

Chapter 4

Developing Disease-Suppressive Soil Through Agronomic Management

R.S. Yadav, Jitendra Panwar, H.N. Meena, P.P. Thirumalaisamy, and R.L. Meena

4.1 Introduction

Plant diseases need to be controlled for maintaining the quality and quantity of food, feed, and fiber. Soilborne plant pathogens are one of the major limiting factors in most of the agroecosystems for the production of economical yields. Mostly they survive in bulk soil, but the parasitic relationship with crop plants is established in the rhizosphere. Soilborne pathogens caused numerous diseases like seed decay, pre- and postemergence damping off, wilting of roots, root rot, stem rot, crown rot, collar rot, decay of collar and fruits in trees, etc., and made serious losses to agricultural crops. These pathogens produce resting bodies in the soil which are long lasting and difficult to eliminate. The various diseases and symptoms are manifested by the plants which are difficult to diagnose and generally confused with the nondistinct symptoms caused by abiotic factors and/or due to lack of nutrients. Various approaches have been used to prevent, mitigate, or control the plant diseases. The practices for managing plant disease are largely based on genetic resistance in the host plants, management of the plant and its environment, and use of synthetic chemicals (Strange 1993). However, the use of agrochemicals needs to be ensured for safety of human health and environment (NRC 1996).

R.S. Yadav (✉) • H.N. Meena • P.P. Thirumalaisamy
ICAR-Directorate of groundnut Research, Junagadh 362001, Gujarat, India
e-mail: yadavrs2002@gmail.com; hariagro@gmail.com; thirumalaisamyp@yahoo.co.in

J. Panwar
Department of Biological Sciences, Centre for Biotechnology, Birla Institute of Technology and Science, Pilani 333031, India
e-mail: drjitendrapanwar@yahoo.co.in

R.L. Meena
Sardarkrushinagar Dantiwada Agricultural University, Sardarkrushinagar 385506, India
e-mail: ramji_meena@yahoo.com

Moreover, issues like legal control on pesticide use (NRC 1996), their nontarget effects (Elmholt 1991), development of resistance in pathogens (Russell 1995), political pressure to ban the use of such hazardous chemicals, etc., are the concerns to think about other eco-friendly alternatives for stable agroecosystems. For this, developing disease-suppressive soils is one of the most eco-friendly viable options to reduce the plant disease pressure as well as to strengthen the agroecosystems for sustainable agriculture. Generally, competition, antibiosis, parasitism, enhancement of plant resistance, etc., are the major mechanisms employed in developing suppressive soils. Numerous factors like soil properties (Hoepfer and Alabouvette 1996), soil microbial activity or the soil respiration (Van Os and Van Ginkel 2001), microbial diversity and composition (Garbeva et al. 2006), microbial population density (Tuitert et al. 1998), presence of antibiotic genes (Garbeva et al. 2006), agronomic management (Hoitink and Boehm 1999; Berg et al. 2002; Larkin and Honeycutt 2006), etc., are the key factors to determine the soil suppressiveness. Although, the mechanism behind soil suppressiveness is still not clear in many pathosystems. Both positive and negative correlations were reported between soil characteristics and suppressiveness, depending on the pathogens and the agroecosystems involved (Janvier et al. 2007).

The farm management practices used for crop cultivation not only promote the plant growth but also the soil suppressiveness having high efficacy for disease control without any additional cost and effect on the environment. Therefore, agronomic management practices are of multidimensional effects and have the high priority in contemporary agriculture (Martin 2003). The agricultural practices like crop rotation, tillage, fertilizers and organic amendments, use of microbes, etc., influence disease suppressiveness considerably. Nonetheless, many soil characteristics could interact, and hence, it will be very difficult to predict the precise effects of the agricultural practices on suppressiveness for specific disease and soil type (Janvier et al. 2007). Probably the soil suppressiveness is a combined effect of general and specific suppression, where the first relates to activity, biomass, and diversity and the second is the result of the presence of specific antagonistic groups. Therefore, knowledge about the process that results in increased soil suppressiveness is a prerequisite for its application under natural conditions. In this review, agronomic strategies for developing disease-suppressive soils for improved soil and plant health and productivity as well as for environmental benefits are discussed.

4.2 Suppressive Soils

The soils in which pathogens fail to establish or to produce disease are called disease-suppressive soils (Baker and Cook 1974). Two types of disease suppression have been described on biological basis, i.e., general and specific suppressions (Fig. 4.1). General suppression is the overall effect of the microbial community principally through resource competition which differs from specific suppression. The specific suppression relates with specific mode of action against pathogen populations (Weller et al. 2002). It is evident that most of the soils possess both

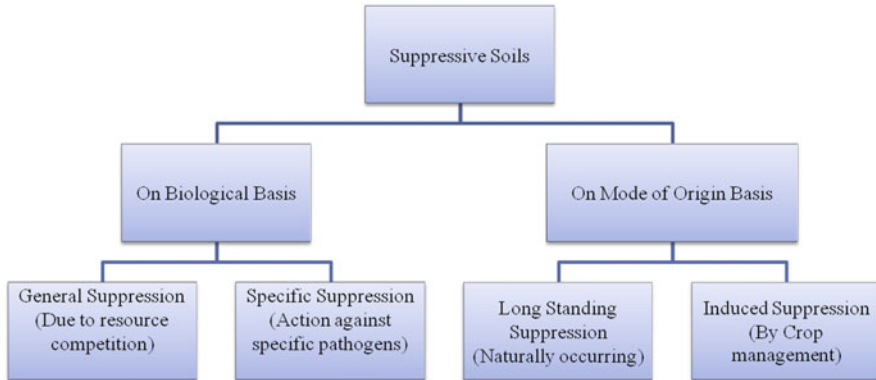


Fig. 4.1 Types of suppressiveness occurred in soils under different agroecosystems

general and specific suppressive activities at varying degrees which are greatly altered by management practices (Weller et al. 2002). The suppressive soils are also known for multiple soilborne pathogens and have been further categorized as long-standing or induced (Hornby 1983). Long-standing suppression is naturally associated with soil and is of unknown origin, whereas induced suppression develops as a result of crop management (Fig. 4.1). Some well-known examples of specific suppressive soils are *Fusarium* wilt of watermelon, take-all decline of wheat (Weller et al. 2002), *Rhizoctonia* damping off of cucumber, scab decline of potato, etc. (Menzies 1959).

Naturally occurring disease-suppressive soils have been well documented in a variety of cropping systems, and in many instances, the biological attributes contributing to suppressiveness have been identified. In spite of an understanding for mechanisms leading to the suppressive state, it is very difficult to realize the transfer of this knowledge into achieving effective field-level disease control. This might be due to the complex nature of biological control system and the inconsistent results for disease control in different agroecosystems under disease-suppressive soils (Pal and Gardener 2006). Therefore, greater emphasis is to be placed on manipulation of the cropping system to manage resident beneficial rhizosphere microorganisms as a means to suppress soilborne plant pathogens. Maintaining high levels of organic matter on the soil surface and incorporated into soil generally is associated with lower incidence and severity of root diseases (Bailey and Lazarovits 2003).

