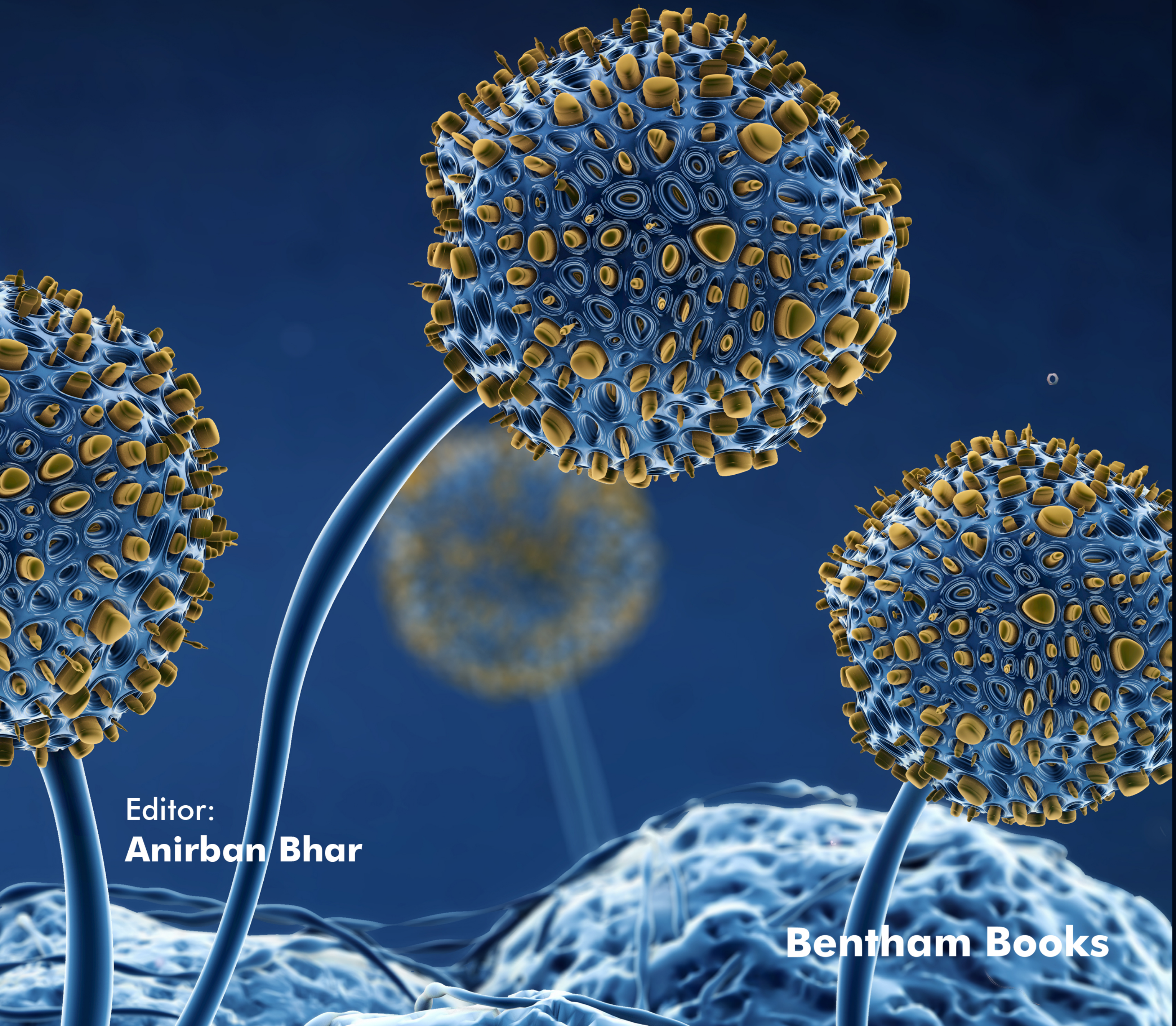
PLANT-MICROBE INTERACTIONS:
A COMPREHENSIVE REVIEW



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Plant-Microbe Interactions: A Comprehensive Review

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Plant-Microbe Interactions: A Comprehensive Review

