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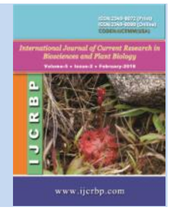

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A Review: Suppressive Soils and its Importance

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ABSTRACT

Microbial communities play a vital role in functioning of plants in respect to their growth and development. The activity of rhizospheric microbial community is higher than the surrounding environment. Microorganisms are colonizing near the plant roots thus affecting their growth and development either by promoting growth or developing diseases. Soil borne pathogens are commonly associated with causing diseases in the plant. Naturally occurring beneficial microbes may inhibit their growth and retention in soil. These beneficial microbes may serve as an agent to suppress these diseases in that particular soil. Therefore, greater emphasis has been laid on manipulation of cropping system to manage native beneficial microorganisms as a means to suppress soil borne plant pathogens. The mechanism following this suppressiveness might be due to various biological attributes like production of antibiotics, competition for nutrients and space, parasitism and predation. Natural biological suppression of soil-borne diseases is a function of the activity and composition of soil microbial communities. Many soils possess similarities with regard to microorganisms involved in disease suppression, while other attributes are unique to specific pathogen-suppressive soil systems. For example, non pathogenic *Fusarium* spp. and fluorescent *Pseudomonas* spp. play a critical role in naturally occurring soils that are suppressive to Fusarium wilt. Suppression of take-all of wheat, caused by *Gaeumannomyces graminis* var. *tritici*, is induced in soil after continuous wheat monoculture due to presence of fluorescent Pseudomonads with capacity to produce the antibiotic 2,4-diacetylphloroglucinol. Rhizoctonia root rot caused by *Rhizoctonia solani* may be suppressed by specific fluorescent Pseudomonad genotypes with antagonistic activity toward this pathogen. The enhancement of soil suppressiveness using organic amendments has also been widely described, especially for soil-borne diseases. However, there is great variability in the effectiveness of suppression depending on the nature of the amendment, the crop, the pathogen, and the environmental conditions. Moreover managing soil physico-chemical properties also suppresses certain pathogen thus improving soil health and quality. Managing soil parameters and microbial communities also proved to be suppressing weeds. Methods that transform resident microbial communities along with improving soil health and quality in a manner which induces natural soil suppressiveness have potential as a component in environmentally sustainable systems for management of soilborne plant pathogens.

Introduction

Plant-microbe-soil interactions play a vital role in maintaining plant health and productivity in agricultural crops. Plants are colonized by numerous numbers of (micro) organisms that can count up to a very high cell count much greater than the number of plant cells and the number of microbial genes in the rhizosphere outnumbers the number of plant genes by far (Mendes et al., 2013). So, rhizosphere reserves high amount of microbial community in the soil. The rhizosphere, that is, a micro-ecological zone in direct proximity of plant roots, is a hot spot for numerous organisms and is considered as one of the most complex ecosystems on Earth (Hinsinger and Marschner, 2006; Pierret et al., 2007; Jones and Hinsinger, 2008; Hinsinger et al., 2009; Raaijmakers et al., 2009). The extent of rhizosphere is dependent on the zone of influence of the plants and associated microorganisms. The activities of the microbes are faster and competitive than the surrounding soil. Organisms found in the rhizosphere include bacteria, fungi, actinomycetes, nematodes, protozoa, algae, viruses, archaea, and arthropods (Fig. 1) (Bonkowski et al., 2009; Buèe et al., 2009; Raaijmakers et al., 2009).

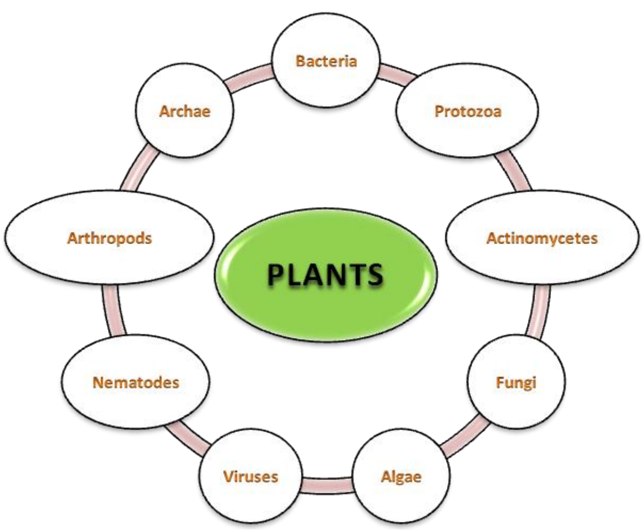


Fig. 1: Overview of (micro)organisms present in the rhizosphere.

