standing suppression operates in most Fusarium wilt-suppressive soils, but there are only a few examples of induced suppression. For example, suppressiveness to *F. oxysporum* f. sp. *niveum* (Larkin et al. 1993) was induced following continuous cropping of melon and watermelon, respectively. Interestingly, the induced suppressiveness in these cases was associated with continuous cropping of partially resistant cultivars, whereas induction of suppressiveness against other soilborne pathogens normally involves monoculture of susceptible cultivars (Whipps 1997). Incorporation of certain organic amendments into the soil may induce soil suppressiveness against soilborne and foliar pathogens. The soil microfauna/soil microbiome plays a significant role in natural and induced disease suppression. The possible mechanisms of induced soil suppressiveness include pathogen suppression, induced systemic resistance within host, and microbial interaction which takes place in the rhizosphere and which involves competition for nutrients and antibiosis (Andrews and Harris 2000). An example of induced soil suppressiveness with wild rocket (WR) found that sustainable disease suppression was maintained for 21 days after *F. oxysporum* f. sp. *radicis-cucumerium* inoculation of cucumber seedlings and transplantation into the WR-amended soil. It was observed that there was delayed onset of disease with reduced incidence, which demonstrates that the impact of soil suppressiveness on root diseases begins after inoculation of the pathogen. Among the bacterial and fungal genera responsible for Fusarium wilt suppressiveness are *Alcaligenes* sp. (Sayyed and Patel 2011), *Bacillus, Trichoderma* (Sivan and Chet 1989; Jambhulkar et al. 2011), *Pseudomonas* spp. (Mazurier et al. 2009), actinomycetes (Larkin et al. 1996), and nonpathogenic *F. oxysporum* (Olivain et al. 2006). Although the introduction of representative strains of each of these genera increased the level of soil suppressiveness in most cases, the introduction of large populations is unlikely to reproduce the microbial community structure and interactions that occur naturally in suppressive soils. In these soils, natural suppressiveness is associated with a reduction in the saprophytic growth and inhibition of chlamydospore germination of pathogenic *F. oxysporum* (Weller et al. 2002). This suppressiveness has been attributed mainly to the activity of nonpathogenic *F. oxysporum* and fluorescent *Pseudomonas* spp., and for both microbial groups, similar mechanisms including competition and induced systemic resistance were shown to be active (Fravel et al. 2003). Particularly interesting from the work of Lemanceau et al. (1993) is the intimate and complementary association between these two groups of microorganisms; in combination they provided enhanced disease suppression mediated by competition for iron via siderophores produced by the pseudomonads and for carbon by nonpathogenic *F. oxysporum* strain Fo47 (Lemanceau et al. 1993). The work by Duijff et al. (1998), using a glucuronidase GUS-marked strain of pathogenic *F. oxysporum* f. sp. *lini* and a pvd-inaZ-marked derivative of *P. putida*, WCS358, supported and extended earlier observations that suppression by the nonpathogenic *Fusarium* strain is related to reductions in both population density and metabolic activity of the pathogen on the root surface; it also showed that competition for iron both contributes to the suppression by *Pseudomonas* and enhances the biological activity of the nonpathogenic *F. oxysporum* strain. Among a large collection of bacteria, fungi, and actinomycetes isolated from this suppressive soil, only nonpathogenic *F. oxysporum* isolates consistently suppressed the disease in both microwave-treated and natural soil. Induced systemic resistance was the primary mode of action for several of these isolates, but it is not yet clear if the mechanism is similar to that described for induced systemic resistance by rhizobacteria. Strains of nonpathogenic *F. oxysporum* differ considerably in their efficacy against Fusarium wilt. For example, strain Fo20 was the least effective of eight strains tested, whereas Fo47 proved to be the most effective against Fusarium wilt (Alabouvette et al. 1993). From this observation, we can infer that the composition of nonpathogenic *F. oxysporum* populations remained relatively stable over a considerable period of time, consistent with the long-standing nature of the suppressiveness of these soils.