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FOREWORD

Plants, being sessile organisms, are constantly exposed to the infection and disease caused by different microbial pathogens, including bacteria and fungi. The resistance of a plant to a pathogen attack depends on its efficiency in the elicitation of defense molecules like phytoalexins, salicylic acid, jasmonic acid, *etc*., as well as on the activation of diverse signaling pathways and induction in *resistance* (*R*) and *pathogenesis-related* (*PR*) genes, altogether triggering plant immunity. However, certain infections caused by microbes are beneficial in nature as well, especially the legume-*Rhizobium* interaction that facilitates symbiotic nitrogen fixation *via* nodule formation, or the microbiome association in the rhizosphere region that allows stress tolerance, phytoremediation of heavy metals in soil or stimulates nutrient absorption in nutrient-depleted soil. Hence, plant-microbe association is a double-edged sword, having both detrimental and beneficial consequences. It is therefore crucial to understand this association by identifying and characterizing the biochemical and molecular pathways, using high throughput genomics, proteomics, metabolomics, and genetic engineering techniques. In this regard, this book titled, "*Plant-Microbe Interactions: A Comprehensive Review*" encompasses quite an exhaustive coverage of important topics, supported by contemporary literature.

The chapters include various facets of co-evolutionary dynamics of plant-microbe interaction, understanding the fungal and viral interactions from a broader perspective, and assuming case studies with particular plant species. Emphasis has been given to the association of nitrogen-fixing bacteria and the biotechnological perspective of legume-pathogen interaction. The inclusion of chapters on rhizosphere and phyllosphere microbiome in the context of stress resistance and increased nutrient acquisition also appears justified, since a lot of research is currently going on in these areas. Researchers working in the field of salt tolerance would benefit from the chapter on halotolerant plant growth-promoting rhizobacteria. The chapter on understanding plant-microbe interaction, based on artificial neural networks is also unique. The chapters presented in this book will collectively address the critical need to understand plant-microbe interactions for the benefit of both the plant community as well as the environment.

I am delighted that this edited volume "*Plant-Microbe Interactions: A Comprehensive Review*" is finally being published. The chapters are elaborately written by established and active scientists and researchers, working in the concerned area.

Finally, I congratulate the editor for making sincereefforts to unravel this illustrious volume, and I am sure that this book will highly cater to the needs of all researchers, students, and academicians, working in the relevant field.

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PREFACE

The plants are constantly interacting with diverse microbial communities in the environments. The constant co-evolution of microbes with plants not only shapes the ecological balance but also determines plants' fitness in a particular environmental condition. The plant-microbe interaction has always been an interesting field of study to decipher unsolved puzzles in these intriguing relationships. Such interactions are of two types, beneficial and harmful interaction. The harmful interaction determines pathogenesis and biotic stress in plants. The beneficial interactions, on the other hand, help plants in nutrient acquisition, nitrogen fixation, and biological control systems against diverse pathogen groups. Although, many studies have been reported demonstrating, biotic stress and beneficial microbes act as plant growth-promoting microorganisms (PGPM) or biological control agents. These two interactions were always studied separately, but in nature both harmful and beneficial microbes interact with the plants synergistically. The in-depth knowledge about the entire interacting microbiome community with plants is necessary to describe this interaction more efficiently. At the same time, knowledge of this balanced interaction would also be useful for future biotechnological and agronomic applications. Recently, many pieces of research have focused on decrypting phyllosphere and rhizosphere microbial communities associated with economically important crop plants to analyze pathovar, core microbiome, and PGPMs. In this view, the present book has been designed to comprehensively accrue contemporary scientific knowledge encompassing all types of plant-microbe interaction for knowledge updation as well as for future agro-biotechnological applications.

In summary, the book is believed to advance our knowledge in the field of plant-microbe interaction, inform practical applications, and contribute to sustainable agriculture, ecosystem conservation, and biotechnological innovations. It addresses the critical need to understand these interactions for the benefit of both plants and the environment.

I would like to thank all the contributing authors for sharing their experiences and enriching the book with their valuable research findings.

My sincere thanks and gratitude are also extended to all the editorial and managerial team of Bentham Science Publishers for their continuous support.

