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interactions between non-pathogenic soil microorganisms and plants

Y.R. DOMMERGUES
AND S.V. KRUPA
(EDITORS)

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INTERACTIONS BETWEEN NON-PATHOGENIC SOIL MICROORGANISMS AND PLANTS

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FOREWORD

During its life in the soil, a plant root is associated with a myriad of soil microorganisms. These associations are qualitatively and quantitatively dynamic.

Non-pathogenic microorganisms associated with roots are known to affect plant growth, their effect being either detrimental or beneficial. The magnitude of microbial activity depends not only on the partners (plant and root microorganisms) but also on the environmental (climatic and edaphic) conditions. Thus the study of the interactions between soil microorganisms and plants should not be restricted to the soil compartment but should be considered within the framework of the whole soil—plant—atmosphere system. This book is an attempt to bring together all these different aspects of the science. The contributors come from different fields of research: plant physiology and anatomy, microbiology, soil science, general ecology and agronomy. The contributions vary in detail and presentation, but the scope is always that of presenting an overall summary of our current knowledge, together with general concepts and ideas of the individual contributors.

We hope that this book will serve as a useful focal point for further studies on the interactions between plants and soil microorganisms, thus providing an impetus for the development of agricultural practices which could maintain or expand the potential for food production while avoiding anthropogenic pollution of agrosystems and waste of energy resources.

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CONTENTS

Chapter 1

THE PLANT—MICROORGANISM SYSTEM

Y. R. DOMMERGUES

1. INTRODUCTION

"A distinction needs to be made between the knowledge obtained from impressive laboratory studies on an isolated culture of bacteria taken from the soil, and bacterial activities as they involve processes occurring under natural conditions; much more is known of the former than the latter at present." (Doetsch and Cook, 1973)

1.1 The plant—microorganism system

The high complexity of interactions between plants and microorganisms prompts plant physiologists and microbiologists to use simple models, namely sterile or sub-sterile hydroponic plant cultures, or pure cultures of microorganisms. Such investigations were and are still very productive, but they tend to mask the role of interactions that are the rule in nature. Actually plant roots growing in soil are never sterile, but always surrounded or invaded by large numbers of microorganisms with potentially intense activity. Thus, plant scientists should not overlook the effect on the metabolism of the plant of microorganisms associated with plant roots. On the other hand microbial populations associated with plant roots cannot be studied independently from the plant. It then follows that root microbial populations must be viewed as an integral part of a system or association which can be termed the *plant—microorganism system*. Such a concept has been widely used when dealing with the different categories of associations (root-nodule symbioses with *Rhizobium*, root-nodule symbioses with actinomycete-like organisms, ecto- and endomycorrhizae, rhizosphere systems, root-pathogen complexes, etc.).

1.2. The plant—microorganism system as a compartment of the soil—plant—atmosphere system

In spite of its advantages, the concept of plant—microorganism system may appear to be inadequate in some circumstances, in that it is restricted to the study of interactions between the plant and the associated soil microorganisms, thus overlooking the influence of the soil environment and the atmospheric parameters upon these interactions. Hence it may be appropriate to consider the plant—microorganism system as a compartment of the whole soil—plant—atmosphere system, a sub-unit of the ecosystem.

According to Tansley's definition (1935), the term *ecosystem* is used to describe "a system resulting from the integration of all living and non-living factors of the environment" (Fig. 1). To many authors, this term refers to a particular biological entity, a unit of landscape or a limited universe; for others the term ecosystem refers to a concept, the emphasis being put upon the interactions between biotic and abiotic components. Although Tansley's definition does not imply any lower limit for a given biological entity, the term "ecosystem" is not applied to simpler complexes such as the soil—plant—atmosphere usually designated as a system. This system is actually a subunit of an ecosystem, and one must consider the interactions between its different biotic and abiotic components.

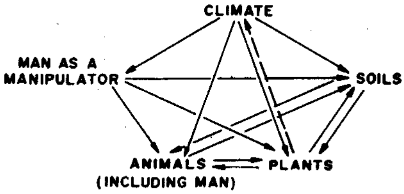

Fig. 1. Interactions among the different components of an ecosystem (Van Dyne, 1969).

The concept of the soil—plant—atmosphere system is not new. As early as 1928, Gradman used it when studying the flow of water through this system (Kramer, 1973). Gradually our knowledge of the functioning of the soil—plant—atmosphere system appeared to increase the understanding of how plants grow. On the other hand the concept of the plant—microorganism system presented in the first paragraph of this chapter emerged at the beginning of this century. Surprisingly, the concept of soil—plant—atmosphere and the plant—microorganism concept have been and are still referred to separately. This is indeed unfortunate since the microbial associations of plant roots make up a unique complex which must be considered as a compartment of the soil—plant—atmosphere system. This latter concept will prove to be most useful for the understanding of the interrelations between the plant and the soil microorganisms ranging from neutralism to various degrees of symbiosis and parasitism.

