International Journal of Current Research and Review
DOI: http://dx.doi.org/10.31782/IJCRR.2022.14807

Review Article

IJCRR
Section: Life Sciences
ISI Impact Factor (2021-22): 2.176
IC Value (2020): 91.47
SJIF (2020) = 7.893

Soil Microbiota and Its Plant Interactions

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ABSTRACT

Microbial biodiversity comprises microorganisms belonging to all kingdoms: from prokaryotes (archaea and bacteria) to eukaryotes (fungi, microalgae, moulds, yeasts and protists). Microorganisms make up a large part of the earth's biomass, are extraordinarily diverse and are widespread in all habitats. More than two thirds of the total biodiversity consists of bacteria, while archaea and eukaryotes occupy less than one third. Microorganisms interact with each other and with the biotic and abiotic components of their environment, creating ecosystems in which there is a dynamic balance between the different components. The rhizosphere is the portion of soil surrounding the roots of plants, from which they absorb the essential nutrients and water they need to grow. In addition to the roots, there are further biotic components in the rhizosphere, such as: symbiotic microorganisms, beneficial and pathogenic bacteria, microscopic and macroscopic fungi. The aim of this review is to increase the knowledge about the interactions between plants and soil microorganisms.

Key Words: Sustainable agriculture, Microorganisms, Plants interaction, Soil research, Plant growth promoting rhizobacteria; Rhizosphere

INTRODUCTION

Since ancient times, some farmers have marvelled at how forests and grasslands could grow and vegetate without any fertilisation. Through long studies and after a long time we have been able to understand how this could happen. Much of what seems supernatural happens through a huge underground network of fungi and micro-organisms which, by interacting continuously, transfers and distributes large quantities of vital plant components such as nitrogen, phosphorus, manganese, sulphur as well as carbohydrates produced by plants.[1] Among the major players in this, are arbuscular mycorrhizae, symbiotic associations established between thousands of species of soil fungi and the roots of most terrestrial plants. Mycorrhizae are essentially filaments (hyphae) that support themselves on the roots of the host plant and permeate the surrounding soil, progressively probing it for nutrients.[2] Their combined action with a specific associated microbiome can extract key nutrients from the soil, store large amounts of carbon from the soil, retain and distribute water, buffer acidity and alkalinity and improve soil structure like no other. Unfortunately, some agronomic practices contribute to tearing apart this underground network with extremely negative results.[3] The distribution of this natural resource through deep tillage, forced cultivation, uncontrolled fertilisation and long resting periods has led to the need to use mineral substances, which are obtained with enormous expenditure of energy, depletion of natural resources and non-renewable fossil fuels.[4] One of the synthesis products of arbuscular mycorrhizae is glomalin, a glycoprotein containing 30-40% carbon. Glomalin is produced in large quantities by arbuscular mycorrhizal fungi (AM). In soils, the amount of glomalin was found to be correlated with the main fertility parameters. Laboratory analyses have shown that glomalin has a high affinity for iron and a strong ability to bind to heavy metals.[5] Under normal conditions, these elements are used by the associated plant for its metabolic functions, whereas in seriously contaminated soils, glomalin effectively sequesters the metals from the soil and then transfers them to the host plant if the latter is able to tolerate them: the higher the tolerance of the host plant, the greater the quantity of elements extracted.[6] Metal immobilisation of a highly stable protein fraction such as glomalin may be of considerable significance in al-

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ISSN: 2231-2196 (Print) **ISSN:** 0975-5241 (Online)

Received: 10.02.2022 **Revised:** 05.03.2022 **Accepted:** 22.03.2022 **Published:** 19.04.2022

leviating toxicity due to excess metals. The metal contained GSRP (Glomalin Related Soil Protein) may represent a system to avoid the loss of metals contained in the soil through leaching and their percolation into groundwater. Glomalin, thanks to its long persistence period in the soil, would act in this sense as a trap system capable of storing mineral nutrients and immobilising them. Glomalin is capable of creating aggregates by promoting flocculation and storing carbon in the protein and carbohydrate (glucose and sugars) subunits of the soil, preventing leaching. It has been discovered that the weight of glomalin is 2 to 24 times that of humic acids (the products of plant decomposition hitherto considered to be most responsible for storing carbon in the soil). Humic acids would contribute only 8% of the soil carbon.[2]