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CHAPTER 1

Co-Evolutionary Dynamics of Plant-Microbe Interaction; A Comprehensive Outlook

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Abstract: The co-evolution of plants and their associated diverse microorganisms has been a field of wide scientific research since the past. However, the ecological relevance of such co-evolution has recently been realized. According to the theories of evolution, 'survival of the fittest' has been an age-old fundamental concept, where every organism modifies itself to adapt to its changing environment while sustaining its vital processes. Understanding the interactions at the molecular level between the stationary plants and their diverse interacting partners has not only helped in deciphering the basis of evolution but also provided a better outlook towards the multidimensional interactions between the organisms of the plant microbiome. Ideally plant 'holobiont' comprises the host and all microbial partners of its different locations such as the rhizosphere, endosphere, and phyllosphere. The behavioral patterns of the microbes with their hosts located at different zones designate them as symbionts, commensals, and/or pathogens. Each type of relationship has its basis of establishment and evolution. The present study aims to explain the basis of the evolution of plant-microbe interaction ranging from symbiosis to parasitism and understanding its evolutionary dynamics from an ecological perspective. Besides, the study shall also explain the role of microbiome in plant-microbe interaction and its ecological significance when subjected to climatic undulations. Overall, the study aims to put forth a comprehensive outlook on the understanding of ecology-driven evolutionary changes of plant-microbe interaction and its relevance in the present age of climate change.

Keywords: Antagonism, Climate change, Commensalism, Ecology, Exosphere, Holobiont, Microbiome, Mutualism, Mycorrhizal fungi, Phyllosphere, Plant-microbe interaction, Rhizobacteria, Rhizosphere, Symbiont, Terrestrialization.

INTRODUCTION

The origin of land plants dates back to 420 million years ago during the period of late Silurian, while the origin of microbes is reported to have occurred much ear-

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lier around 3.4 billion years ago [1, 2]. Timeline analyses have shown that the diversification and establishment of plants on land have taken place when the microbial world had already been well settled on Earth. Thus, under the profound ancestral influence of microbial communities how the plants originated, established themselves, and functioned as one of the pivotal entities of almost all ecosystems on Earth, is undoubtedly an intriguing question of evolutionary biology [3]. Plants are not only termed as the food producers of the biotic world but also referred to as niche providers that provide shelter to numerous micro and mega organisms of diverse structures, functions, and behavioral patterns [4, 5]. The history of the origin of photosynthesis however dates back to 1967 when scientist LynnMarguilis (then Lynn Sagan) in her article 'On the Origin of Mitosing Cells', published in the Journal of Theoretical Biology hypothesized the origin of solar energy trapping organelle 'the Chloroplast'. Chloroplast originated when a non-photosynthesizing bacterium engulfed a photosynthesizing cyanobacterium through the unique process called 'endosymbiosis'. The same process also gave rise to the oxygen-generating organelle 'the mitochondria' when an aerobic prokaryotic (possibly alpha-proteobacteria) bacterium was engulfed by a heterotrophic anaerobe. Lynn also suggested that the eukaryotic flagellum (named undulipodium) and the mitotic apparatus were formed from a spirochaete-like organism by endosymbiosis [6]. Increasing phylogenomic evidence has, however, suggested that the present-day distribution of photosynthetic machinery within six phyla, namely 1) cyanobacteria or blue-green algae,2) proteobacteria of purple bacteria, 3) green sulfur bacteria, 4) heliobacteria or firmicutes, 5) green non-sulfur bacteria and 6) acidobacteria have taken place by horizontal gene transfer (HGT) through independent phylogenetic lineages, which makes the evolutionary tree of photosynthetic very complex. All the above-mentioned bacteria were phototrophic except proteobacteria [7]. Although photosynthesis is known as a well-concerted metabolic process its various subsystems such as photosynthetic pigments, light-harvesting antenna systems (LH), reaction centers (RCs), electron transport, and carbon fixation pathways are believed to have originated *via* diverse evolutionary trails [8].

Besides photosynthesis, plants are known for their distinctive ability to provide habitation to diverse groups of organisms. Plants are believed to have probably acquired the said property because of their sessile nature, which occurred with the migration, settlement, and colonization of plants from aquatic environments to land locations. The aquatic paraphyletic group of green algae belonging to Charophyta with the order Zygnematales is reported to be the nearest ancestor of land plants [9]. Zygnematales members were marked for the absence of motile sperms which the remaining Charophytes possessed. Such gradual retraction of flagella leading to the cessation of motility possibly was a transition where mobile lower groups of plants started adapting to land habitats [3]. Interestingly, the origin of land plants from the algal ancestral lineage showed exciting illustrations of bacterial-algal interactions that put possible endorsements to the fact that biotic interactions not only shaped the algal evolution but also had a signature role in the colonization of land plants [10]. Phylogenomic studies suggested Zygnemataceae family members *Spirogloea muscicola* gen. nov. and *Mesotaenium endlicherianum* to be the closest members of earliest diverging embryophytes and bryophytes; all of which shared similar sub aerial/terrestrial traits. Genetic analyses further indicated the presence of significant genes that controlled biotic and abiotic stress resilience properties (desiccation tolerance) both in Zygnematacean members as well as early land colonizing embryophytes and bryophytes. These genes were found to have originated from soil bacteria by HGT [11]. Hence, it remains clear that the event of terrestrialization of plants, considered one of the most significant phenomenons of the evolution of life on Earth, was predominantly controlled by the primeval residents of Earth, the microorganisms.