If the association between plants and soil microorganisms is assumed to be a component of the soil—plant—atmosphere system, the role of the physical and chemical environments, as far as these interactions are concerned, can be more easily explained. The factors affecting the activity of root microorganisms are shown diagrammatically in Fig. 2. Two categories of factors

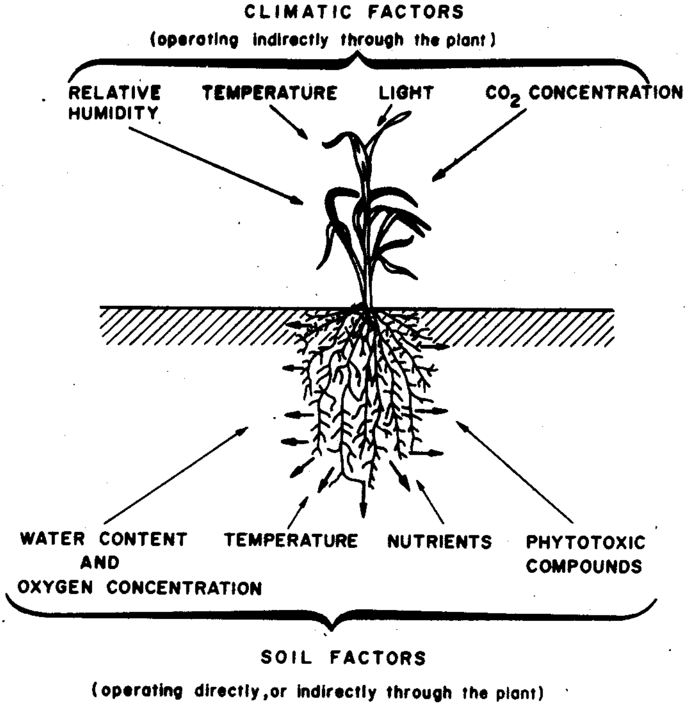

Fig. 2. Climatic and soil factors affecting activity of the root microorganisms.

are involved. (1) climatic factors such as light, which have often been overlooked by soil microbiologists, (2) soil factors, which can be divided into factors operating directly upon the microorganisms and factors operating indirectly through the plant.

Among the different climatic factors, light is probably of paramount importance. This parameter is known to affect the composition of the rhizosphere population (Rovira, 1965), but its influence on the activity of microorganisms associated with the roots has not received enough attention. However, our knowledge concerning this specific problem is progressively improving (p. 28). On the other hand, direct influence of soil factors is well known: a simple example is that of the repression of nitrogenase synthesis in N_2-fixing bacteria when soil ammonium content exceeds a critical threshold. Indirect influence has less frequently been studied, although it is of consequence in many instances. Thus the number of bacteria living in the rhizosphere of *Phaseolus vulgaris* well supplied with potassium was only 65 percent of that of plants grown in a low potassium medium. The reason for this depressive effect of high potassium level is that plants well supplied with potassium released through exudation only half the amount of organic compounds as did the plants low in potassium (Trolldenier, 1972). The influence of some of these environmental factors on exudation is discussed in detail on p. 181.

1.3. Biological equilibrium of the plant—microorganism system

Many ecosystems are characterized by a steady state balance, an equilibrium which is maintained by homeostatic mechanisms (Odum, 1971). The plant—microorganism system behaves roughly in the same way; nevertheless, microbial populations in this system do not exhibit a perfectly stable equilibrium, but rather an ever fluctuating one. The related fluctuations are either short-term ones, such as fluctuations induced by exudation rhythms, or long-term and more progressive fluctuations such as those linked to the plant growth cycle. As long as environmental conditions remain fairly constant, the aforementioned fluctuations are maintained within certain limits.

This equilibrium of the plant—microorganism system can be upset by different types of stresses, such as chemical or heat treatments, drought, irrigation or drainage, addition of organic matter, etc. The degree of stress required to upset the equilibrium varies according to the level of buffering of the plant—microorganism complex. Some systems are well buffered, such as those met with in plants growing in soils with high organic content harboring a host of saprophytic microorganisms. Others are poorly buffered, such as situations in plants growing in sandy soils. In well buffered systems a drastic shock is necessary to modify the structure of the microbial population: in the first step autochthonous microorganisms must be eliminated by heat or fumigation; in the second step alien microorganisms are introduced. This procedure has been successfully used for inoculating *Pinus radiata* with the mycorrhizal fungi *Rhizopogon luteus* and *Boletus granulatus* into nursery soils partially sterilized with methyl bromide. However, in some instances successful superimposition of selected mycorrhizal fungi on an existing microflora has also been reported (Theodorou and Bowen, 1973). This success is presumably attributable to the absence or at least the low density of competitive or antagonistic organisms.