To date, soil suppressiveness to Fusarium wilt disease has been ascribed to carbon and iron competition between pathogenic *F. oxysporum* and nonpathogenic *F. oxysporum* and fluorescent pseudomonads. Mazurier et al. (2009) studied the role of bacterial antibiosis in Fusarium wilt suppressiveness by comparing the densities, diversity, and activity of fluorescent species producing DAPG (*phl*D+) or phenazine (*phz*C+) antibiotics (Fig. 5.2). The frequencies of *phl*D+ populations were similar in the suppressive and conducive soils but their genotypic diversity differed significantly. However, *phl*D+ genotypes from two soils were equally effective in suppressing Fusarium wilt, either alone or in combination with nonpathogenic *F. oxysporum* strain Fo47. A mutant deficient in DAPG production provided a similar level of control as its parental strain, suggesting that this antibiotic does not play a major role. In contrast, phzC+ pseudomonads were only detected in suppressive soil. Representative phzC+ isolates of five distinct genotypes did not suppress Fusarium wilt on their own but acted synergistically in combination with strain Fo47. This increased level of disease suppression was attributed to phenazine production as the phenazine-deficient mutant was not effective. These results suggest, for the first time, that redox-active phenazines produced by fluorescent pseudomonads contribute to the natural soil suppressiveness to Fusarium wilt disease and may act synergistically with carbon competition by resident nonpathogenic *F. oxysporum*.

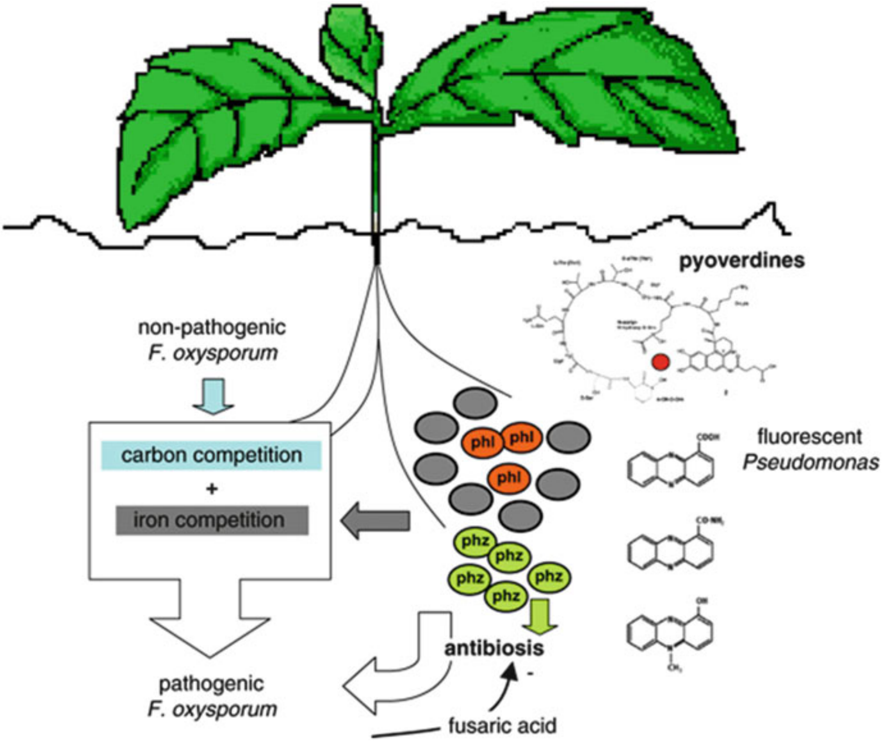

Fig. 5.2 Schematic model presenting the proposed mechanisms that contribute to the natural soil suppressiveness to Fusarium wilt. *phl* 2,4-diacetylphloroglucinol (DAPG), *phz* phenazine (Mazurier et al. 2009; reproduced with permission)

A higher level of carbon competition in the suppressive soil is generated due to the significantly higher microbial biomass in the suppressive soil as compared with the conducive soil. On this background of general competition, the higher density of nonpathogenic *F. oxysporum* in the suppressive soil further increases the carbon competition. The suppressive soil also differs from the conducive soil in its lower concentration of extractable iron, due to a high pH and $CaCO_3$ content, making pyoverdine-mediated iron competition between the pathogen and the fluorescent pseudomonads stronger in the suppressive than in the conducive soil. Carbon and iron competition act in synergy to suppress the saprophytic growth of pathogenic *F. oxysporum*, leading to a reduced activity and rate of root infection (Mazurier et al. 2009).

