Dhananjaya Pratap Singh
Harikesh Bahadur Singh
Ratna Prabha *Editors*

Plant-Microbe Interactions in Agro-Ecological Perspectives

Volume 1: Fundamental Mechanisms, Methods and Functions

Springer

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ISBN 978-981-10-5812-7 ISBN 978-981-10-5813-4 (eBook)
DOI 10.1007/978-981-10-5813-4

Library of Congress Control Number: 2017953933

Printed on acid-free paper

This Springer imprint is published by Springer Nature
The registered company is Springer Nature Singapore Pte Ltd.
The registered company address is: 152 Beach Road, #21-01/04 Gateway East, Singapore 189721, Singapore

Foreword

त्रिलोचन महापात्र, पीएच.डी.
एफ एन ए, एफ एन ए एस सी, एफ एन ए ए एस
सचिव एवं महानिदेशक
TRILOCHAN MOHAPATRA, Ph.D.
FNA, FNASc, FNAAS
SECRETARY & DIRECTOR GENERAL

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Interactions of diverse microbial communities with plants and soils have been an integral part of our agro-ecosystem. Plants and soils recruit their own microbiome that interact with them and their abiotic environment through a cross-talk mechanism, which have remained central to the idea of studying the basis of microbial interactions. Such studies, after long efforts, have paved the way for the understanding of intrinsic biochemical, molecular and genetic mechanisms of plant microbe interactions and deciphering the ultimate benefits to plants and soils. Research efforts on plant-microbe interactions have further been facilitated with the developments in isolation and characterization of microbial communities, studies on the biology of community structure and functions, chemistry and biology of root rhizosphere, epiphytic and endophytic microbial associations, identification and behavior of phytopathogens and beneficial impacts of microbial interactions on plants and soils. Such studies have strengthened the prospect of manipulating plant and soil biology and root rhizosphere with beneficial microbial population at a greater pace.

The book, *Plant-Microbe Interactions in Agro-ecological Perspectives: Volume I – Fundamental Mechanisms, Methods and Functions*, presents a detailed account of principles and mechanisms of microbial communities, methods used to decipher such interactions and functional mutual benefits to plants, microbes and soils. In this well-compiled volume, the authors have presented widened views on microbial interactions taking into account various plant-microbe association systems, emphasizing on various mechanisms, different tools involved to decipher results and evaluating functional benefits out of such interactions. I am very sure that this compilation will attract a wide readership of researchers, students, scholars, agricultural professionals and all those who are interested in this area of research and development.