Thus, once settled, plants gradually acquired roots and vascular systems giving rise to different classes of plants that adapted to the land habitats. On the other hand, the rooted nature made the plants sessile and exposed them to diverse groups of interacting partners with varied behavioral patterns. Although remarkable developments have taken place over the past few decades in establishing the modes and mechanisms of plant-microbe interaction, even then research, long-standing discussions, and debates continue to argue about why and when a plant and microbe/s enter into communication. However, high throughput experimental studies have established that signal-mediated sensory manipulation of both interacting partners termed the 'Coercion' property is the main guiding force behind the initiation of communication [12]. Previous research on coercion suggested having two modes of stabilized coercive communication where microbial coercion means manipulating plant phytohormones while plant coercion suggests maneuvering quorum sensing infochemical of microbes [12]. Amongst several interacting partners, plants coexist with some microbes that facilitate their growth and development and are called symbionts, some remain as commensals with no advantage to the host plant, while a handful modify themselves and compete with the host plants for nutrition and space and get transformed into pathogens [13]. Besides some other microorganisms which surround the host plant may have no direct influence on the host performance under a particular spatial and temporal scale, but may reprogram themselves to hold direct or indirect influence on the host plant under changing climatic conditions. All the above microbes with their differential behavioral patterns are referred to as the 'plant microbiome' where all the organisms individually serve as a 'metaorganism' [14, 15]. The entire plant microbiome is reported to have an impact on shaping the ecological evolutionary trajectories with 'plant holobiont'

CHAPTER 2

Decoding the Role of Rhizosphere and Phyllosphere Microbiome in Biotic Stress: A Treasure Trove of Nature

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Abstract: Biotic stress imposes several detrimental effects such as nutritional and physiological imbalance that subsequently leads to a huge yield loss of crop plants. Climate change and rapid urbanization also act as positive catalysts for the prevalence of biotic stressors. Acquiring the knowledge of dynamic rhizosphere and phyllosphere microbes has opened a new horizon of eco-friendly, economical biotic stress management of plants that can also overcome the drawbacks of traditional agricultural practices. Plant growth-promoting rhizobacteria (PGPR) are potent biocontrol agents that can mitigate biotic stress by several mechanisms such as by modulating plant growth regulators, producing extracellular polysaccharides (EPS), up-regulating defence responsive genes, and stimulating Induced Systemic Resistance (ISR), which subsequently increase plant productivity and stress tolerance. Moreover, with respect to above-ground plant-microbe interaction *i.e.* Phyllosphere microbial communities (PMC) have immense potential to ameliorate biotic stress by modulating phytohormone and changing existing microbial communities. Even though, our knowledge about these hyper-diverse beneficial plant-microbe interactions is still illusive. In this chapter, we have critically analyzed the role of PGPR and PMC in biotic stress management, in light of promoting this agricultural practice on a large scale.

Keywords: Biotic stress, Climate change, Plant growth promoting rhizobacteria, Phyllosphere microbial communities, Plant-microbe interaction.

INTRODUCTION

Plant stress may be defined as the external factors that impose several detrimental effects on plant growth, development, and yield [1]. Being sessile in nature, plants

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are always exposed to a wide range of environmental stresses namely biotic and abiotic stress conditions [2]. Living organisms such as bacteria, viruses, nematodes, fungi, and insects are primary causative agents of biotic stress in plants [1] that are responsible for the yield loss of about 35% [3]. Although biotic stressors of plants are quite dynamic, interestingly plants may anticipate the predictable pattern of stressors in their life cycle [4]. Wilting of plant parts, root rotting, seed damage, and leaf spot are some common symptoms of biotic stress [5].

Climate change has multidimensional effects on agricultural crop productivity. Therefore, it is inevitable to develop environmentally friendly and sustainable agricultural policies to cope with the food security challenges [6]. Global warming and rapid climate change induce the prevalence of biotic and abiotic stress in plants [7]. Atmospheric CO_2 concentrations and secondary air pollutants are increasing rapidly due to the indiscriminate use of fossil fuels in this anthropogenic era, reducing the nutritional content of staple crops. Furthermore, climate change also enhances reproductive potential and expands the geographical distribution of pathogens, thus leading to a drastic change in the disease dynamics of plants [8]. According to WHO reports, the population on the Earth will reach about 8.8 to 11.6 billion in the year 2100, and also the demand for food for an energy-rich diet will increase from 59% to 98% in 2050 [9].