Most members of the rhizosphere microbiome are part of a complex food web that utilizes the large amount of nutrients released by the plant. The chemistry of plant nutrients is governed by rhizosphere thus affecting the growth of plants. Along with plant growth enhancement, some of the soils are suppressing diseases either specific or general and this activity is very much active in the zone of rhizosphere as the habitat around the rhizosphere soil is favorable for microbes which are believed to be an important agent for disease suppression. An overwhelming number of studies have revealed that many plant-associated microorganisms can have profound effects on plant growth promotion, plant disease suppression, nutrition and tolerance to abiotic stress (Fig. 2). Till date, the interplay between plants and microorganisms has been studied in depth for various leaf pathogens, symbiotic rhizobia, and mycorrhizal fungi by many researchers. However, there is limited knowledge of their impact on plant growth, health, and disease. Hence, deciphering rhizospheric microorganisms is critical to identify microorganisms that can be exploited for improving plant growth and health.

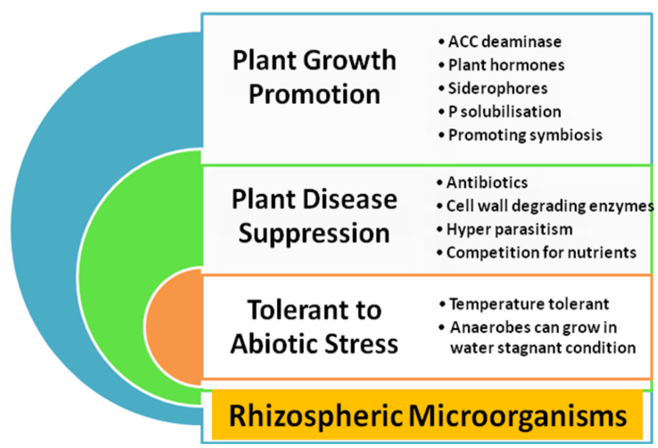


Fig. 2: Overview of functions and impact of Rhizospheric microorganisms on plant growth (Mendes et al., 2013; Palaniyandi et al., 2013).

Plant diseases caused by soilborne pathogens result in substantial losses to agricultural production worldwide (Jeger et al., 1996; Duveiller et al., 2007). Soilborne plant pathogens causing root and crown rots, wilts, and damping-off are major yield-limiting factors in the production of food, fiber, and ornamental crops. Roots of cereals, pasture plants and oil seed crops are prone to attack by soilborne necrotrophic pathogens such as *Rhizoctonia solani, Fusarium pseudograminearum, Gaeumannomyces graminis* var. *tritici* and *Pythium* spp. These are among the most difficult groups of plant pathogens to control due to their ability to persist in crop residues (Neate, 1994). Soil fumigation is the most effective chemical treatment but is too expensive for many crops, and fumigants like methyl bromide are being phased out for environmental reasons. And most soilborne pathogens are difficult to control by conventional strategies such as the use of resistant host cultivars and synthetic fungicides. The lack of reliable chemical controls, the occurrence of fungicide resistance in pathogens, and the breakdown or of host resistance by pathogen populations are among the key factors underlying efforts to develop other control measures. The search for alternative strategies also has been stimulated about the adverse effects of soil fumigants such as methyl bromide on the environment and human health (Weller et al., 2002). In this context, much is to be learned from disease-suppressive soils, where susceptible plants are protected from soil-borne pathogens by the indigenous microbiota which is antagonistic to the pathogen. However, knowledge of plant-protecting microorganisms and biocontrol mechanisms involved in soil suppressiveness are very much limited, as the studies are mostly restricted to individual plant-protecting microbial populations, mostly fluorescent *Pseudomonas* and *Trichoderma* species.