New Delhi
10th April, 2017

T. Mohapatra

Preface

Agriculture is a live, dynamic, and ecologically sustained system based on key constituents like plants, soils, biological diversity, and the environment. The ecological dynamics and sustainability of this system can be witnessed in terms of multipronged interactions among its constituents. Microorganisms (microfauna and microflora) constitute numerous small- to micro-scale stakeholders of interactions, and their interactions among themselves and with plants, soils, and the environment make the whole agroecological system so vital and live that even at a time scale of microseconds, multifarious biological, biochemical, physiological, and molecular events are organized, disintegrated, and reorganized at the cellular level of all the living cells that interact. The total output of these interactive events can be calculated in terms of plant health and development, soil health, and ecological balance of the whole system toward sustainability. This is why the importance of multiphasic plant-microbe interactions and its impact on native soils, microbial communities, and the plant itself have been recognized in the past few decades. This realization has yielded numerous work from all corners of the world on various plant-microbe systems on which in-depth data has been generated to decipher the mode of interactions; direct and indirect impacts on plants, microbes, other communities, and soil health; assays at cellular, ultrastructural, physiological, biochemical, and enzymatic levels; mechanisms at genetic, genomic, transcriptomic, proteomic, metabolomic, and phenomic levels in both plants and microbes; and benefits to both the partners (plant and microbes) due to environmental adversities. The research reflected that the benefits arising due to tripartite interactions among plants, microbes, and the environment (soil conditions, drought, temperature, etc.) can be helpful in obtaining better yield, better crops, and better environment at the field level. This directly transferable benefit of results at laboratory scale to the field level is the actual practical relevance of this subject area having precise, proven, and impactful benefit transfer to the farms. The book *Plant-Microbe Interactions in Agro-ecological Perspectives* is dedicated to the real work of researchers all across the world who, by their continuous efforts, made this area as dynamic and live as it remains in the fields. In a series of two volumes, the first volume "Fundamental Mechanisms, Methods, and Functions" shares with its readership the work that has been conducted to decipher plant-microbe interactions, the methodology to obtain genuine results, and the functions related to the interactive partnering in soils and plants. This volume presents pertinent topics on soil-plant-microbe interactions and their impact on plant and soil health; dynamics of rhizosphere microbial communities; molecular tools to study communities and community functions (metagenomics); microbe-root interactions in the rhizosphere; belowground microbial crosstalk and rhizosphere (root-associated) microbial communities; genomics at plant-virus interface; microbiome in interactive mode in conventional vs. organic production system; symbiotic and pathogenic associations; plant-fungi interactions; endophytic and epiphytic interactions and benefits; microbial functions in the hotspot, i.e., rhizosphere; molecular signaling determinants in rhizosphere; quorum sensing in plant-microbe interactions; arbuscular mycorrhizal interactions with roots; genetically modified crop-mycorrhizal symbiosis; microbial interactions to improve soil structure and function; nutrient mobilization and soil fertility benefits due to interactions in climate change era; microbial interactions and induced resistance in plants; pathogenic interactions and disease suppression due to biological control; interaction of entomophagous fungi for soilborne pest control; and interaction competence of bioinoculants in the field. We believe that this volume will attract a wide readership because of its integrated and holistic endeavor of describing microbial communities, their interactions with plants and soils, and the functional role of microbial interactions with plants for crop benefits. The views of the authors are authoritative, thorough, well-thought, and based on their long experiences while working over the subject area. We hope that this volume will benefit a wide readership of researchers, academicians, students, and those who are looking for practically sound and workable solutions to the heavy chemicalization of present-day agricultural systems.

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Harikesh Bahadur Singh is presently Professor and Head of the Department of Mycology and Plant Pathology at the Institute of Agricultural Sciences, Banaras Hindu University. He served the State Agriculture University, Central University, and CSIR institutes in teaching, research, and extension roles. His major research focus is on bioinoculants, biological control of plant pathogens, and nano-biotechnology. In recognition of his scientific contributions and leadership in the field of plant pathology, he has been honored with several prestigious awards, notably being the CSIR Technology Prize for Biological Sciences by the Honorable Prime Minister of India, M. S. Swaminathan Award by the Society for Plant Research, Vigyan Bharti Award, Prof. V. P. Bhide Memorial Award by the Society for Plant Research, Scientist of Excellence Awards, BRSI Industrial Medal Award, Jyoti Sangam Award, Akshyavat Samman Award, Distinguished Scientist Award by the Society for Research Development in Agriculture, Prof. Panchanan Maheshwari Medal by the Indian Botanical Society, Rashtriya Gaurav Award by IIFS, Plant Pathology Leader Award by IPS, CSIR Award for S&T Innovation for Rural Development (CAIRD), Environment Conservation Award, and Vigyan Ratna Award by the UP Council of Science and Technology. Dr. Singh has been a fellow of the National Academy of Agricultural Sciences. Currently, he is also serving as an associate/academic/board editor in journals of international repute. Professor Singh has published more than 300 publications, several training modules/manuals, 17 edited books, and 20 patents (USA, Canada, PCT).

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Microbial Interactions and Plant Growth

1

Sh.M. Selim and Mona S. Zayed

Abstract

Microbial interactions in soil are considered as one of the most important activities that occur in the terrestrial ecosystem. They affect all the dynamic processes of plants and other living organisms that live near from them either directly or indirectly. There are two types of microbial interaction that occur in soil. The interactions that occur between individuals within the same species are called intraspecific interaction, and those that occur between organisms of different species either two microbial populations or microbial population and plants or animals are called interspecific interactions. Each microorganism could perform more than one type of interaction depending on the sounding environmental conditions, its partner in the interaction. Microbial interactions are very essential for plant growth and health.