4.3 Factors Responsible for Enhancing Soil Quality, Plant Health, and Crop Productivity

The agronomic operations like plant species, land preparation, irrigation, and manure and fertilizer application are generally used by the farmers for crop cultivation. These practices considerably influenced the soil rhizosphere and biogeochemistry as well as growth and composition of microbial communities around plant roots. Plant roots and microorganisms are the vital component of the rhizosphere, and the total biomass and composition of rhizosphere microbial populations markedly affect interactions between plants and the soil environment. Therefore, the beneficial conditions for plant growth could be created by the use of amendments in the soil, breeding or engineering better plants, and manipulating plant/microorganism interactions. Plant root system, rhizosphere and rhizodepositions, soil properties, microbial diversity and microbiome, cultural practices, etc., are some of the major factors responsible for soil health and productivity of the crop plants (Fig. 4.2). These factors have positive influence on plant growth and development by facilitating plant establishment, enhanced nutrient availability, tolerance to stresses, improved plant protection, induced systemic plant disease resistance, etc. However, the benefits of root zone microbial biodiversity are still not certain in managed agroecosystems. Further management for disease control and yield maximization often minimized the community complexity and also disrupted the ecosystem stability. Therefore, the complexity of plant–soil–microbial interactions varied greatly, and the complete understanding of all the relationships involved is very difficult to be understood. Nevertheless, these beneficial biological

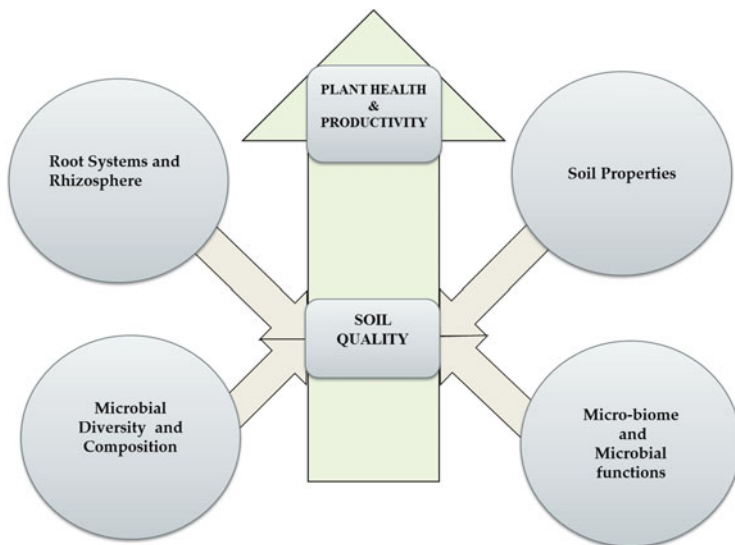


Fig. 4.2 Factors interacting with soil quality and affecting the plant health and productivity

interactions can be evaluated for better soil and plant health and also devised the management strategies accordingly.

4.3.1 Root System and Rhizosphere

Traditionally the root system was thought to provide anchorage and uptake of nutrients and water. However, it is the key element to a plant interacting with its surroundings by secreting various biochemical compounds as root exudates (Bais et al. 2006). Secretion of these compounds varies between different plant species (Rovira 1969), ecotypes (Micallef et al. 2009), and even distinct roots within a plant (Uren 2007). The diverse compounds released by plants as root exudates including sugars, proteins, fatty acids, flavonoids, amino acids, aliphatic acids, etc., create a unique environment in the rhizosphere (Badri and Vivanco 2009). All these different compounds are able to attract and initiate both symbiotic and pathogenic interactions within the rhizosphere (Bais et al. 2006).

Rhizodeposition that comprises of border cells, root debris, and root exudates are the major organic carbon source to the soil (Uren 2007) which could probably attract microorganisms that service the plant via biochemically active root system. Root exudates varied in composition and concentration depending on many factors like edaphic conditions, agronomic management (Bowen and Rovira 1999), age of the plant (De-la-Pena et al. 2010), soil type (Rovira 1969), biotic and abiotic factors (Flores et al. 1999), etc. All these factors also alter the microbial composition of the rhizosphere (Micallef et al. 2009) as these exudates are also used as growth substrates (Vandenkoornhuysen et al. 2007) by soil microbes for their population density and activities. Hence, the rhizosphere harbors many organisms having multiple effects on the plants like deleterious, beneficial, and neutral in action. The rhizosphere is also a battlefield where the complex rhizosphere community, both microflora and microfauna, interact with pathogens and influence the outcome of pathogen infection. Therefore, rhizosphere engineering may ultimately reduce our reliance on agrochemicals by replacing their functions with beneficial microbes, biodegradable biostimulants, or transgenic plants. For further details, see Ryan et al. (2009).

4.3.2 Soil Properties and Plant Health

Soils are highly diverse and dynamic in nature, allowing for habitation to diverse communities of microorganisms (Schloss and Handelsman 2006). The diverse communities of microbes have been associated with soils of varying texture (Girvan et al. 2003), nutrient content (Frey et al. 2004; Faoro et al. 2010), and soil pH (Fierer and Jackson 2006; Rousk et al. 2010). The bacterial community in soils was greatly influenced by soil pH (Fierer and Jackson 2006), and a strong

correlation was observed between soil pH and the diversity and composition of bacterial communities across the biomes (Rousk et al. 2010). Thus, soil factors and plant root activities have been shown to strongly influence the soil microbial community.

Physicochemical properties of the soils like texture, structure, density, pH, EC, carbon content, nutrient content, C:N ratio, altitude, ratio of cations (Ca^{2+} , Mg^{2+} , and Al^{3+}), etc., were more or less correlated to suppressiveness (Faoro et al. 2010). These suppressive effects were found variable among different soil types like more effective in sandy organic matter poor soils (Tenuta and Lazarovits 2004) and reduced *Fusarium* diseases at high soil pH (Borrero et al. 2004). Soil biological properties like enzymes, respiration, microbial functions, etc., strongly influenced the soil suppressiveness against multiple soilborne pathogens. Fluorescein diacetate (FDA) hydrolysis is consistently related to suppressiveness of composts on *Pythium* (Chen et al. 1988). FDA hydrolysis was also proposed as a promising indicator for predicting organic matter suppressiveness (Hoitink and Boehm 1999). However, subsequent studies reported contrasting relationships for disease suppression in relation to both OM type and pathogen species (Yulianti et al. 2006). The substrate respiration was also considered as an important indicator for disease suppression as FDA hydrolysis which could be explained by the model of general suppression (Weller et al. 2002).