MICROBIAL BIOMASS

The term microbiome is often mistakenly used to refer to the set of microorganisms that inhabit a living being or part of it. However, the correct term to use here is 'microbiota'. Instead, the microbiome refers to the totality of the genetic make-up possessed by the microbiota, i.e. the set of their genes.[7] Almost all of us have been used to associating microbes and bacteria with a negative image since childhood. The 'bad' microbes that cause disease and infection are only a small part of the hidden world around us. Microbes are everywhere and not only live in close contact with us, but are indispensable for our survival and for the life of our entire ecosystem.[8] Preserving the life and diversity of microorganisms is just as important as combating the 'bad' ones, just think of the beneficial effects that taking probiotics (good microorganisms) can have on our health. This is why the use of substances that can harm this 'invisible' population is counterproductive. Several studies correlate the microbiome with the health status of the host, making microbiome analysis a new frontier not only in medicine, but also in agriculture.[9] Microorganisms can boost the immune system and prevent diseases, determine the productivity of soils and crops and thus improve growing conditions (Figure 1). Knowing the micro-organisms that colonise different soils and the relationship between the microbiome and the environment, which is strongly involved in the fate of ecosystems, is crucial in the interaction between plants and the land. Recent studies show that a strong correlation exists between the microbiome of the land and the microbiome of plants, resulting in an impact on food. Also in the food sector, the microbiome plays an important role in various productions, such as fermented products.[10] The microbial biomass represents a reserve of available nutrients, so soils with a high microbial mass have a higher capacity to make them available. Enzymatic activity is the ability of a soil to stimulate certain spontaneous biochemical reactions in the soil. Some reactions occur faster (e.g. urea degradation) if the catalysts are enzymatic. Intracellular and extracellular enzymes are present. Intracellular enzymes within microbial cells are responsible for normal metabolism, while extracellular enzymes make certain compounds available to organisms that are otherwise unusable.[11] The majority of enzymes in the soil are microbial in origin, so enzyme activity is an indicator of the presence of microorganisms in the soil. Micro-organisms interact with soil surfaces, so the greater the specific surface area, the greater the presence of micro-organisms.[12] In clay soils their presence is greater. Enzyme activity is also influenced by crop rotation (a maize-oats rotation results in an average presence and persistence 2/3 times higher than a single-crop maize rotation), tillage (less tillage, higher content) and pH. Among the enzymes, dehydrogenase is the one most involved in the early stages of organic matter degradation, its presence depending on the biological activity of microbial populations.[13]

BENEFICIAL MICROORGANISMS AND RHIZOSPHERE INTERACTION AND AGRONOMIC PRACTICES INTERFERENCE

Micro-organisms can adversely affect plant development without necessarily acting as plant pests.[14] Their action can alter the water supply, the uptake of ions and substances useful for growth, altering root functionality and/or limiting the harmonious development of the plant (Table 1). The main mechanism of action of the specific micro-organisms that improve the rhizosphere is competition with the harmful strains in the soil, thus favouring the availability and uptake of nutrients.[15]The various classifications of microorganisms in the rhizosphere distinguish between "major pathogens" and "minor pathogens", with the former penetrating the plant and causing the most damage, and the latter including obligate and facultative parasites.[16] Within the minor pathogens there are some, non-psraxic, growth-altering with their metabolites (DRMO Deleterious Rhizosphere Microorganisms), while others are parasites of plant tissue (Parasitising Minor Pathogens).[17] The pathogenicity of DRMOs is not easy to prove, as their effect on plants is limited to a delay in root growth without any other distinctive symptoms. The hypotheses that DRMOs belong mainly to different families, including *Enterobacteriaceae*, *Corynebacteriaceae*, *Pseudomonaceae* and *Bacillaceae*, are fairly consistent but not fully clarified.[18]

MECHANISMS OF MICROORGANISM ACTIVITY

Microorganisms can interfere with plant growth through competition and interference with the microflora naturally present in the soil.[19] Root growth, the length and number of root hairs and an efficient metabolism of the root cells are key aspects for an optimal uptake of water and less available ions in the soil such as P and K (Figure 2). There are micro-organisms that produce metabolites that hinder these processes and have a negative effect on plant growth.[20] Others, such as *Pseudomonas fluorescens*, produce secondary metabolites such as growth-promoting substances and antibiotics. The action of metabolites can alter cell wall structure, cell permeability, polysaccharide and acid secretion and enzyme release, all of which interfere with physiological processes.[21] We have to consider that for the plant the uptake of nutrients is an energy-intensive process and involves 60% of the root respiration under normal conditions.[22] The increased availability or ease of uptake, assisted by specific micro-organisms, contributes to the availability of energy that the plant can use for other more useful metabolic activities (Table 2). Changing the composition of the microbiome also serves this purpose.[23]

ROOTS COLONISATION WITH PGPR (PLANT GROWTH PROMOTING RHIZOBACTERIA)