2. INTERRELATIONS BETWEEN PLANT ROOTS AND MICROORGANISMS

2.1. The different plant—microorganism systems

Microorganisms are associated either with the aerial parts (e.g. phyllosphere) or with the underground parts. Only systems related to the underground parts will be dealt with here. These systems can be subdivided into different groups on the basis of the type of function of microorganisms involved or the type of existing structure.

2.1.1. Nodule symbiosis between roots and Rhizobium

Legume root nodules may vary markedly in structure, but usually four main regions can be recognized.

(1) Nodule cortex. This outer cortical zone is composed of 4—10 layers of undifferentiated, uninfected parenchymatous cells. Peripheral cells are often suberized and thickened in perennial nodules.

(2) Meristematic region. This growing region provides specialized nodule tissue. The shape and size of the nodule varies, depending on the characteristics of the meristem.

(3) The vascular tissue, which is connected with the root vascular system, is internal to the cortex.

(4) The central infected zone, which is separated from the vascular tissue by several layers of parenchymatous cells. This region is composed of swollen cells infected by the *Rhizobium* (bacteroids) and contains leghaemoglobin. In some cases, this zone may be composed of both infected and uninfected cells.

2.1.2. Nodule symbiosis between roots and actinomycete-like microorganisms

Alnus nodules exhibit the following structure:

(1) An enlarged outer cortical region composed of infected cells dispersed among the uninfected.

(2) An uninfected apical meristem, the growing region.

(3) A stele surrounded by an endodermis.

The nodule endophyte shows three different forms: (1) branched or unbranched hyphae, (2) septate vesicles developed at the hyphal tips; and (3) bacteria-like cells (Lalonde and Fortin, 1973).

2.1.3. Ectomycorrhizae

The structure of ectomycorrhizae varies depending on the plant species and the associated mycorrhizal fungus. However, it is possible to give a general picture of the ectomycorrhizal structure. The arrangement of this system is as follows:

(1) The fungus sheath or mantle, surrounding the feeder or young root tip.

(2) The Hartig net or intercellular network of fungal hyphae in the host cortex.

(3) Strands of hyphae and rhizomorphs growing from the sheath into the soil.

(4) Free living microorganisms (bacteria or fungi) thriving in or on the fungal sheath and forming the *ectomycorrhizosphere* (Bowen, 1973).

2.1.4. Endomycorrhizae

Among the different categories of endomycorrhizae, vesicular-arbuscular mycorrhizae (VA) are of paramount importance. In contrast to the ectomycorrhizal infection, VA mycorrhizal infection results in very little change in the external morphology of the root. VA mycorrhizal associations exhibit the following structure:

(1) Extramatrical mycelium formed by different degrees of hyphal growth on the roots. Fruit bodies and spores are found on the extramatrical mycelium.

(2) Epidermal and cortical zones of the root are invaded by internal hyphae which are inter- and/or intracellular, depending on the host species. Within the host cells the internal hyphae produce repeated branches termed *arbuscules*, similar to the haustoria of pathogenic fungi. The tips of hyphae often end in sac-like swellings called *vesicles* which are either inter- or intracellular.

2.1.5. Symbioses between roots and algae

The roots of many genera of the gymnosperm family Cycadaceae (e.g. *Cycas*, *Macrozamia*) form N_2-fixing nodules when they are infected by blue-green algae of the genera *Anabaena* or *Nostoc*. The structure of these nodules is different from that induced by actinomycete-like endophytes. According to Becking (1974), it comprises:

(1) An outer secondary cortex derived from a terminal meristem.

(2) An infected zone, filled with blue-green algae, developed from the protoderm (layer of cells analogous to the epidermis of uninfected roots).

2.1.6. Rhizosphere systems

In spite of the looseness and instability of this association and the variations occurring in the composition of the microbial populations, certain generalizations are possible. Typically the rhizosphere can be divided into three areas:

(1) The rhizosphere sensu stricto (= outer rhizosphere) comprising the region of the soil immediately surrounding the plant roots and the microbial populations inhabiting this.

(2) The rhizosplane (= root surface) formed by the root surface and the microorganisms living on it (Clark, 1949).

(3) The endorhizosphere (= inner rhizosphere) formed by the root cortical tissue invaded and colonized by saprophytic soil microorganisms (non-pathogenic host infection).

"To some degree these three areas should be regarded as a single microbial milieu with no sharp demarcations between them" (Old and Nicolson, 1975).

2.1.7. Root—pathogen complexes

Pathogenic soil microorganisms that invade plant roots and grow in their tissues are mostly fungi. Some of them are almost completely confined to the host tissues during the active phases of their lives, while others can grow