4.4 Microbial Diversity and Disease Suppression

The microorganisms in the rhizosphere are the key agents for changes in soil agroecosystems. The interactions between plant root systems and microorganisms have an intense effect on crop health, yield, and soil quality. Microorganisms like pathogenic fungi, oomycetes, bacteria, and nematodes adversely affect plant growth and health. In contrast, a wide range of microorganisms are also present which are beneficial to the plant and include nitrogen-fixing bacteria, endo- and ectomycorrhizal fungi, and plant growth-promoting bacteria and fungi (Pal and Gardener 2006). Several microorganisms have been suggested to be involved for general soil suppressiveness like *Trichoderma* spp. (Wiseman et al. 1996), *V. biguttatum* (Velvis et al. 1989), *Pseudomonas* population (Mazzola and Gu 2002), combination of *Pantoea*, *Exiguobacterium*, and *Microbacteria* (Barnett et al. 2006), etc., but their mode of action is still not clear. The nonpathogenic *fusaria* (the most common components of soil microbial communities) and deuteromycetes such as *Penicillium* species are strongly antagonistic to pathogenic *fusaria* (Fravel et al. 2003; Sabuquillo et al. 2005). Actinomycetes are also known to be a strong producer of antibiotics and have a direct influence on disease suppression (Mazzola et al. 2001). Recently fluorescent pseudomonads attained the highest percentage of positive correlation (73 %), followed by sporigenus bacteria (60 %) and *Trichoderma* spp. (56 %) with no cases of negative correlation with suppressiveness (Pal and Gardener 2006). These microbial groups are able to

increase plant growth and development through production of phytohormones (Patten and Glick 1996), as biocontrol of phytopathogens in the root zone (Weller 1988), manipulation of ethylene levels (Glick et al. 1998), enhanced availability of minerals (Marschener and Römheld 1994), etc. Several species have been developed as biocontrol agents, with modes of action such as antibiotic production (Whipps 1997) and mycoparasitism (Harman et al. 2004).

Mycorrhizae are the dynamic symbionts between fungi and plants and occur on most terrestrial plant species. These fungi can prevent root infections by reducing the access sites and stimulating host defense. Various mechanisms employed by mycorrhizae to suppress plant pathogens includes intricate network of fungal hyphae around the roots, physical protection, chemical interactions, and other indirect effects like enhanced plant nutrition, increased root lignifications, biochemical changes of the plant tissues (Morris and Ward 1992), alleviation of abiotic stress, changes in mycorrhizosphere biology (Linderman 1994), etc. Specifically, disease protection by ectomycorrhizal fungi may involve multiple mechanisms including antibiosis, synthesis of fungistatic compounds by plant roots in response to mycorrhizal infection, and a physical barrier of the fungal mantle around the plant root (Duchesne 1994). Hence, the rich diversity of the soil microbes provides apparently the incessant resource for suppression of plant diseases (Elizabeth and Jo 1999).

4.5 Role of the Microbiome in Plant Health and Productivity

Soil microbiome provides an important role in disease-suppressive soils along with increased plant productivity (Mendes et al. 2011). Enhanced species richness and diversity resulted into quick recovery from the stresses which might be due to high functional redundancy within the soil microbiome (Nannipieri et al. 2003). The high functional redundancy in soil microbial diversity also confers protection against soilborne diseases (Brussaard et al. 2007; Mendes et al. 2011). This balanced microbiome due to enhanced microbial diversity does not allow pathogens to flourish (Mendes et al. 2011; Schnitzer et al. 2011). Many studies on disease-suppressive ability of particular taxons or group of microbes have been correlated with soil community as a whole (Garbeva et al. 2004; Mendes et al. 2011). For further details, see Chaparro et al. (2012).

Microbial community evenness has been also identified as one of the important factors for community functioning, soil health, and plant productivity (Crowder et al. 2010; Wittebolle et al. 2009). It ensures that no individual microbial taxum is able to flourish and/or upsetting the ecological balance (Elliott and Lynch 1994). Increased competition found in diverse and even microbial communities reduces the niche spaces available for potential invaders (Hillebrand et al. 2008; Naeem et al. 2000), and a lack of community microbial evenness has been associated with

reduced plant productivity (Wilsey and Potvin 2000). It is suggested that when environmental fluctuations occur, even communities are quickly able to adapt to the new environment and sustain high productivity over time (Hillebrand et al. 2008; Wittebolle et al. 2009). These examples highlight the benefits of ensuring even and diverse microbial communities to produce healthy soil, high levels of nutrient cycling (Elliott and Lynch 1994) and to combat stress and disease (van Bruggen and Semenov 2000).

4.6 Mechanisms of Suppressive Soils

The ability of soil to suppress disease is of key importance in measuring soil productivity (Janvier et al. 2007). Many factors as discussed in the previous section determine the effectiveness of suppressive soils to combat the invading pathogens in soil–plant systems. The soil suppressiveness encompasses various mechanisms including competition, antibiosis, allelopathy, hyperparasitism, and induction of plant disease resistance (Fig. 4.3), which are being operative through different precursors like soil microbes, soil amendments, cropping systems, etc. (Haas and Défago 2005). Various soil bio-indicators like microbial biodiversity and composition (Garbeva et al. 2006), population density (Postma et al. 2008), the presence of specific antagonists (Postma et al. 2008), the presence of antibiotic genes (Garbeva et al. 2006), or combination of these have been related to soilborne disease suppressiveness. However, these mechanisms responsible for soil suppressiveness are not fully understood, and the effect may also differ depending on the host–pathogen systems (Janvier et al. 2007). The airborne diseases may also be reduced

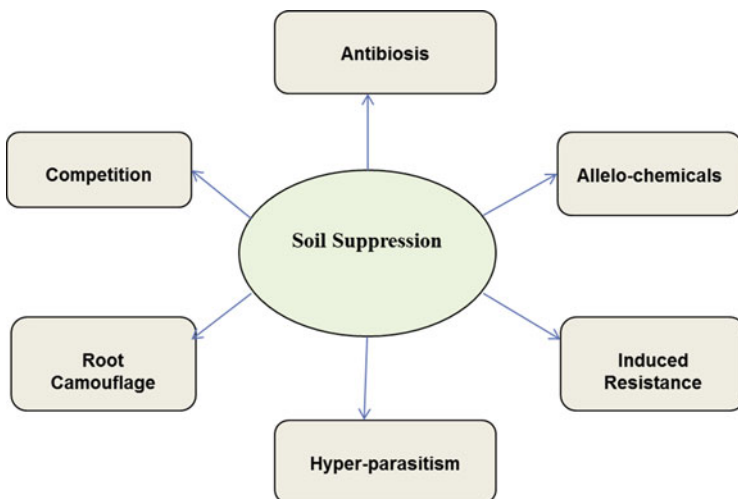


Fig. 4.3 Mechanisms of soil suppression in different agroecosystems

by soil microorganisms and induced systemic resistance (ISR) as reported in experiments under controlled conditions (Kloepper et al. 1999).