Plants have evolved sophisticated defence responses to mitigate the adverse effects of biotic stress; they may sense the environmental cues and modulate several genetic changes to survive by synthesizing defensive secondary metabolites and proteins. Moreover, phytohormones Salicylic acid (SA), Jasmonic acid (JA), and Ethylene (ET) play a crucial role in activating systemic defence response in plants, in response to biotrophic, hemibiotrophic and necrotrophic pathogens [10]. Transcription factors (TFs) have a significant role in genetic modulation under stress conditions; WRKY, NAC, bZIP, and MYB are some reported TFs that enhance stress tolerance by the upregulation of several stress-responsive genes in crop plants [3]. As plants are devoid of adaptive immune systems and specialized immunological cells, plants' immunity to pathogens mainly relies on an intricate signalling cascade. Signature molecules of invading pathogens such as Pathogen-associated molecular patterns (PAMP) and microbe-associated molecular patterns (MAMP) help the host plant to identify a class of pathogens and subsequently develop pattern recognition receptor (PRR). MAMPs/PAMPs-PRR interplay stimulates PAMPs-triggered immunity (PTI) by the upregulation of Ca^{2+}accumulation and ROS generation that leads to oxidative burst [11].

Hybridization, backcross breeding, and composite crossing are some of the most primitive and tedious methods of crop improvement to cope with stress conditions. Thereafter, several molecular genetics approaches have evolved such as marker-associated selection (MAS) and virus-induced gene silencing (VIGS) to mitigate the deleterious effects of stress [12]. Breeding programs for crop improvement become unfeasible due to the non-availability of appropriate resistance sources. It develops new alternative approaches referred to as plant genetic engineering. The most prominent example of genetic engineering is the development of insect-resistant plants by cry gene, isolated from *Bacillus thuringiensis* [13].

The plant system is encompassed by microorganisms; there are three main hot spot regions for plant-microbe interaction namely phyllosphere (above-ground microbiome), rhizosphere (roots associate microbiome), and spherosphere (seed microbiome). Plants can modulate the surrounding microbial population by secreting organic compounds and complex molecular signalling [14]. The Rhizosphere, the surrounding zone of plant roots is a specialised ecological niche that contains a wide diversity of microorganisms. On exposure to insects and pathogens, plants recruit beneficial microbes that subside the activity of the pathogen. Nevertheless, they also promote nutrient uptake and boost host immunity. *Arthrobacter Azotobacter, Azospirillum, Alcaligenes, Klebsiella, Bacillus, Enterobacter*, and *Pseudomonas* are some dominant PGPRs that promote plant growth and disease resistance [15, 16]. Whereas, dynamic communities of above-ground microbes inhabit as epiphytic (on the external surface) and endophytes (internal spaces) referred to as phyllosphere microbiome, also impart disease resistance from pathogens [17].

In this study, we have critically evaluated the remarkable role of rhizospheric and phyllospheric microbiomes in biotic stress amelioration. Rhizosphere and phyllosphere are the two most prominent zones of plant-microbe interaction (Fig. **1**). Our knowledge about the phyllosphere and rhizosphere microbiome is still elusive. Therefore, they deserve more attention from plant biologists regarding the dynamics of microbiomes, and the mechanism of action of these microbiomes, which will ultimately help us to cope with the increasing biotic stress condition and food security.

CHAPTER 3

The Application of Artificial Neural Network in Plant-Microbe Interaction and Future Crop Health Surveillance

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Abstract: Plants are the most important constituents of our environment. Despite their function in producing energy by capturing photons from sunlight, they are the only source of atmospheric oxygen by the process of photosynthesis. Since the last 100 years, a huge amount of agrobiodiversity has been lost and many are at risk of extinction. The existing crop plants are also at the constant threat of different biotic and abiotic stress factors. Every year yield of the agricultural crops is curtailed dramatically by changing environmental pressure and associated pathogenic ingression. Many works are carried out in this field to demonstrate defense signaling in plants in response to either biotic or abiotic interactors. Artificial neural networking (ANN) system is a revolutionizing bioinformatic technology that can predict any problem with maximum logic depending on the weights given in different situations. The application of this ANN in predicting biological networks will be capable of changing the scenario of plant infection biology completely. In such context, the present article intends to demonstrate basic ANN and their probable application in future plant-microbe interactions to develop a sustainable agrosystem.