Keywords

Microbial interactions • Intraspecific interaction • Interspecific interactions and plant growth

1.1 Introduction

Soil is the biggest active terrestrial ecosystem, and this activity is determined by the numerous and diverse interactions among its physical, chemical, and biological components, which are controlled by the environmental conditions (Barea et al. 2005;

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D.P. Singh et al. (eds.), *Plant-Microbe Interactions in Agro-Ecological Perspectives*, DOI 10.1007/978-981-10-5813-4_1

Buscot and Varma 2005). Through these interactions, varieties of relationships occur between different microorganisms either between themselves or with plants.

The rhizosphere's content regularly contains thousands of interactions between its different constituents. These processes include exudation, water uptake, nutrient mobilization, organic matter decomposition, and respiration (DeAngelis 2013; van der Heijden and Hartmann 2016). By comparing the properties of both root-associated soil and root-free soil, there were major differences in their biological, physical, and chemical properties, which are responsible for changing in microbial diversity, numbers, and activity (Barea et al. 2005).

This chapter is concerning about illustrating different microbial interactions that occur in the soil especially the rhizosphere and linking these relations with their effects on plant growth and performance.

Symbiosis in Biology

The term symbiosis is taken from the Greek sym which means "with" and biosis that means "living" at which is defined as "living together," which is usually defined as long coexistence of two organisms. The term was first coined in 1879 by the German mycologist, Heinrich Anton de Bary, as "the living together of unlike organisms" (Das and Varma 2009; Martin and Schwab 2012, 2013). He believed that this terminology should include parasitic, communalistic, and mutualistic relationships between different species of microorganisms.

This terminology faced a lot of confusion and variation for over 130 years since Anton de Bary (1879) coined the word (Martin and Schwab 2012, 2013; Paracer and Ahmadjian 2000). For example, some biologists believed that mutualism is considered common restrictive definition of symbiosis. Furthermore, Pianka (2000) reformed the definition of symbiosis to comprise the interactions at which no species is harmed (i.e., mutualism, commensalism, and neutralism) (Martin and Schwab 2012). Therefore, in this chapter we decided not to discuss this term or insert it into the types of microbial interactions because of the confusions that face it.

1.2 Microbial Interactions in Soil

Soil microorganisms perform a number of interactions during their presence in the soil that comprise interaction with plant roots in the rhizosphere, interaction with soil constituents, as well as the interaction with other microbial communities that inhabit the rhizosphere (Barea et al. 2005; Bowen and Rovira 1999; Kennedy 1998). Microbial interactions regularly improve the sustainable development of agroecosystem, plant growth, and health.

The microbial community that existed in the rhizosphere is different forms that could be found in the bulk soil, as it was affected by root exudates that lead to high availability of nutrients and microbial biomass, which change the environmental conditions in the rhizosphere as a consequence of interactions between microorganisms as well as microbial interactions with higher plants and animals (Barea et al. 2005).

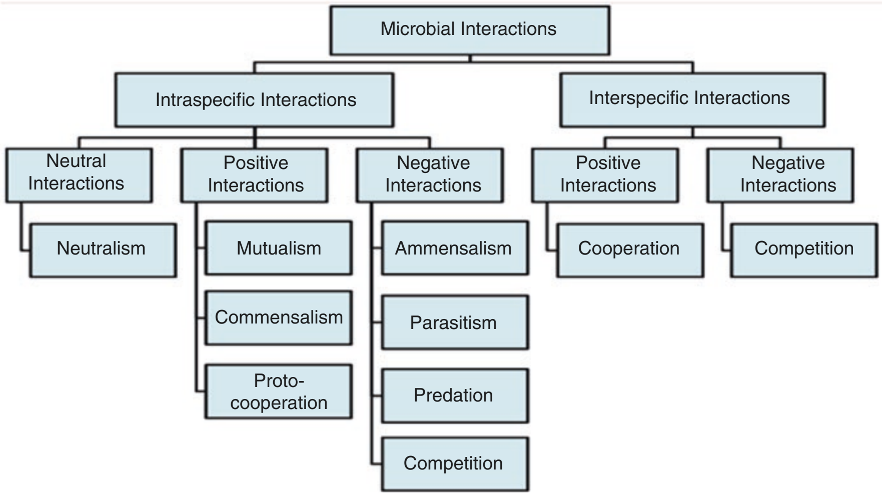

Fig. 1.1 Simplified scheme of microbial interactions

There are two types of microbial interactions that transpire in the rhizosphere: intraspecific interactions and interspecific interactions (Fig. 1.1). Intraspecific interactions occur between organisms of the similar species, while interspecific interactions occur between organisms of dissimilar species either two microbial populations or microbial population and plants or animals.