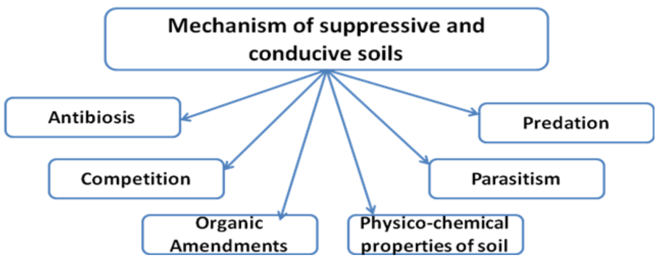
Every natural soil possesses some ability to suppress the activity of plant pathogens due to the presence and activity of soil microorganisms. This can be described in terms of general suppression and specific suppression (Mazzola, 2002). The phenomenon of general suppression is thought to be directly related to the total microbial community resulting in suppression of the diseases. Specific suppression accounts for suppression of pathogen by a specific microorganism. The study of specific suppression is the major concern nowadays compared general suppression in order to understand the potentiality of a particular microorganism in respective soil offering resistance to diseases (Cook and Baker, 1983). The role of microorganisms in disease suppression was supported by several studies which demonstrated that the disease suppressive factor could be transferred to a conducive soil through the introduction of very small amounts of the suppressive soil (Mazzola, 2002).

Manipulation of rhizosphere microbial community to induce suppressive soil

Management of resident bacterial communities colonizing the plant rhizosphere can lead to effective control of specific soilborne diseases. Modification or enhancement of the disease-suppressive rhizobacterial community can be attained via crop rotation, organic amendments, moisture content, nutrient availability, etc. For example, compost has shown significant levels of efficacy in controlling the environment for microbial communities in the soil (Mandelbaum and Hader, 1990; Widmer et al., 1998). Mazzola (1999) observed that soil collected from a continuous wheat monoculture field was suppressive to disease incited by the apple pathogen *Rhizoctonia solani* AG-5 but immediately adjacent ground where recently apple has been grown was conducive to disease development. The change in rhizospereic microbial community due to change in crop type may be correlated with conducive nature of the sol towards diseases. Reduction in soil suppressiveness of the soil towards *R. solani* has also been noted and this decrease in suppressiveness corresponds with a decline in rhizosphere populations of *Burkholderia cepacia* and *Pseudomonas putida* (Mazzola, 1999).

Mechanism of suppressive soil

The exact mechanism of suppressive soils is unknown or unproven till now, but most explanations for suppressiveness include microbial antagonism, *i.e.*, antibiosis, competition and parasitism and predation. Managing the quality and health of soil may also induce suppressiveness to the pathogen by altering their habitat in the soil. These processes may include managing drainage, pH, organic matter content, cation exchange capacity, etc. Addition of organic amendments may also serve as an important soil borne disease suppressor.



1. Production of antibiotics

Production of antibiotics plays an important role in biological control of soilborne pathogens. Antibiotics like phenazine- 1-carboxylic acid, 2,4 diacetylphloroglucinol (2,4- DAPG), pyoluteorin and pyrrolnitrin by certain strains of fluorescent *Pseudomonas* spp. are produced which make them an important candidate of biocontrol agents (Thomashow and Weller, 1988; Keel et al., 1992; Kraus and Loper, 1995). Different species of *Streptomyces* which are non pathogenic have been reported to be producing antibiotics inhibitory to *Streptomyces scabies* which causes potato scab disease (Liu et al., 1996; Eckwall and Schottel, 1997).

2. Competition for nutrients and space with pathogens

Microbial communities spreading in the soil may compete with the pathogenic microorganisms for nutrients as well as space. Some saprophytic microbial community has been reported to be suppressing Fusarium wilt by competition and induced systemic resistance (Lemanceau et al., 1992; Lemanceau et al., 1993; Duijff et al., 1999).