4.6.1 Allelochemicals

Allelochemicals are well known to influence a wide variety of soil and crop management-related processes (Sturz and Christie 2003). These processes include soil health, nutrient transfer, weed control, crop compatibility within rotations, residue management, plant growth and development, and disease-suppressive soils (Narwal 2000). Various plant-derived allelochemicals have been identified for weeds (Hoagland and Cutler 2000), fungal pathogens (Lovett and Hoults 1995), nematodes (Sukul 1992), and insects (Jacobsen 1989). Allelochemicals are secondary metabolites comprising lytic agents and enzymes (Glick et al. 1998), antibiotics (Bender et al. 1999), siderophores (Marschener and Crowley 1997), auxins (Patten and Glick 1996), volatile compounds (Claydon et al. 1987), and phytotoxic substances (Hoagland and Cutler 2000). However, the major source of allelochemicals in the rhizosphere is believed to be the plants. These allelochemicals are generated directly or indirectly, from precursor compounds released into the root zone and subsequently transformed through abiotic (i.e., oxidation) or biochemical reactions through the action of microbes or higher organisms (Tang et al. 1989). Suppression of *Meloidogyne incognita* by entomopathogenic nematodes has been proposed to be an allelopathic event mediated by symbiotic bacteria (Grewal et al. 1999).

4.6.2 Niche Competition and Microbiostasis

These are the mechanism that exists between pathogens and other microbial populations (Stephens et al. 1993). The siderophore-producing bacteria with high affinities for iron have been found to inhibit certain phytopathogens in iron-limited soils due to iron deficiency (Dowling et al. 1996). Similarly, by establishing partial sinks for nutrients, rhizobacteria can reduce the amount of carbon and nitrogen available for fungal spore germination and phytopathogen growth in the root zone (Elad and Baker 1985). The action of microbial population against pathogens was also proposed by altering the physical habitat rather than denial of the food source (Lockwood 1988) which were described as substrate antagonism (Lockwood 1986). In soil biostasis, microbial decomposers produce inhibitors during competitive interactions. The spectrum of inhibitors varies with microbial community composition. The inhibitors do not only affect the direct microbial competitors but have also negative effect on other soil-inhabiting organisms (Fig. 4.4). This ability of certain portions of a soil microbial population to impose fungistasis/biostasis appears to be relatively nonspecific. Thus, most isolates of actinomycetes, bacteria, and fungi were capable of initiating some degree of fungistasis (Lockwood 1964) or

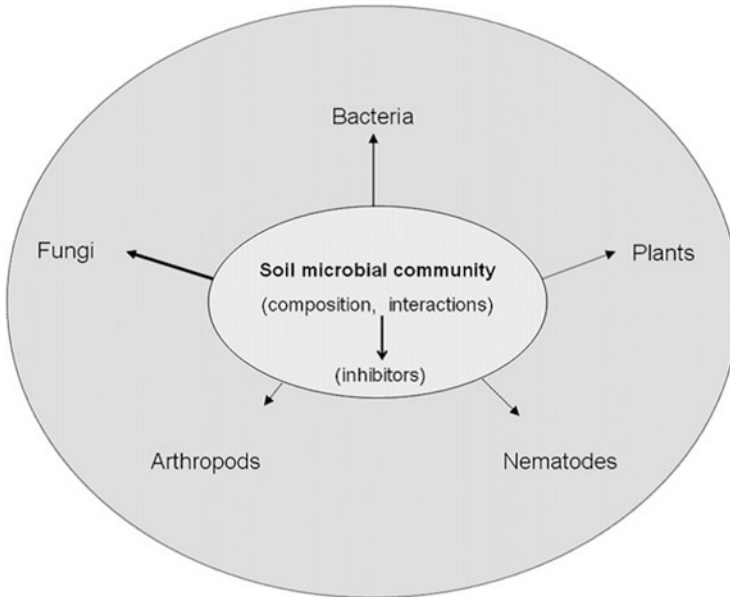


Fig. 4.4 Illustration of the soil biostasis concept. The length, weight, and pattern of the *arrows* illustrate the amount of supporting evidence for this concept (*Source*: Garbeva et al. 2011)

general microbiostasis (Ho and Ko 1986) when applied to sterilized soil or artificial soil, respectively. A more detailed discussion on biostasis can be found in Garbeva et al. (2011).

4.6.3 Antibiosis

Production of specific or nonspecific microbial metabolites, lytic agents, enzymes, volatile compounds, or other microbial toxins is often reported as agents of disease suppression (Fravel 1988; Lambert et al. 1987; Leyns et al. 1990). Antibiotics synthesized by rhizobacteria can contribute to microbial antagonism and persistence in the root zone soil (Kerry 2000). Antibacterial, antifungal, and antineematode activity has been identified in the antibiotic-producing strains of a wide range of bacterial genera, but most notably from *Agrobacterium* spp., *Pseudomonas* spp., *Bacillus* spp., *Trichoderma virens*, *Lysobacter* spp., *Pantoea agglomerans*, *Burkholderia cepacia*, etc. (Table 4.1). *P. fluorescens* bacteria that produce the antibiotic 2, 4-diacetylphloroglucinol (DAPG) are well known for their capacity to suppress diverse soilborne diseases (Weller et al. 2002), especially take-all disease of wheat (Raaijmakers and Weller 1998). Antibiotic production confers a competitive ecological advantage to the producer microbe; plants that stimulate root zone colonization by beneficial rhizobacteria will also benefit through the development

Table 4.1 Some of the antibiotics produced by biocontrol agents

Antibiotics	Source	Target pathogen	Disease	References
2, 4-diacetylphloroglucinol	<i>Pseudomonas fluorescens</i> F113	<i>Pythium spp.</i>	Damping off	Shanahan et al. (1992)
Agrocin 84	<i>Agrobacterium radiobacter</i>	<i>Agrobacterium tumefaciens</i>	Crown gall	Kerr (1980)
Bacillomycin D	<i>Bacillus subtilis</i> AU 195	<i>Aspergillus flavus</i>	Aflatoxin contamination	Moyné et al. (2001)
Bacillomycin fengycin	<i>Bacillus amyloliquefaciens</i> FZB 42	<i>Fusarium oxysporum</i>	Wilt	Koumoutsis et al. (2004)
Xanthobaccin A	<i>Lysobacter sp.</i> Strain SB-K88	<i>Aphanomyces cochlioides</i>	Damping off	Islam et al. (2005)
Gliotoxin	<i>Trichoderma virens</i>	<i>Rhizoctonia solani</i>	Root rots	Wilhite et al. (2001)
Herbicolin	<i>Pantoea agglomerans</i> C9-1	<i>Erwinia amylovora</i>	Fire blight	Sandra et al. (2001)
Iturin A	<i>B. subtilis</i> QST713	<i>Botrytis cinerea</i> and <i>R. solani</i>	Damping off	Paulitz and Belanger (2001), Kloeppe et al. (2004)
Mycosubtilin	<i>B. subtilis</i> BBG100	<i>Pythium aphanidermatum</i>	Damping off	Leclere et al. (2005)
Phenazines	<i>P. fluorescens</i> 2-79 and 30-84	<i>Gaeumannomyces graminis</i> var. tritici	Take-all	Thomashow et al. (1990)
Pyoluteorin, pyrrolnitrin	<i>P. fluorescens</i> Pf-5	<i>Pythium ultimum</i> and <i>R. solani</i>	Damping off	Howell and Stipanovic (1980)
Pyrrolnitrin pseudane	<i>Burkholderia cepacia</i>	<i>R. solani</i> and <i>Pyricularia oryzae</i>	Damping off and rice blast	Homma et al. (1989)
Zwittermicin A	<i>Bacillus cereus</i> UW 85	<i>Phytophthora medicaginis</i> and <i>P. aphanidermatum</i>	Damping off	Smith et al. (1993)