1.3 Intraspecific Interactions

It could be defined as interactions among individuals of single microbial population. This could be classified into two types:

1.3.1 Positive Interaction

This type of interaction is called cooperation or intraspecific cooperation as it improves the growth of the microbial population (Tarnita 2017). It appears in different types such as:

- Extended lag phase if small inoculum is used (less than 10% inoculum used) to avoid failure to grow
- Adherence of microcolonies to normal habitats by the minimum infectious dose
- Motile bacteria that remain in colonies during the growth by making synchronized immigration (mass movement) to appear in the form of colony
- Attaching of the cells to the matrix during biofilm formation

- Cooperation of the cells in degrading insoluble substrates such as lignin and cellulose by production of suitable enzymes
- Genetic exchange between members of the same population through transformation, transduction, and conjugation to acquire resistance to different abiotic stress

1.3.2 Negative Interaction

Intraspecific competition occurs as a negative interaction between the individuals of the same population (competition within population). It is considered as a very important factor that regulates population size and density. Also it is responsible for the equal distribution of individuals within population in the ecosystem (Atlas and Bartha 1986). It appears in different types such as:

- Low concentrations of available nutrients in natural habitats since all the cells use the same substrates and occupy the same ecological niche
- High microbial densities in natural habitat that lead to accumulation of some toxic products

1.4 Interspecific Interactions

It occurs among diverse microbial population that exhibit many different types of interactions. When it leads to increase the growth rate, it is called positive interaction, while it is referred to as negative interaction when it leads to decrease the growth rate, while some interactions are indifferent or neutral. In accordance to Burkholder (1952), different researchers illustrated different microbial interactions by using his famous symbols +, −, and 0 for any pair of interacting species at which + = beneficial effect, − = harmful effect, and 0 = neutral effect (Martin and Schwab 2012, 2013). Most microbial interactions are illustrated in Fig. 1.2, by considering that interaction occurs between to different populations at which one of them is (A) and the other is (b), and the type of interaction is symbolized as + 1 = beneficial effect, − 1 = harmful effect, and 0 = neutral effect.

1.4.1 Neutral Interactions (Neutralism)

It is a neutral association between dissimilar microorganisms inhabiting the same environment without impacting each other (the two members neither losing nor achieving anything from the relationship). Such association mostly is not a prevalent form of interaction (it is rare) as it is always transitory since environmental conditions always change.

This relationship occurs if the populations are living in culture with distinctive characteristics (Freilich et al. 2011; Weiner et al. 2012), such as:

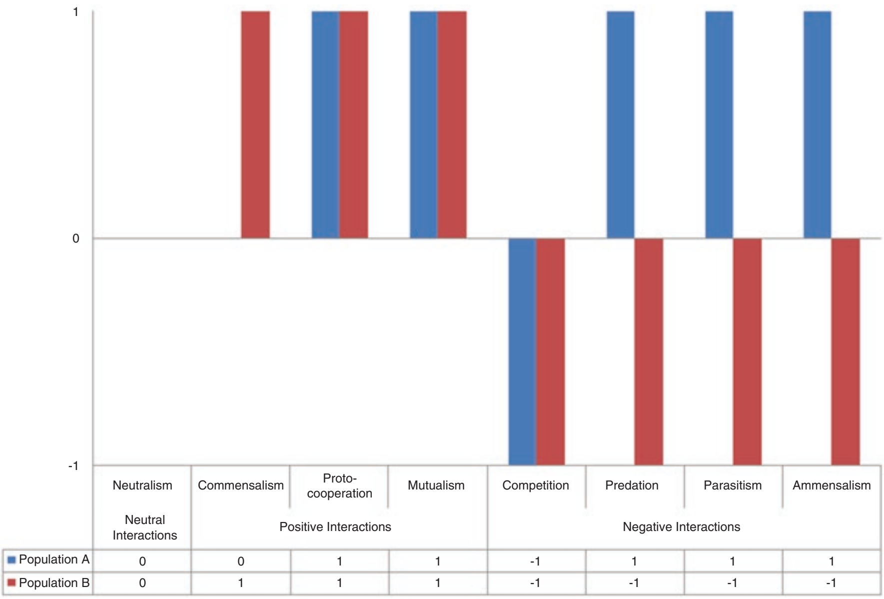

Fig. 1.2 Microbial interactions, basic characteristics of neutral, and positive and negative interactions that occur between different microorganisms (+ 1 = beneficial effect, − 1 = harmful effect, and 0 = neutral effect)

1. Separated by vast distance
2. Having dissimilar nutrient requirement
3. Living in oligotrophic lakes or marine habitats
4. Living in environment that does not authorize microbial growth like frozen products, polar ice, and frozen habitats

1.4.2 Positive Interactions

Such interactions consist of different relationships between different populations at which one population at least is benefited while the other is either benefited or not affected.

1.4.2.1 Mutualism

It is an obligatory or highly specific interaction between two populations in which both of them benefit from each other. It usually required close physical connection in which both partners may act as if they are one. When they exist separately, the physical tolerance and metabolic activities will be different for each single symbiont. Theoretically, mutualism could lead occasionally to the assembling of a new species (Freilich et al. 2011; Leung and Poulin 2008; Weiner et al. 2012).

1.4.2.1.1 Types of Mutualism

Mutualism could be classified into different types according to partner's selection and function or purposes of the relationship.

1.4.2.1.2 Types of Mutualism According to Interaction Patterns

According to the partner's selection, mutualism could occur in two forms:

- *Obligate Mutualism*: It occurs when both microorganisms live together in close proximity, and both species cannot survive without its mutualistic partner.
- *Facultative Mutualism*: It occurs when one of the two partners can survive without its mutualistic partner by itself in some conditions.

1.4.2.1.3 Types of Mutualism According to Interaction Purposes

Mutualistic relationships between different populations have three main purposes**:**

Trophic Mutualism It is also called *resource-resource interactions*. It is a type of mutualistic association, which comprises the exchange of nutrients between two species. Also, it is called "*syntrophism*" (Greek meaning: syn = mutual and trophe = nutrition)**.**

Defensive Mutualism It is also called *service-resource relationships*. It appears when one organism provides shelter or protection from predators or pathogens, while the other provides food.

Service-Service Mutualism It appears when one species receives service from its partner in return for transporting another service to the other organism. This type of mutualism is not common between microorganisms in the soil.

1.4.2.1.4 Some Examples of Mutualism

No clear or sharp type of mutualism could be detected between microorganisms in the soil since two or more types could be integrated together in nature.

a. Lichen

The most common example for mutualism is the lichen, which is an association between fungus (ascomycetes) and algae (green algae) or cyanobacteria (blue green algae), since most types of mutualisms occur between the two symbionts. Fungal partner surrounds the algal partner's cells within fungal tissues that are exclusive to lichen associations.

In this type of association, algae get benefits through protection afforded to it by fungal hyphae from environmental biotic and abiotic stresses and excess light intensity as well as it is provided with water and minerals that help it to grow while fungal partner obtains nutrients and oxygen from alga. When the blue green algae are the partners in the lichen association, the fungus gets benefit also from the fixed nitrogen.

Although lichen association improves the range of ecological survival for both partners, nonetheless, this relationship is not permanently necessary for their growth and reproduction in natural environments especially algae, since many of the algal symbionts can live independently (Aislabie et al. 2013; Lutzoni et al. 2001; Nash 1996).

b. Mycorrhizae

It is a mutualistic association among mycorrhizal fungi and plant roots, in which plants provide fungus with carbohydrates and offer it protection. In turn the fungus increases the surface area of plant roots for absorbing water, nitrogenous compounds, phosphorus, and other inorganic nutrients (e.g., phosphate) from the surrounding soil and delivers them to the plant which improves plant growth and health (Zayed et al. 2013). Also, mycorrhizal fungi shelter plant roots from invasion by soilborne root-infecting pathogens.