Keywords: Artificial intelligence, Biological network, Gene interaction, Neural network, Plant-microbe interaction.

INTRODUCTION

Intelligence is nothing but the ability to acquire and at the same time apply knowledge promptly by analyzing temporal as well as spatial situations of a phenomenon. Colloquially "artificial intelligence (AI)" is an improvisation of mechanical algorithms to learn, analyze, and demonstrate a particular problem of any kind by using its analytical power. AI is used in wide fields including scienti-

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fic studies and big data analysis to maximize its chance of achieving a cognitive goal and successful predictions [1]. "Neural network system" is a modern application-bound algorithm deploying AI as its core. The analysis power of any animal including human beings is dependent on its billions of neural connections concentrated mostly in the brain. The neural network system is an AI-based network that can analyze a problem with all the possible angles and give an output (suggestions) with maximum logic [2]. Nowadays neural networking systems (NNS) are a popular tool for analyzing different complex biological networks. Plant science, the most important branch of biological science is not an exception to employ the AI system to solve different problems associated with it. The important issue associated with plant science is its production, yield, and quality improvements. All the above-mentioned criteria are well connected with the global economy and nutrition [3]. Besides, population outbursts and rapid urbanization are other threats to mankind to meet the needs of these unexpected oversized citizens of Earth. Biotic stresses of plants are responsible for dramatic curtail in the yield of crops globally. Scientists across the globe are tirelessly searching the ways to minimize yield loss due to biotic ingressions. Advancements in different scientific tools including computational techniques enable modern agriculture to analyze the gross health of the crops by employing different algorithms. The development of AI has the tremendous possibility of predicting diseases and other health conditions of plants related to yield and acting accordingly to meet global demand. The present article tries to emphasize concepts of basic artificial neural network systems for biologists and the probable application of NNS to solve the complex metabolic networks in a plant-microbe interaction. Further insight is given into chickpea networks under *Fusarium* attack to predict clues in defense signaling pathways to restrict the pathogen attack and improve yield. The enormous possibilities and some obvious future questions are also discussed.

Artificial Neural Network (ANN)

The artificial neural network system is an application of "artificial intelligence" categorically inspired by the nervous system in animals. Mainly, the neural network system is used to solve complex biological networks that are hard to analyze or difficult to infer for the human brain instantly [4]. It has long been used in the field of computer technology but has very recently been applied in biological systems too. Although successful applications can be found in speech processing, image recognition, pattern classification, visualization, robotics, marketing systems, numerical variation, *etc.* application in biological systems, particularly plant science is elusive. Mature functionality as well as 100 percent accuracy is long-awaited but constant incorporation of newly built problems leads to modification and improvements of the networking system day by day [5].

ANN, The Basic Architecture of the Networking System

The neural network system was inheritable from the pioneering work of Warren Mc Cullock and Walter Pitts demonstrating logical calculation popularly known as threshold logic [6]. "The nets without circles" emanating into modern-day artificial neural network systems with their semi-absolute reasoning compatibility. The neural network relies on computational neurons called "perceptrons" that can analyze single to multiple binary inputs and express a single binary output [7]. The perceptrons (X1, X2, X3,……..Xj) analyze the inputs based on their weights (W1, W2, W3,….. Wj) in real numbers. The sum of the inputs along with their weight is finally calculated by the system and a particular threshold value is given for a particular problem. The output result depends on the weighted value that is below the threshold (0) [∑j WjXj ≤ Tj= 0] or above the threshold (1) [∑j WjXj ≥ Tj=1] (Fig. **1**).