Source: Pal and Gardener (2006)

of a protective root zone microflora. Similar antibiosis responses may also be delivered by a protective bacterial endophyte flora localized within specific tissues of the host (Sturz et al. 1999).

4.6.4 Induced Systemic Resistance in Plants

Induced systemic resistance (ISR) in plants occurs when root colonization by certain nonpathogenic rhizobacteria stimulates defense-related genes such as those encoding the production of jasmonate (van Wees et al. 1999), peroxidase (Jetiyanon et al. 1997), and enzymes involved in the synthesis of phytoalexins (van Peer et al. 1991). ISR is often described as a heightened state of defense-related preparedness, which may be expressed locally or systemically within the activated plant, and results in either delayed symptom development or reduced disease expression (Liu et al. 1995) but only after pathogen penetration. While bacterial strains can differ in their ability to induce resistance, multiple pathogens may be inhibited by individual strains of rhizobacteria, indicating a general defense mechanism being induced in the plant (Hoffland et al. 1996). Even so, no consistent structural alterations have been identified in plants subjected to ISR, and cultivar-specific variations in the level of the ISR response have been reported (see review by Van Loon et al. 1998; Sturz and Christie 2003). Some of the bacterial determinants and type of host resistance induced by biocontrol agents as described by Pal and Gardener (2006) are given in Table 4.2.

4.6.5 Root Camouflage

Root camouflage (Gilbert et al. 1994) is the concept to explain decreased microbial population densities in the rhizospheres of disease-resistant cultivars (Lochhead et al. 1940). This mechanism was postulated to attract soil pathogens on plant roots (i.e., rhizosphere) than in root-free soil so as to targeting the root system for pathogen attack. A reduction in the population densities of root zone microbial communities was observed to the levels of resistant donor parent in wheat cultivars and to that of the surrounding soil (Neal et al. 1970, 1973). Thus, the presence of the root system is believed to be masked. Further it refers to the mechanisms involved in regulating disease suppression and pathogen reduction as described by Sturz and Christie (2003).

Table 4.2 Bacterial determinants and types of host resistance induced by biocontrol agents

Bacterial strain	Plant species	Bacterial determinants	Type	References
<i>Bacillus mycoides</i> strain Bac J	Sugar beet	Peroxidase, chitinase, and β -1,3-glucanase	ISR	Bargabus et al. (2002)
<i>Bacillus pumilus</i> 203-6	Sugar beet	Peroxidase, chitinase, and β -1,3-glucanase	ISR	Bargabus et al. (2004)
<i>Bacillus subtilis</i> GB03 and IN937a	Arabidopsis	2,3-butanediol	ISR	Ryu et al. (2004)
<i>Pseudomonas fluorescens</i> strains CHA0	Tobacco	Siderophore	SAR	Maurhofer et al. (1994)
	Arabidopsis	Antibiotics (DAPG)	ISR	Iavicoli et al. (2003)
WCS374	Radish	Lipopolysaccharide	ISR	Leeman et al. (1995a, b)
		Siderophore		Leeman et al. (1995a, b)
		Iron-regulated factor		Leeman et al. (1995a, b)
WCS417	Carnation	Lipopolysaccharide	ISR	Van Peer and Schippers (1992)
	Radish	Lipopolysaccharide	ISR	Leeman et al. (1995a, b)
		Iron-regulated factor	ISR	Leeman et al. (1995a, b)
	Arabidopsis	Lipopolysaccharide	–	Van Wees et al. (1997)
	Tomato	Lipopolysaccharide	–	Duijff et al. (1997)
<i>Pseudomonas putida</i> strains	Arabidopsis	Lipopolysaccharide	–	Meziane et al. (2005)
WCS 358	Arabidopsis	Lipopolysaccharide	–	Meziane et al. (2005)
		Siderophore	–	Meziane et al. (2005)
BTP1	Bean	Z,3-hexenal	–	Ongena et al. (2004)
<i>Serratia marcescens</i> 90–166	Cucumber	Siderophore	ISR	Press et al. (2001)

Source: Pal and Gardener (2006)

4.7 Agronomic Management Practices to Develop Suppressive Soils

Agricultural practices like crop rotation (Cook et al. 2002), intercropping (Schneider et al. 2003), tillage and organic amendments (Tilston et al. 2002; Mazzola 2004; Stone et al. 2003), and their combinations (Garbeva et al. 2004)

spectacularly influenced the disease suppressiveness. Although the changes in soil suppressiveness due to altered agricultural management are often site-specific (Cook 2007). It is a well-known fact that agronomic practices have often lead to decreased soil fertility by loss in soil organic matter, soil microbial biomass, soil organisms, and soil structure (Bellamy et al. 2005; Khan et al. 2007); consequently, it affected the soil suppressiveness to control the diseases (Van Bruggen and Semenov 2000). Therefore, better understanding of the processes and the potential to maintain or reestablish disease suppressiveness is essential for developing sustainable agricultural practices.

It is uncertain up to what extent soil suppressiveness could be reestablished by agronomic management practices or by introduction of soil microbial communities in disturbed soils. Numerous strategies have been investigated, altering soil microbial communities to develop soil capacity for suppression of soilborne plant diseases. Crop management practices including crop rotation (Huber and Schneider 1982), input system like organic versus conventional (Workneh et al. 1993; van Bruggen 1995), and tillage and fertilization (Smiley 1978) will influence ecological processes that affect microbial communities involved in the suppression of soilborne plant pathogens. All these observations inferred that based on the knowledge of the operative biological mechanisms, the capacity exists to enhance or diminish the suppressive nature of the resident microbial community through timely application of the appropriate agronomic practices (Hoepfer and Alabouvette 1996; Pankhurst et al. 2002). It is well evident that induction of soil suppressiveness is often mediated through transformations in soil microbial communities over time (Liu and Baker 1980; Larkin et al. 1993; Raaijmakers et al. 1997; Mazzola and Gu 2002). Hence, there may be a commendable opportunity to enhance the disease-suppressive state in the soils using various agronomic practices which would be the prerequisite for successful adoption of such disease control strategy. Some of the agronomic practices enhancing soil suppressiveness are summarized as mentioned below.