The effectiveness of PGPR activity on stimulating plant growth depends mainly on the timely establishment and persistence of DRMOs.[24] The greatest effectiveness is obtained by treating the seeds and tubers from which they will colonise the root systems (Figure 3). It has been noted that PGPRs introduced via this route remained during the growing season even though their numbers gradually decreased compared to the total (more stable) population of fluorescent Pseudomonas.[25]Competition between micro-organisms increases as the overlap of their ecological niches increases. Some unfavourable environmental factors may reduce the effectiveness of PGPRs. The availability of $Fe3+$ is limited in alkaline and neutral soils and increases with increasing acidity. A higher activity of DRMOs and a lower suppressive activity of PGPRs on DRMOs could be expected as soil acidity increases.[26] Some clay minerals appear to have a pronounced effect on siderophore-mediated microbial activity. For example, the presence or absence of certain clay minerals has been correlated with the suppressiveness of certain soil-borne diseases. The presence of illite inhibited the antagonistic activity of *Pseudomonas fluorescens* on root pathogens such as Thielaviopsis basicola, whereas this activity was favoured by vermiculite. The inhibition seems partly attributable to the interference of clay with the ferric nutrition of the fungi. The environment may also affect the rate of exudate emission by the roots and their composition.[27]

PHOSPHORUS AVAILABILITY AS A RESULT OF MICROBIAL ACTIVITY

Phosphorus is a poorly mobile element in the soil and highly insoluble in non-neutral soils. Phosphorus is an essential element for plant development and is present in fair quantities in soils throughout Europe. However, it is always added to fertilisation plans because it is scarcely available to plants.[28] However, this route is not sustainable given the limited availability of mineral phosphorus (stocks are expected to run out by 2033), the very low yield (only 5% of the added P is assimilated by plants) and the negative impact (e.g. eutrophication of water). Given the type of soil on the European continent, new solutions are being developed that are both environmentally sustainable and economically advantageous.[29] The forms in which it is found in the soil are mainly phosphates (Fe, Al and Ca) or as gradually mineralised organic phosphorus. The reaction of the soil strongly influences its bioavailability: at a pH of less than 6, ferric phosphate prevails, and at a pH of more than 7, calcium phosphate, all stable and insoluble forms.Micro-organisms act on the breakdown of phosphorus organic compounds and the organification of mineral phosphorus. Mycorrhizae play a key role in phosphorus uptake by acting as root extensions and having high uptake efficiency even in more stable forms. Inorganic phosphorus present in the soil is transformed into soluble and available phosphorus by certain bacteria such as *Pseudomonas fluorescens*, *Bacillus amyloliquefaciens* and *Bacillus megaterium*. These bacteria are naturally present in our soils, but as they are sensitive to pollution and over-fertilisation, their presence is low if not absent in highly polluted soils.[30] A solution could therefore be to multiply them in the laboratory and inoculate specific microbial consortia for each plant, thus overcoming the problem of pollution and natural competitors.Organic phosphorus is made available to plants by enzymes (phytase and phosphatase) present in certain endomycorrhizal fungi. Endomycorrhizae live on the roots of plants and a symbiosis is established between them and the plant. Some of them are capable of supplying phos-

Table 1: Bacteria number per g of dry soil in the rhizosphere[39]

Root distance	Wheat	Swiss chard	Bean
50cm	2 x 107	1,5 x 107	1,7 x 107
35 cm	2 x 107	1,8 x 107	2 x 107
15 cm	3 x 107	2,2 x 107	2,2 x 107
0,2 cm	5 x 107	3 x 107	2,7 x 107
in contact	28 x 107	30 x 107	9 x 107

Table 2: Soil microflora processes that promote plant growth[33]

Diagnosis	Infant%
Organic matter decomposition	Bacillus, Streomyces, Clostridium
Symbiotic nitrogen fixation	Rhizobium, Bradyrhizobium, Frankia
Free nitrogen fixation	Azotobacter, Azospirillum
Nitrogen mineralisation	Bacillus, Pseudomonas, Serratia
Nitrification	Nitrobacter, Nitrosomonas
Denitrification	Achromobacter, Pseudomonas
Phosphorus solubilisation	Azotobacter, Enterobacter, Bacillus
Sulphur processing	Desulfovibrio, Thiobacillus
Iron processing	Ferribacterium, Leptohrix
Phytohormone production	Azotobacter, Azospirillum, Pseudomonas
Siderophores production	Erwinia, Pseudomonas, Aeromonas
Biocontrol	Pseudomonas, Bacillus, Streptomyces