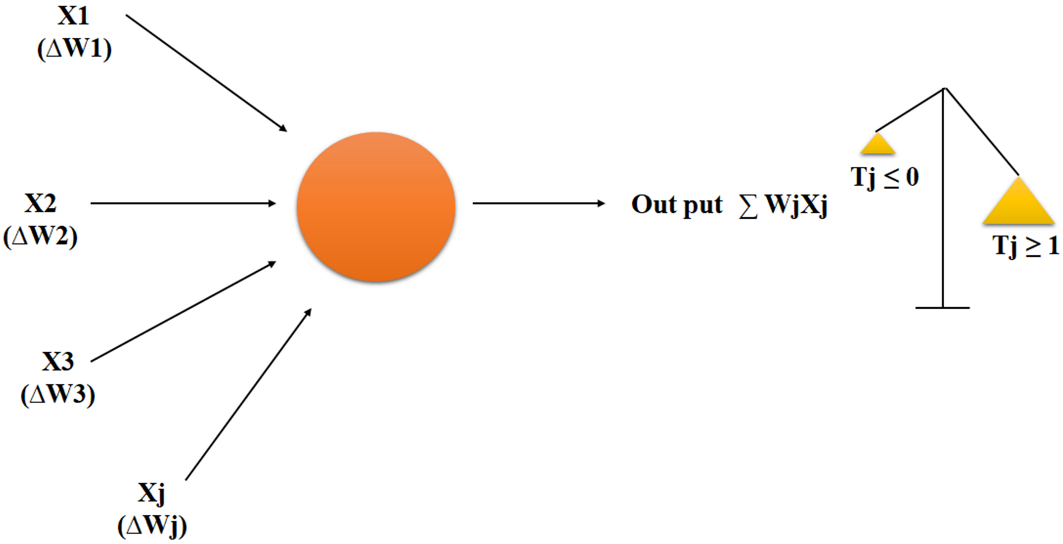

Fig. (1). Schematic representation of basic neural network system where outputs are based on the weighs of different controllers and threshold values designated on them.

Biological systems are complex, so it is difficult to infer based on a single perceptron. Further, a single target can be modulated by so many different factors with different modes of inference. All of these factors further do not have equal power to modulate a particular phenomenon, *i.e.*, having different threshold weights of the threshold we can easily modify the decision of a neural network. The more weight of the threshold of a factor demonstrates that the factor has greater abilities to modify the reaction and the phenomenon is called network biasness [8]. Hence, perceptrons can analyze a particular problem and give a

CHAPTER 4

Mixed Virus Infections in Rice

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Abstract: Rice is one of the highest consumed food gains in the world and is a key commercial product in the world economy. However, recurring outbreaks of viral diseases in rice lead to a significant loss of yield and economy in several Asian, African, and Latin American countries. Mixed virus infections are common in field conditions. They often lead to synergistic enhancement of the pathogenicity of one or both infecting viruses. However, in certain cases, antagonistic interaction between the viruses leading to the suppression of infectivity of one by the other virus has also been reported. Out of all rice-infecting viruses, 4 pairs of viruses are known for being involved in mixed infection, where symptom development and pathogenicity of the diseases get synergistically enhanced. Rice tungro disease is one of the most well-known diseases in this category that occurs due to simultaneous infection by the *Rice tungro spherical virus* and *Rice tungro bacilliform virus* and is responsible for major economic losses in South and Southeast Asia. On the other hand, mixed infection by Southern rice black-streaked dwarf virus and Rice ragged stunt virus came into the picture rather recently. Interestingly, all the mixed virus infections in rice are transmitted by insect vectors. Therefore, elucidating the complex interactions between the host-virus-vector pathosystems is pivotal for finding ways to control both single and mixed virus infections in rice.

Keywords: Antagonistic interaction, Leafhoppers, Mixed virus infection, Rice virus, Synergistic interaction, Tungro disease.

INTRODUCTION

Hosts and pathogens coevolve in the never-ending evolutionary arms race. The pathogens are a threat to hosts. Therefore, the host develops different defense mechanisms to counter the pathogens. As a reciprocal effect, pathogens also develop adaptive genetic change to overcome the defense [1]. However, the gradual course of plant-pathogen co-evolution significantly accelerated due to different factors like the domestication of plants, and the introduction of agricultures [2]. As per the general consensus, the spread and movements of

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human started approximately 8000 years ago leading to the gradual distribution of crops from their original centers of domestication [3 - 5]. Interestingly, the history of plant-virus co-evolution and spreading also follows this trend closely. For example, the spread of potyviruses, the largest group of plant-infecting RNA viruses, to the high number of species seen today was shown to be triggered by the introduction of agriculture around 6600 years ago [6], while the spread of *Banana streak virus*, (family *Caulimoviridae*), in East Africa, was dated around 5000 years ago [3]. Currently, the threat to food production by viruses is increasing rapidly due to increased human activities like trades and movements of plants away from the centers of domestication leading to alterations in plant-viru--vector pathosystems [2]. As a direct result of these activities, there is an expansion in the host range of the viruses as they can now spread from native plants to introduced crops. Similarly, the risk of emergence of more severe diseases due to the symbiosis between multiple viruses has also increased [7, 2]. For instance, cassava was originally domesticated in Central America, and thereafter it was introduced to Africa. Indigenous African begomoviruses like *African cassava mosaic virus* (ACMV) and *East African cassava mosaic virus* (EACMV), earlier infected native plants and then started spreading to cassava to cause cassava mosaic disease (CMD). This disease was first reported in 1894 in Tanzania, while by 1940, it spread across the whole of Africa. The most severe variety of CMD was reported in Uganda in 1990 that was caused by the synergistic interaction between ACMV and a virulent recombinant EACMV-like virus with concomitant appearance of a new virulent whitefly vector biotype [2, 8].