4.7.1 Organic Amendments

Various organic amendments like cover crops, animal and green manure, organic wastes, plant residues, composts and peats, etc., have been proposed to provide plant nutrition as well as control of diseases caused by soilborne pathogens (Steinberg et al. 2004; Widmer et al. 2002; Cotxarrera et al. 2002). These organic amendments have been successfully used to increase the soil suppressiveness to different diseases in agricultural and horticultural crops (Table 4.3). The effectiveness and the level of disease control obtained depend on many factors like chemical nature of the materials used, the composting process and degree of decomposition, type of microorganisms present, etc. These factors might be the probable reasons for contradictory reports for efficacy of disease control by organic amendments in the soil which seriously hinder the practical use of these amendments as

Table 4.3 Organic amendments and plant disease suppression

S. No.	Organic amendments	Disease suppression	References
1.	Vermicompost	<i>Phytophthora</i>	Szczech and Smolinska (2001)
2.	Vermicompost	Chickpea collar rot disease (<i>Sclerotium rolfsii</i>)	Sahni et al. (2008)
3.	Vermicompost	<i>Verticillium</i> wilt of eggplant	Elmer and Ferrandino (2009)
4.	Hairy vetch (<i>Vicia villosa</i>)	Fusarium wilt of watermelon	Zhou and Everts (2004)
5.	Swine manure	Microsclerotia of <i>Verticillium dahliae</i>	Tenuta et al. (2002)
6.	Compost tea	Damping off (<i>Pythium ultimum</i>)	Scheuerell and Mahaffee (2004)
7.	Composted hardwood bark	<i>Rhizoctonia</i> damping off	Nelson et al. (1983)
8.	<i>Brassica napus</i> seed meal amendment	Apple root pathogens	Mazzola et al. (2001)
9.	Broccoli residues	<i>Verticillium</i> wilt of cauliflower	Koike and Subbarao (2000)
10.	Composted swine Waste	<i>Rhizoctonia solani</i> on <i>Impatiens</i>	Diab et al. (2003)
11.	Composts	Damping off and root rot (<i>Pythium graminicola</i>) of creeping bent grass	Craft and Nelson (1996)
12.	<i>Brassica napus</i> seed meal	<i>Rhizoctonia</i> root rot	Cohen et al. (2005)
13.	Hardwood bark media	<i>Rhizoctonia solani</i>	Chung, et al. (1988)
14.	Synthetic and organic soil fertility amendments	Southern blight of tomato	Bulluck and Ristaino (2002)
15.	Composted municipal biowaste Composted cow manure	<i>Sclerotinia minor</i> (garden cress)	Pane et al. (2011)
16.	Vegetal composts	<i>Rosellinia necatrix</i> (avocado)	Bonilla et al. (2009)
17.	Fresh farmyard manure	<i>Rhizoctonia solani</i> (basil)	Tamm et al. (2010)
18.	Viticulture waste compost Composted cow manure	<i>Rhizoctonia solani</i> (garden cress)	Pane et al. (2011)
19.	Bark compost	<i>Pythium ultimum</i> (garden cress)	Erhart et al. (1999)

(continued)

Table 4.3 (continued)

S. No.	Organic amendments	Disease suppression	References
20.	Animal and vegetal composts	<i>Pythium ultimum</i> (garden cress)	Pane et al. (2011)
21.	Chipped eucalyptus trimmings	<i>Phytophthora cinnamomi</i> (avocado)	Downer et al. (2001)
22.	Sludge vermicompost	<i>Phytophthora cinnamomi</i> (avocado)	Bender et al. (1992)
23.	Fresh and composted chicken manure	<i>Phytophthora cinnamomi</i> (white lupin)	Aryantha et al. (2000)
24.	Vegetal composts	<i>Fusarium spp.</i> on several hosts	Yogev et al. (2006)
25.	Vegetal compost Poultry manure Green manure (legumes)	<i>Sclerotium rolfsii</i> (tomato)	Bulluck and Ristaino (2002)
26.	Horse manure Municipal green waste Wood shavings	<i>Verticillium dahliae</i> (eggplant)	Malandraki et al. (2008)
27.	Sewage sludge	<i>Laetisaria fuciformis</i> , <i>Pythium graminicola</i> , <i>R. solani</i> , <i>Sclerotinia homoeocarpa</i> , and <i>Typhula incarnate</i>	Nelson and Boehm (2002)
28.	<i>Brassica napus</i> seed meal	<i>Rhizoctonia</i> root rot (<i>Rhizoctonia solani</i> AG-5) in apple	Cohen et al. (2005)
29.	<i>Cruciferous</i> soil amendments	<i>Aphanomyces</i> root rot of peas	Papavizas (1966)
30.	Organic amendments	<i>Thielaviopsis basicola</i>	Papavizas (1968)
31.	Organic amendments	<i>Gaeumannomyces graminis</i> var. <i>Tritici</i> in wheat	Mazzola and Gu (2002), Weller et al. (2002), Tilston et al. (2002)
32.	Organic amendments	<i>Pythium splendens</i>	McKellar and Nelson (2003)
33.	Cotton-gin trash	<i>Sclerotium rolfsii</i>	Coventry et al. (2005)
34.	Organic amendments	<i>Macrophomina phaseolina</i>	Lodha (1995)

disease-suppressive materials (Termorshuizen et al. 2006). The effectivity and suppressive potential of organic amendments could be improved by inoculation of decomposed composts with specific strains of antagonistic microorganisms. Substantial effort has been made during the last decade for reliable indicators of organic matter-suppressive capability (Noble and Coventry 2005; Janvier

et al. 2007). Testing of various organic matters on different pathosystems is the traditional approach for identification of characteristics responsible for disease suppression (Scheuerell et al. 2005; Termorshuizen et al. 2007). For instance, FDA hydrolysis assay has been correlated with organic matter decomposition (Schnurer and Rosswall 1982), peat (Boehm et al. 1997), and compost suppressiveness (Chen et al. 1988). The degree of decomposition of the amendments (Hoitink and Boehm 1999; Janvier et al. 2007) is also an important indicator for disease suppression in different plant species.

Significant changes in the correlation between suppressiveness and the level of decomposition have been reported for crop residues (Papavizas and Davey 1960), organic wastes (Kotsou et al. 2004), peats (Boehm et al. 1997), and composts (Diab et al. 2003). The biocontrol effect is sustained for as long as the parent organic matter remains constant for factors like particle size, salinity, pH, carbon-to-nitrogen ratio, lignin-to-cellulose ratio, and moisture (Hoitink et al. 1997). The microbial carrying capacity declines with decomposition of organic matter which ultimately declines the disease suppression. However, mostly biological control agents colonized naturally in the composts at indefinite extent which often leads to reduction in the efficacy or reproducibility effects between batches of composts. Therefore, an understanding of the influence of the degree of organic matter decomposition on the suppression of soilborne disease is essential to improve our predictive capability.