Endomycorrhizal symbiosis increases plant performance through improving their tolerance to different environmental stresses, which may be biotic, e.g., pathogen attack, or abiotic (e.g., drought, salinity, heavy metal toxicity, or presence of organic pollutants (Manaf and Zayed 2015) and also enhancing soil structure through formation of hydro-stable aggregates essential for good soil structure (Barea and Pozo 2013).

c. Symbiotic N_2 Fixation

The nitrogen-fixing bacteria provide the plants with nitrogenous compounds, while in return the plants provide the nitrogen-fixing bacteria with carbohydrates. This mutualistic association improves plant growth and health, and it has different types which include *Rhizobium* spp. with root nodules of legume plants and *Frankia* which is an actinomycete (nodule-forming filamentous bacteria) with the roots of *Alnus* and *Casuarina* trees which are "nonlegumes" (Selim et al. 2003).

1.4.2.2 Commensalism

It is a relationship at which one population benefits, while the other population is unaffected (neither harmed nor benefited). It is a very common relationship between different microbial populations. It is usually unidirectional, not obligatory relationship and occurs when the unaffected population adapts the habitat in such a way that the other population benefits.

1.4.2.2.1 Examples of Commensalism

(a) During the alteration of complex molecules by one population into other substrates in soil, the degraded products are regularly used by numerous other fungi and bacteria which cannot utilize complex molecules in the soil, like conversion of cellulose and lignin by fungi through production of extracellular enzymes**.** This process improves the nutritional properties of the soil which in return improve the activities of microbial communities in soil and improve plant growth and health.

(b) During the growth of facultative anaerobes and obligate anaerobes in the same site, the facultative anaerobes consume the oxygen from the environment which helps the obligate anaerobes to grow. This process occurs commonly in soil (Atlas and Bartha 1986).

1.4.2.3 Protocooperation (Synergism)

Synergism (protocooperation) is a relationship that occurs between two or more populations at which both or all of them benefit. In this relationship microbial populations perform a function which may not be performed individually or produce a new product that neither each population can produce alone.

This relationship is different from mutualism because as it is not an obligatory interaction, none of the species depend on the relationship for existence, as each member can live and produce its own food individually. It is also called loose relationship since one member can be replaced by another microorganism (Atlas and Bartha 1986).

1.4.2.3.1 Types of Protocooperation

There are different types of protocooperation relationship that could be found in the terrestrial ecosystem which is considered very useful in agriculture:

- *Nutritional protocooperation*: It is the most popular relationship between terrestrial populations at which the populations exchange nutrients between each other. Such a cooperation is also called syntrophism protocooperation.
- *Metabolism of toxic end products*: In this type of association one organism embellishes its associate by eliminating toxic substances from the habitation versus obtaining carbon products made by the other associate partner.
- *Production of derivative enzymes*: *Arthrobacter* and *Streptomyces* (soil flora) produce enzymes which collectively degrade diazinon which is an organophosphate pesticide (useful in the degradation of xenobiotics or recalcitrant compounds).

1.4.2.3.2 Examples of Protocooperation

(a) *Thiobacillus* spp. is an autotrophic bacterium which is aerobic, acidophilic, carbon dioxide fixer as well as sulfur and iron oxidizer, while *Beijerinckia* spp. is a heterotrophic bacterium which is an aerobic nitrogen fixer and slow grower. These two organisms could be grown together since *Thiobacillus* spp. fix carbon dioxide for itself and *Beijerinckia* spp., while *Beijerinckia* spp. fix nitrogen to satisfy the need from nitrogenous compounds for itself and *Thiobacillus* spp. in medium devoid of carbon and nitrogen sources. Also, the association of *T. ferrooxidans* with *Beijerinckia lacticogenes* enhanced the ratio and amount of Cu-Ni sulfide concentrate leaking in the medium (Barbosa et al. 2000; Trivedi and Tsuchiya 1975; Tsuchiya et al. 1974). This relationship in the terrestrial ecosystem improves the carbon and nitrogen content in the soil as well as