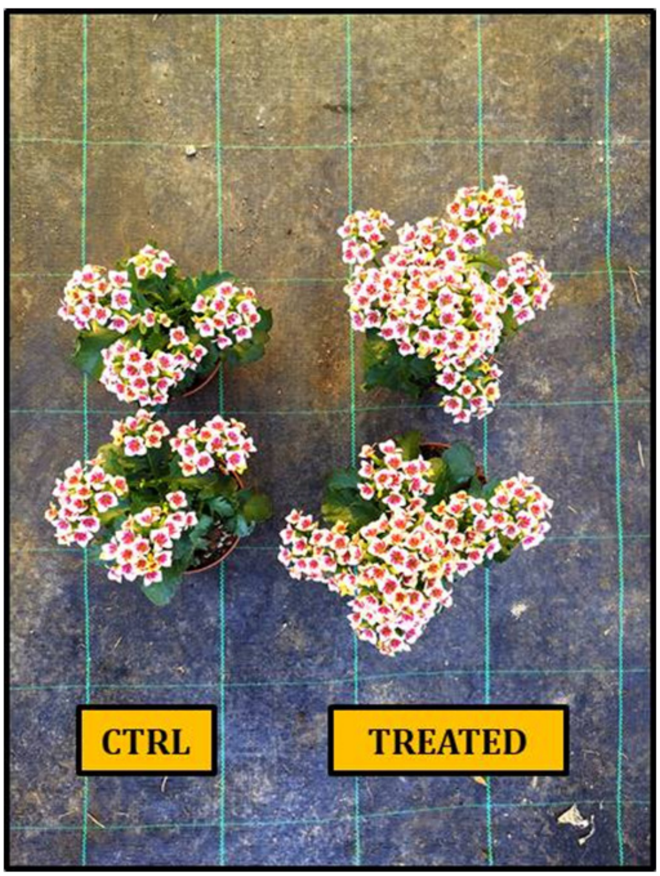

Figure 1: Microorganisms effect on flowering of Kalanchoe blossfeldiana

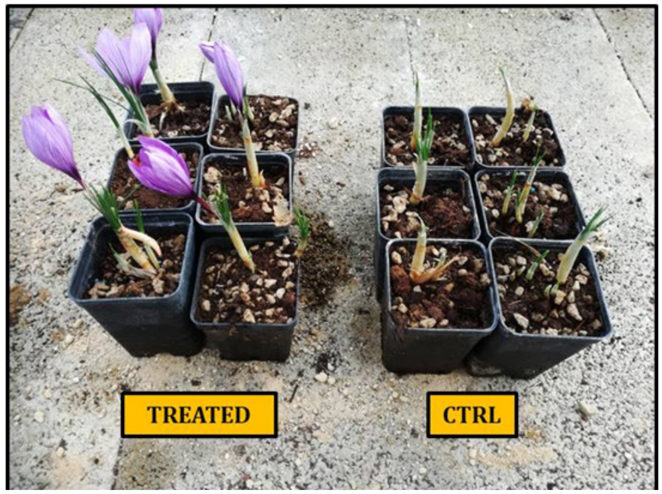

Figure 2: Microorganisms effect on flowering of Crocus sativus

Figure 3: Microorganisms effect on vegetative and roots growth of Kalanchoe tubiflora

phorus and water to the roots and in return take up carbohydrate substances.[31] There are endomycorrhizae that release phosphorus quickly, others that take a long time, others that are able to release phosphorus constantly and finally there are endomycorrhizae that do not interact with phosphorus at all. Combinations of different types of mycorrhizae are optimal as they result in immediate availability of phosphorus that remains constant over time. The endomycorrhizae generally used are *Glomus intraradices*, *Glomus claroideum*, *Gigaspora margarita*. The limit in the use of mycorrhizae is given by the quantity of phosphorus already present in the soil, in fact for the symbiosis to be established there must be a convenience on both sides. If the plant has sufficient phosphorus (a condition which rarely occurs) it has no need to enter into symbiosis with the fungus.[32]Actinomycetes are also present in the soil. They perform an activity of fundamental importance, as they preside over various operations such as: i) active participation in the decomposition of animal and plant tissues resistant to microbial attack; ii) they allow the formation of humus, through the conversion of organic residues into compounds typical of the organic fraction of the soil; (iii) regulate the microbiological balance of the soil through the production of antibiotics and probiotics (group B vitamins) that stimulate growth.[33]