Plant residues left on or near the soil surface may contribute to an increase of disease suppressiveness through the promotion of the general microbial activity. When residues are buried, the pathogens are displaced from their niche to deeper layers in the soil and their ability to survive is severely decreased. Repeated incorporations of crop residues can affect a change in the activity of residue-borne microorganisms that in turn influence the decomposition of crop residues. Carbon released from this decomposition contributes to an increase of soil microbial activity and thereby enhances the level of general suppression. Developing disease-suppressive soils by introducing organic amendments and crop residue management takes time, but the benefits accumulate across successive years, thereby leading to an improvement of soil health and structure (Bailey and Lazarovits 2003).

4.7.2 Soil Solarization and Biofumigation/Biodisinfection

Solarization or solar heating is a method that uses the solar energy to enhance the soil temperature to levels at which many plant pathogens will be killed or sufficiently weakened to obtain significant control of the diseases. Solarization is a hydrothermal process, and its effectiveness is not only related to the temperature but also to the soil moisture. The efficiency of the process can be improved by combining soil solarization and organic amendments (Ndiaye et al. 2007; Oka et al. 2007). The duration of solarization is also an important factor determining

the effectiveness of the treatment. Solarization does not destroy all soil microorganisms, but modifies the microbial balance in favor of the beneficial microorganisms. An important characteristic of soil solarization is its broad spectrum of activity including activity against fungi, nematodes, bacteria, weeds, arthropod pests, and some unidentified agents.

Disease control and yield increase have been reported after 2–3 years of solarization (Gallo et al. 2007). This long-term effect is probably due to both the reduction of the inoculum density and some induced level of disease suppressiveness of the soil. Many studies report that the efficacy of soil solarization is not only due to a decrease of pathogen populations but also to an increase of the density and activity of populations of antagonistic microorganisms such as *Bacillus spp.*, *Pseudomonas spp.*, and *Talaromyces flavus*. Several review papers are available that describe both the technology of solar heating and mechanisms involved in the control of pests, pathogens, and weeds by solarization (DeVay 1995; Katan 1996).

Biofumigation or biodisinfection is the strategy based on plastic mulching of the soil after incorporation of fresh organic matter which is suitable for cooler regions (Blok et al. 2000). Although the mechanisms involved are not fully understood, anaerobic fermentation of organic matter under plastic mulch and production of toxic metabolites are the two mechanisms considered to be contributed to the inactivation or destruction of pathogenic fungi. Therefore, two definitions have been proposed by Lamers et al. (2004), that is, biofumigation corresponds to the use of specific plant species containing identified toxic molecules, whereas biodisinfection refers to the use of high quantities of organic matter resulted in anaerobic conditions mainly responsible for the destruction of pathogens. For example, many species of *Brassicaceae* produce glucosinolates, a class of organic molecules that may represent a source of allelopathic control of various soilborne plant pathogens (Kirkegaard and Sarwar 1998).

4.7.3 Soil Tillage

However, it is very difficult to assess the role of tillage on disease suppression as its evaluation is often combined with the effects of other agricultural practices such as organic amendments and green manure burial, residue management, or crop rotations (Bailey and Lazarovits 2003). Therefore, tillage appears as giving conflicting effects on disease suppression. Conventional tillage results in considerable disturbance of the soil but removes residue from the surface. Tillage also disrupts hyphae, thereby affecting the ability of fungi such as *R. solani* to survive (Bailey and Lazarovits 2003). Reduced tillage can also favor pathogens by protecting the pathogen's refuge in the residue from microbial degradation, lowering soil temperature, increasing soil moisture, and leaving soil undisturbed (Bockus and Shroyer 1998).

A variable impact of conservation tillage practices on plant disease development has been reported depending on the specific regional crop–pathogen–environment

interactions (Sturz et al. 1997; Bailey et al. 2001). Leaving plant debris on the surface or partially buried in the soil may facilitate the survival of some pathogens until the succeeding crop is planted, but conditions favorable for microbial antagonism of plant pathogens may also be increased (Baker and Cook 1974; Boosalis et al. 1981) under such systems. Soil physical and chemical properties, moisture and temperature, root growth, and pathogen vectors are all influenced by tillage practice, and consequently pathogen virulence, diversity, and host susceptibility are likewise influenced (Sumner et al. 1981). A list of the impacts of minimum tillage on specific crops and their associated pathogens can be found in Sturz et al. (1997). Plant residues left on or near the soil surface may contribute to the suppression of soilborne pathogens in minimum tillage systems.

4.7.4 Crop Rotation

Crop rotation is an agricultural management tool with ancient origins (Howard 1996). Besides the benefits like maintenance of soil health, soil organic matter, reduction in soil erosion, etc., crop rotation spectacularly declined the incidence of plant disease caused by soilborne pathogens (Pedersen and Hughes 1992). Monocropping generally led to the buildup of soil populations of specific plant pathogens resulting in the decline of crop yield and quality (Honeycutt et al. 1996). In contrary, crop rotation with resistant and/or less susceptible to specific pathogens enhanced the crop yield and quality because it declined the pathogen populations due to natural mortality and the antagonistic activities of root zone microorganisms (Fry 1982). Rotation is most successful in limiting the impact of biotrophic pathogens that require living host tissues or those pathogens with low saprophytic survival capability (Bailey and Duczek 1996). However, it is least successful in reducing disease caused by pathogens with a wide host range or that produce long-lived survival structures such as sclerotia or oospores (Umaerus et al. 1989). Crop choice in a rotation may also harvest microbial benefits beyond those normally associated with pathogen host range and saprophytic pathogen survival. For example, analysis of microbial populations in plant tissues and soils when clover preceded potato in a rotation revealed that 25 bacterial species were common to both clover and potatoes and represented 73 % of culturable bacteria recovered from clover roots and potato tubers (Sturz et al. 1998). Endophytic bacteria found inhibitorier to *R. solani* than the bacteria present in the root zone. Therefore, it emphasized that adaptation of bacteria to host plants can result in the expression of a mutually beneficial relationship (Sturz et al. 1998). Crop rotation also influences disease suppressiveness of the soil (Garbeva et al. 2006; Postma et al. 2008). The best examples are take-all disease (Weller et al. 2002), *Rhizoctonia solani* in wheat (Mazzola and Gu 2002), potato (Jager and Velvis 1995), sugar beet (Sayama et al. 2001), radish (Chet and Baker 1980), and cauliflower (Davik and Sundheim 1984). However, knowledge on the mode of action of *Rhizoctonia* disease decline is lacking. In most pathogen–crop combinations, it is unknown if the host crop or the

pathogen itself are needed for the development of disease decline. In few cases, it was described that virulent *R. solani* was required to induce *Rhizoctonia* disease decline (Sayama et al. 2001).