5.4.2 Mechanism of Disease Suppressiveness Against **Rhizoctonia** *spp.*

R. solani Kuhn is a soilborne fungus that causes disease in many economically important crop plants worldwide. Strains of the fungus are traditionally grouped into genetically isolated anastomosis groups (AGs) based primarily on hyphal anastomosis reactions and are further subdivided into intraspecific groups (ISGs) (Bolton et al. 2010). *Rhizoctonia*-suppressive soils reduced the severity of diseases caused by *R. solani* due to successive growing of a given plant host, which in general has been attributed to increased antagonism by *Trichoderma* spp. (Liu and Baker 1980). Ghini et al. (2007) evaluated the contribution and relationship of abiotic factors (pH, electrical conductivity, OM content, N total, P, Ca, Mg, S, Na, Fe, Mn, Cu, Zn, B, cation exchange capacity) and biotic factors (total microbial activity evaluated by CO_2 evolution and fluorescein diacetate hydrolysis; culturable bacteria, fungi, actinomycetes, protozoa, fluorescent pseudomonads, and *Fusarium* spp.) to the suppressiveness of soils to *R. solani*. Studies have reported that in highly suppressive soils of forest and pasture/fallow ground areas, several abiotic variables and fluorescein diacetate hydrolysis correlated with the suppression of *R. solani*; and this set of variables have explained more than 98 % of suppressiveness (Ghini and Morandi 2006). However, suppressive soils possessed higher populations of *Trichoderma* spp. than the corresponding conducive soil.

The soil suppressive to *Rhizoctonia* root rot of apple, caused by *R. solani* AG 5, was identified in Washington State (Mazzola and Gu 2002). However, the relative *Rhizoctonia*-suppressive capacity of the indigenous soil microbial community diminished with increasing age of the orchard block. The change in soil suppressiveness corresponded with a decrease in apple root colonization by actinomycetes and *Burkholderia cepacia* and a transformation in species composition of the fluorescent pseudomonad populations. While *P. putida* dominated the fluorescent pseudomonad community in non-planted orchard soil, a precipitous decline in its population was observed with increasing age of the orchard. *P. putida* was supplanted by *P. fluorescens* bv. III and *P. syringae* in the soil in response to planting apple. Likewise, isolates of *P. putida* from these soils provided biological control of *R. solani* AG 5. As observed in other systems, the *Rhizoctonia*-suppressive nature of the non-planted orchard soil was abolished by steam pasteurization (Mazzola 2007).

The mechanism for suppressing the pathogenic activity of *R. solani* differs from that of reducing its saprophytic activity in the case of damping-off. This aspect contrasts with the process during the events of damping-off caused by *Pythium* spp. For the latter, the frequency of seed colonization is directly related to the number of propagules until the colonization frequency reaches its maximum and is also correlated to the incidence of damping-off. Hence, different approaches to biological control need to be employed for *R. solani* and *Pythium* spp. (Kasuya et al. 2006). Microorganisms capable of suppressing these two kinds of pathogens also are known to be different. It was demonstrated that, although >70 different commercial composted pine bark amended potting mixes were effective in controlling damping-off of radish by *Pythium* spp., only one-fifth of those provided adequate control of *R. solani* damping-off because the latter was controlled by a much narrower spectrum of antagonistic microorganisms (Abbasi et al. 1999).

The feasibility of using organic amendments such as compost, animal manures, and organic industrial by-products in order to suppress soilborne plant pathogens has been well documented (Hoitink and Boehm 1999; Cheuk et al. 2005; Noble and Coventry 2005). Composts prepared from agricultural waste and used in container media or as soil amendments may have highly suppressive effects against diseases caused by a variety of soilborne plant pathogens. Barakat and Al-Masri (2009) amended sheep manure with *T. harzianum* and investigated its suppressiveness against damping-off of bean (*Phaseolus vulgaris*) for a 24-month period. Disease reduction was 50 % after 24 months with the highest concentration of organic amendment (10 %). Disease reduction increased with increasing concentration of organic amendment and with the duration of the incubation time. A combination of *T. harzianum* and sheep manure reduced both the total fungal population and the *R. solani* population after 12 and 24 months.