3. Parasitism against pathogen

Parasitism is also one of the important mechanisms in suppressing one group of microbial community by another group and is affected by environmental factors including nutrient availability. Pathogenic fungus *Gaeumannomyces graminis* var. *tritici* have been reported to be parasitised by *Trichoderma* spp. (Cook and Rovira, 1976; Simon and Sivasithamparam, 1989). Mycoparasitism may also destroy propagules of *Phytophthora cinnamomi* thus inhibiting their further in the soil (Malajczuk, 1983).

4. Predation on pathogen

The degree of suppression may be associated with the balance between disease- causing organisms and those organisms which feed on them. Predation on pathogenic microorganism might serve as an important component in suppressing the disease by maintaining their population under control. For example, a study has shown that the preference of feeding habit of earthworms on fungal species differs depending on the ecological niche of earthworms and their preference were favored towards plant pathogenic fungi, such as Fusarium as they frequently consume them while recalcitrant polymers degrader like Basidiomycetes were less preferred by the earthworms (Bonkowski et al., 2000).

5. Organic amendments

Soil organic matter plays a critical role in global biochemical cycles and is fundamental to the long term sustainability (Fonte et al., 2009). With the increasing trend of inorganic fertilizer utilization, there is an imbalance between organic matter input and output. Soil organic amendments can improve soil quality by altering soil parameters like soil aeration, structure, moisture holding capacity, nutrient availability and microbial ecology (Doran and Zeiss, 2000; Bailey and Lazarovits, 2003). Management of these parameters may serve as a means in destroying the favorable habitat of pathogenic microorganisms. Microbial decomposition of the organic residues also releases some allelochemicals which may reduce the growth of soil borne pathogen (Bailey and Lazarovits, 2003). Development of disease suppressive soils through organic amendments and crop residues may take time but the benefits in sustaining agricultural land over the years will improve soil health and quality.

6. Physico chemical properties of the soil

Physico chemical properties of soil may be managed accordingly in order to destroy the unfailing habitat of the pathogenic microorganisms. Soil texture and structure could have effects on plant diseases as they affect water holding capacity, nutrient status and gas exchange as well as root growth. Poor soil aeration caused by poor soil structure, soil type or water logging was associated with the development of cavity spot (*Pythium* spp.) disease in carrot. The severity of the soil borne diseases is greatest near the saturation and is proportional to the amount of soil moisture. *Pythium*, which causes damping off of seedlings and seed decay are affected by increased moisture content (Agrios, 1997). The pea root rot complex (*Fusarium* spp.) is known to be affected by compaction, temperature and moisture of the soils.

Some examples of specific suppressive soils

➢ Fusarium wilt suppressive soils

Fusarium wilt suppressive soil was first recognized by Atkinson followed by other researchers (Hopkins et al., 1987; Peng et al., 1999; Dominguez et al., 2001). Wilt–suppressive soils limit the incidence or severity of wilts of many plant species (Cook and Baker et al., 1983; Alabouvette et al., 1990). The suppressiveness is specific to Fusarium wilts and not effective against diseases caused by non vascular *Fusarium* species including *F. roseum* and *F. solani*, or other soilborne pathogens (Deacon and Berry, 1993). This suppressiveness has been attributed mainly to the activity of non pathogenic *F. oxysporum* and fluorescent *Pseudomonas* spp., and for both microbial groups, similar mechanisms including competition and induced systemic resistance were shown to be active (Lemanceau et al., 1992; Lemanceau et al., 1993; Duijff et al., 1999).

➢ Take-all suppressive soils

Take-all disease develops only in presence of the active pathogen, *Gaeumannomyces graminis* var. *tritici*. Some biological and chemical elements have been reported as the operative factors responsible for take-all suppressive soils (Cook and Baker 1983). However, many of the research conducted indicates the reduction in disease severity and induction of soil suppressiveness due to increased populations and activity of certain antibiotic-producing fluorescent Pseudomonads or parasitism by *Trichoderma* spp. (Cook and Rovira, 1976; Simon and Sivasithamparam, 1989; Raaijmakers et al., 1999).