4.7.5 Use of Beneficial Microbes

Agricultural management practices impact soil and rhizosphere microbial diversity and community structure. Management of soil properties is an important approach to promote the activities of beneficial microbes in the rhizosphere and thus limiting the densities and activities of soilborne pathogens to a tolerable level (Janvier et al. 2007). Furthermore, soil type is known to be a key determinant for soil microbial community structure (Garbeva et al. 2004). Adaptation of cultural practices has been proposed as a means to decrease the soil inoculum potential or increase the level of suppressiveness to diseases (Steinberg et al. 2007). Hence, it is evident that various cultural and management practices significantly influenced the microbial community structures and activities in the rhizosphere. Tillage (Feng et al. 2003), rotation (Lupwayi et al. 1998; Larkin 2003), use of mulches (Tiquia et al. 2002), cover crops (Schutter et al. 2001; Schutter and Dick 2002), and amendments (Parham et al. 2003; Pérez-Piqueres et al. 2006) are also known to influence the structure and activity of microbial communities.

Adding beneficial microorganisms to those already present in the soil can maximize plant nutrient uptake (Kirankumar et al. 2008), increase plant growth (Cummings 2009; Guñazú et al. 2009), confer resistance to abiotic stress (Selvakumar et al. 2012), and suppress disease (De Vleeschauwer and Höfte 2009). These living microorganisms are dynamic and potentially self-sustaining, reducing the need for repeated applications, and can avoid the problem of pests and pathogens, evolving resistance to the treatments (Lucas 2011). A possible management technique is to apply plant growth-promoting rhizobacteria (PGPRs) as an agricultural treatment to minimize niche vacancy and effectively fill vacant niches. It has been shown that PGPRs colonize particularly and effectively in soils with low microbial biomass (Fliessbach et al. 2009) so inoculations are more likely to be successful. Beneficial microorganisms that thrive in this environment can more quickly take up space and nutrients made available for potential pathogen invaders and assist with achieving sustained niche occupancy (Kaymak 2011). In addition, PGPRs offer benefits of increased yields, nutrient acquisition, stress tolerance, and disease resistance to the plant host (Lugtenberg and Kamilova 2009). The application of PGPRs consortia has been shown to be even more effective than one treatment alone in suppressing disease (Ahemad and Khan 2011; Yang et al. 2011). This combination of beneficial microbes also had the added effect of stimulating plant N and P absorption (Hernandez and Chailloux 2004). Formulations of compost with beneficial bacteria have also shown the ability to suppress plant pathogens (Pugliese et al. 2011; Yang et al. 2011). The ability of formulations of multiple beneficial microbes to increase plant productivity and health hints at the

potential of the entire microbiome and plants working together with mutually beneficial outcomes.

Sometimes, the same effect can be achieved by applying a microbial elicitor (compound produced by the microorganism and causes the desired effect). For example, exogenous application of the *Bacillus subtilis*-derived elicitor, acetoin (3-hydroxy-2-butanone), was found to trigger induced systemic resistance (ISR) and protect plants against *Pseudomonas syringae* pv *tomato* pathogenesis (Rudrappa et al. 2008). Similarly, adding low doses of *Chryseobacterium balustinum* AUR9 cell wall lipopolysaccharides, another bacterial elicitor, to *A. thaliana* reproduced systemic induction (Ramos Solano et al. 2008). Applications of living microbes or their elicitors have potential use for agricultural priming, the induction of ISR (Conrath and Loon 2009), which has been shown as an efficient way to increase pathogen resistance with little cost to the plant (De Vleeschauwer and Höfte 2009). An important addition to strategic management practices will be the development of crop species that are able to accomplish their own priming and ISR induction, which will reduce the use of microbial applications. Although, ideally, adding PGPRs as inoculants into the rhizosphere to exploit the immense benefits they provide is, potentially, an easy fix, there is still much inconsistency in their performance at the field scale (Morrissey et al. 2004; Mark et al. 2006). Research has begun to focus on how to cater the rhizosphere environment for PGPR rhizosphere colonization by means of rhizosphere engineering (Ryan et al. 2009), by understanding which PGPR traits are essential for rhizosphere competence (Barret et al. 2011), or by considering which indigenous soil microbial communities respond most favorably to inoculation (Bernard et al. 2012).

4.8 Conclusion

The evergrowing human population coupled with reduced natural resources and the need for more environmentally friendly agricultural practices have highlighted the need for sustainable farming. The intricacies of the plant–microbiome interaction and its impact on plant health and productivity need to be understood for obtaining healthier and more productive plants. Suppressible soils represent an underutilized resource for the control of soilborne pathogens of food, fiber, and ornamental crops. Early research identified the characteristics of soil suppressiveness and the major groups of microorganisms involved, but in recent past due to availability of molecular tools, it has been made possible to characterize and identify the factors and mechanisms responsible for genetic and functional determinants underlying the activity of some biologically suppressible soils. Adoption of different agronomic practices by the farmers spectacularly altered the soil microbiome and considerably enhanced soil suppressiveness to various soilborne diseases. The use of organic amendments or composts for the suppression of plant pathogens could be a promising and environmentally benign alternative to chemical pesticides. The deeper

understanding of microbial ecology processes could also provide directions for possible manipulations of the community, leading to a reproducible suppressive amendment. Combining measures of microbial structural diversity with functional traits should be explored in relation to soil and root health in agricultural systems.

Manipulating soil quality to achieve an economic level of disease control via agronomic management has been deliberately reviewed with some skepticism. However, crop rotation, residue management practices, and various forms of organic amendments do contribute to the suppression of soilborne diseases. However, the level of understanding for the mechanisms involved in suppressive soils is still limited and not so clear. The benefits of applying organic amendments for disease control are incremental and long lasting depending upon soil ecosystems. The conventional agricultural systems need to be discouraged because of poor production efficiency due to reduced crop diversity, increased genetic uniformity, and shorter rotations. More attention is to be paid on conservation agriculture including maximum use of natural resources. Through the application of green and livestock manures, mulches, and composts, it is hoped that plant beneficial soil microbial populations will develop spontaneously. Selection of complementary rotation crops may also increase the buildup of beneficial microflora during successive field seasons. Plants can manage the development of beneficial microbial populations through the release of specific root exudates in the root zone. Recently, it has been proposed that plants may also be able to camouflage their presence to phytopathogens by blending into the soil microbial background through restricting the proliferation of root zone bacterial populations. Therefore, the future studies of biologically based soil suppressiveness will put new insights into the microbial ecology of agricultural soils and lay the foundation for the development of creative management strategies for the suppression of soilborne diseases.

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