5.4.3 Mechanism of Disease Suppressiveness Against **Pythium** *and* **Phytophthora**

Damping-off and root rot caused by *Pythium* are considered to be the most devastating diseases of greenhouse crops. Biological control of *Pythium* is a promising environmentally friendly approach. Many factors affect the suppression of diseases in compost-amended soil affected with *Pythium* spp. These factors include compost type, OM quality and quantity, and associated level of microbial activity. Lightly decomposed OM colonized by a diverse microflora is very suppressive to diseases caused by *Pythium* spp. in container systems (Stone et al. 2004). This mechanism is being exploited by many nursery growers using tree barks in container system to suppress root rots in woody perennials. Apart from this, much of the evidence suggests damping-off of cucumber is suppressed with composts prepared from cattle manure, licorice roots, municipal biosolids, and sugarcane residues (Jenana et al. 2009). *Pythium* species are poor microbial competitors that strictly depend on the production of effective survival structures. They have the ability to germinate rapidly and grow in response to plant-derived seed or root exudate molecules to initiate plant infections. Carbohydrates and amino acids are the primary exudate components responsible for stimulating sporangium and oospore germination and initiating *Pythium*-seed interaction in the soil. Suppressive soil has greater mean concentrations of sodium, sulfate, and chloride than conducive soils; only chloride is inhibitory to *P. ultimum*. When conducive soils were amended with chloride at concentrations found in suppressive soil, colonizations of leaf debris by *P. ultimum* were partially suppressed. In suppressive soils, *P. oligandrum* was the most commonly isolated primary colonizing fungus and tended to be found at higher propagule densities than observed in conducive soils. When propagule densities of *P. oligandrum* were increased artificially in conducive soils, colonization and subsequent inoculum increases of *P. ultimum* were reduced. Suppressiveness was overcome by successive soil amendments with dried leaf debris, which resulted in progressive reductions in the frequencies of colonization by *P. oligandrum*. Apparently, soils with elevated chloride concentrations allow *P. oligandrum* to successfully compete with *P. ultimum*, and thus, the former increases its propagule density and further suppresses the saprophytic activity of *P. ultimum* (Martin and Hancock 1986).

The sphagnum peat system has been used as a model system to investigate the impact of OM quality on *Pythium* damping-off suppression (Boehm and Hoitink 1992; Boehm et al. 1997). Peats harvested from the top layers of a bog (very slightly decomposed sphagnum moss or light peat) are suppressive to *Pythium* damping-off. As a light peat decomposes, it loses the ability to suppress *Pythium* damping-off. Suppression is supported for 1–7 weeks. The loss of suppressiveness is related to (1) a decline in microbial activity as measured by the rate of hydrolysis of fluorescein diacetate (FDA) activity, (2) a shift in the culturable bacterial community composition from one in which 10 % of the isolates have the potential to suppress *Pythium* damping-off to one in which less than 1 % have this potential, and (3) a decline in carbohydrate content as determined by ^{13}C NMR spectroscopy (Boehm et al. 1997).

The following characteristics of the container system are responsible for suppression of *Pythium* damping-off:

1. Many types and sources of organic amendments consistently generate suppression.
2. Suppression is generated immediately after high-rate organic amendment (unless the organic substrate is raw).
3. Suppression is for a short duration (ranges from 1 week to 1 year).
4. Suppression is positively related to microbial activity.

Soil suppressiveness of diseases caused by *Phytophthora* spp. is considered to be the result of general suppression. Many types of organic materials suppress diseases caused by *Phytophthora* spp. The duration of suppression is similar to that of diseases caused by *Pythium* diseases, and suppression occurs soon after organic amendment. However, in contrast to suppression of *Pythium* spp., in which pathogen populations typically do not decline, in most documented systems of *Phytophthora* spp., propagules undergo microbial colonization, germination, and lysis. Bioassays determining the suppressiveness of soils have been used widely for various diseases with a variety of approaches and indicator plants. Such techniques may be used to determine the relative potential of the antagonistic population of a soil. Thus, blue lupin seedlings are used as indicator plant hosts to measure the suppressiveness of soils that are infested with *P. cinnamomi* (Duvenhage et al. 1991).

5.5 Conclusion

Soil suppressiveness research has clearly demonstrated that the phenomenon exists and is microbiologically mediated. However, there is considerably more uncertainty surrounding the identity of causal microbial agents and ecological processes that result in disease-suppressive soils. Many studies appear to have commenced with an assumption that suppression is specific. While it is likely that the principal mode of suppression will vary with each incidence of pathogen-suppressive soil, each study should commence by attempting to ascertain whether suppression is specific or general. We believe that this approach is justified as the outcomes provide a sound rationale for allocating resources toward future research efforts. The past dominance of culture-based studies has imposed limitations on our ability to test a specific suppression hypothesis. While not without their limitations, microbiomic methods currently provide the best tool for examining this question. Suppression cannot be achieved for all pathogens in question as the factors predicted to suppress different diseases are different for each pathogen. Suppressive soils are an asset to mankind as suppressive OM or compost can be produced but suppressive soil is not a renewable resource.

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