AGRONOMIC PRACTICES EFFECT ON MICROBIAL ACTIVITY

The effects of micro-organisms, irrespective of the quantity present in a given soil, appear to be influenced by the agronomic practices carried out in that soil. Numerous studies and observations have suggested that microbial factors, more than the presence of normal pathogens, play a decisive role in, for example, plant yield. Among these factors, non-spore farming harmful microorganisms can play a decisive role.[34] The effect on yield reduction increases in some species (potato) as the cropping sequence is intensified, although the mechanism generating this effect is not yet fully understood. The effect is certainly related to host specificity as in crops other than potato (wheat, beet) the effects are less evident. One of the explanations may be that some harmful strains survive on the root residues of the crop, representing a potential inoculum for the colonisation of subsequent crops. As the frequency of cultivation increases, the phenomenon widens. Another hypothesis is the accumulation of compounds that stimulate the production of toxic metabolites. In the case of cyanide, glycine could be its precursor, as well as some ferric metals. Glycine and, to a lesser extent, proline, increase cyanide production by some microbial strains and both are constituents of radical exudates.[35] Studies have shown that glycine is resistant to microbial degradation and that proline and glycylglycine have a high affinity for certain clay minerals, remaining in the soil for a long time. One of the possible causes of the disease known as replant disease (the reduction in vigour and reseeding yield of the same species) is attributable to fluorescent and non-fluorescent strains of Pseudomonas. There is therefore evidence that part of the microflora present in the rhizosphere can adversely affect plant growth and development and that the activity of this microflora is influenced by agronomic practices.[5] Frequent tillage, especially deep tillage, has deleterious effects on soil microflora. In general, symbiotic microorganisms such as Rhizobium, some actinomycetes, mycorrhizal fungi and saprophytes increase the availability of nutrients and/or growth stimulating substances as well as suppressing parasitic and non-parasitic pathogens.[10]The inoculation of micro-organisms specific to the colonisation of the rhizosphere can lead to extremely positive effects.[36]The production of siderophores under Fe-limiting conditions is one of the effects observed. This results in strong competition with harmful microorganisms for Fe^{3+} ions in the rhizosphere. Siderophores are small molecules with a high affinity for iron and capable of effectively chelating it, generally produced by certain microorganisms, fungi and grasses. Siderophores are among the strongest Fe^{3+} chelating agents known.[37] The growth-promoting effect attributed to the removal of Fe available to harmful micro-organisms (DRMO) has been demonstrated in various experimental studies. Siderophores chelate Fe^{3+} that is no longer available to DRMOs, leading to a decrease in growth and virulence.[38,39]

DISCUSSION

In recent years, agriculture has faced the challenge of economic and environmental sustainability, reducing fertiliser use while adopting strategies to increase water use efficiency. Many microorganisms or fungi can promote the plant's use of nutrients and water in the soil.[7] There are numerous bacterial strains that promote root growth and are classified according to acting at the level of the rhizosphere and rhizoplane. Many studies carried out with growth-promoting bacteria (PGPR), which have given interesting results in a controlled environment or in vitro, have not been as effective in field crops in promoting plant growth. One of the problems encountered in the field with the use of microbial biostimulants is the use of live microbial mediums which make application by the farmer difficult.[5] To overcome this problem, microbial biostimulants are formulated and encapsulated with calcium alginate, which facilitates the retention and release of PGPR bacteria into the soil after application. Microorganisms that stimulate plant growth and resistance include arbuscular mycorrhizal fungi (AMF). They are effective in nutrient uptake but also in improving tolerance to abiotic stresses. One of the key characteristics of AMF is that they can only survive in symbiosis with the roots of the host plant. The improved quality of the plant in the nursery phase also has an impact on its behaviour in the subsequent cultivation phase. MFAs ensure a symbiotic relationship with the host plant, which makes it possible to overcome transplant stress and reduce the acclimatisation period.[15]

CONCLUSIONS

As is well known, fertility depends on the physical, chemical and biological properties of the soil. However, biological soil fertility is often forgotten and is much less studied than the others. It is linked to the activity of micro-organisms, on which the balance of nutrient cycles such as nitrogen, phosphorus and sulphur depend. It is therefore necessary to investigate a number of aspects related to plant growth promotion such as: (i) how the action of DRMO siderophores on plant growth and field yield occurs and takes place; (ii) whether siderophores of PGPRs are produced in the rhizosphere; (iii) whether it is possible to genetically manipulate siderophores to increase the effectiveness of PGPRs.

ACKNOWLEDGEMENT

The author would like to express his heartfelt gratitude to his colleagues at CREA Research Centre fr Vegetable and Ornamental Crops in Pescia and to all other sources for their cooperation and guidance in writing this article.

Source of Funding:

None

Conflict of Interest:

The author declares no conflict of interest.

Authors' Contribution:

The author confirms sole responsibility for the following: study conception and design, data collection, analysis and interpretation of results, and manuscript preparation.

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