➢ *Rhizoctonia* suppressive soils

Rhizoctonia solani has great importance among soil borne plant pathogens and damages a wide range of hosts worldwide. Decline in the severity of disease caused by *R. solani* has been documented in response to increased parasitism by *Trichoderma* spp. Liu and Baker (1980) identified *T. harzianum* as the primary cause of the disease decline in these soils. Soil suppressiveness was induced in apple field and it was found to be associated with increased colonization of apple roots by actinomycetes and a reversal in the composition of the fluorescent Pseudomonad population (Mazolla, 2002).

➢ *Phytophthora cinnamomi* suppressive soils

Well drained soils having pH between 5.5 and 7.0 and possessing high levels of NH_4, NO_3, Ca ions, Cation Exchange Capacity (CEC) and organic matter content have been found to be suppressing *Phytophthora cinnamomi* (Broadbent and Baker, 1974). *P. cinnamomi* is a weak saprophytic competitor (Malajczuk, 1983), inhabiting poorly in surface organic layers where large numbers of saprophytes dominate (Downer et al., 2001). Suppression of *Phytophthora* by soil bacteria has also been reported. Direct antagonism may be one of the processes which suppress the pathogen (Broadbent and Baker, 1974). Some bacteria and actinomycetes may also utilize *P. cinnamomi* as a substrate for their growth thus suppressing the disease (Downer et al., 2001). Mycoparasitism and/or production of metabolites by fungi may also inhibit or destroy *P. cinnamomi* propagules (Malajczuk, 1983). Table 1 provides the overview of some of the important diseases and their probable mechanisms for suppression.

Table 1. Some of the important diseases and their probable mechanisms for suppression.

Disease	Causal Organism	Probable mechanism for suppression
Fusarium wilt	*Fusarium oxysporum*	Growth of saprophytic microbial community
Take-all	*Gaeumannomyces graminis* var. *tritici*	Activity of certain antibiotic producing fluorescent Pseudomonads or parasitism by *Trichoderma* spp.
Collar rot, Root rot, Damping off	*Rhizoctonia solani*	Increased parasitism by *Trichoderma* spp.
Root rot	*Phytopthora parasitica*	Rhizobacteria and parasitism by *Trichoderma* spp.
Potato Scab	*Streptomyces scabies*	Production of antibiotics inhibitory to the pathogen by diverse species of non pathogenic *Streptomyces.*
Root rot or Dieback	*Phytophthora cinnamomi*	Direct antagonism, mycoparasitism and/or production of metabolites by fungi

Weed suppressive soils through improved soil quality

Nowadays, weeds are also gaining importance so as to improve soil quality and health as it deteriorates the soil and compete with the crop for space, nutrients, sunlight, moisture etc. thus reducing the yield of crops. Management of these soils with some beneficial microbes can be included in the integrated management system to suppress weed. Only few studies have been done on the development of agroecosystems with the capacity to suppress weeds using naturally occurring soil–weed interactions (Gallandt et al., 1999). This type of management could be used to promote the development of beneficial organisms as 'biological control' thereby undertaking weed management with reduced or no herbicide use (Parr et al., 1992). Identification of these biological control agent is a must step in managing these problems. Introducing environment friendly microbes or managing the soil physico chemical properties in weed overloaded field may be an alternative to high dose of chemical herbicides.

Conclusion

Although the importance of rhizosphere microbime in functioning of plant ecosystems has been widely recognized but the recognition on its importance towards disease suppression in soil are limited. Investigation on soil microbial communities along with soil quality and health is a must in order to obtain a full understanding of disease suppressive community. Identification of their mechanism in soil suppressiveness towards diseases is important in order to convert conducive soil to suppressive soil so as to improve crop protection and soil health. Along with the mechanisms associated with (micro)organisms *viz.*, antibiotics, competition, parasitism and predation, maintaining soil health and managing soil quality by agronomic practices and addition of organic matter in the soil may account to disease suppressive property of the soil. The use of organic amendments or organisms for the suppression of plant pathogens could be a promising and environmental friendly alternative to chemical pesticides. Moreover, some studies have shown that the weed can also be suppressed by certain soil using naturally occurring soil–weed interactions. Overall, the study clearly demonstrates the need to include soil suppressiveness property towards soilborne pathogen in the integrated pest management system.

Conflict of interest statement

Authors declare that they have no conflict of interest.

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