Viruses are a major cause of plant diseases, and they comprise approximately 50% of pathogens responsible for emerging and reemerging plant diseases worldwide [9]. Stunted growth, deformed appearance, reduced crop yield, and lower quality are some of the commonly associated viral infections [9]. While begomoviruses, tospoviruses, and potyviruses are the major groups of plant viruses that pose an imminent threat to global food security, individual members from other virus groups like *Rice tungro spherical virus* (RTSV), *Rice tungro bacilliform virus* (RTBV), *Faba bean necrotic yellows virus*(FBNYV), *Banana bunchy top virus*(BBTV), *Rice yellow mottle virus* (RYMV), and *Groundnut rosette virus*(GRV) with its satellite RNAs are responsible for causing the emergence of major plant diseases in certain parts of the world. Cumulatively, they account for crop losses of more than $30 billion annually [10]. Rice (*Oryza sativa*) is one of the most important staple food crops consumed by humans worldwide for nutrition and calories [11]. However, viral diseases pose a major threat to global rice production. Currently, 17-19 rice viruses are reported to cause intermittent outbreaks of diseases in rice in different parts of Asia, Africa, and Latin America [12, 13]. RTBV, RTSV, *Rice grassy stunt virus* (RGSV), *Rice* *ragged stunt virus* (RRSV), *Rice black-streaked dwarf virus* (RBSDV), *Rice stripe mosaic virus* (RSMV), RYMV, *Rice gall dwarf virus* (RGDV), *Rice dwarf virus* (RDV), *Rice stripe virus* (RSV) and *Rice stripe necrosis virus* (RSNV)are among the notable ones causing significant yield losses in rice production [11 - 13] Chen *et al.*, 2019a [14 - 16] Teng *et al.*, 1988; Tantera 1985). Table **1** presents the major rice viruses, their host ranges, and geographical distributions compiled from the public database https://www.dpvweb.net/ [16]; and other kinds of literature [12, 17 - 21].

Table 1. List of rice infecting viruses with family, host range, and geographical distribution.

Virus Name	Genus and Family	Host Range	Geographical Distribution
Rice dwarf virus(RDV)	*Phytoreovirus, Sedoreoviridae*	Restricted to a few species of Gramineae	Japan and Korea
rice stripe virus (RSV)	*Tenuivirus, Phenuiviridae*	Rice, maize, wheat, oat, foxtail millet and wild grasses	China, Japan, Korea, Taiwan
rice black-streaked dwarf virus (RBSDV)	*Fijivirus, Spinareoviridae*	All known host plants are members of the Gramineae	China, Japan, Korea
rice grassy stunt virus (RGSV)	*Tenuivirus, Phenuiviridae*	Rice is the only natural host	India, Indonesia, Japan, Malaysia, Philippines, Sri Lanka, Taiwan and Thailand
rice tungro bacilliform virus (RTBV)	*Tungrovirus, Caulimoviridae*	*Echinochloa crus-galli, E. glabescens, E. colona, Eleusine indica, Leptochloa chinensis, Leersiahexandra, Oryza sativa, Panicum repens, Cyperus rotundus.*	The virus is found in most of the rice-growing countries of South and Southeast Asia.
rice tungro spherical virus (RTSV)	*Waikavirus, Secoviridae*	*Echinochloa crus-galli, E. glabescens, E. colona, Eleusine indica, Leptochloa chinensis, Leersiahexandra, Oryza sativa, Panicum repens, Cyperus rotundus.*	The virus is found in most of the rice-growing countries of South and Southeast Asia.
rice yellow stunt virus (RYSV)	*Alphanucleo-rhabdovirus, Rhabdoviridae*	Rice is the only natural host	Taiwan
rice bunchy stunt virus (RBSV)	*Phytoreovirus, Sedoreoviridae*	Rice is the only natural host	China

CHAPTER 5

Navigating Legume Pathogen Interactions: A Biotechnological Perspectives

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Abstract: This book chapter explores the complex landscape of pathogens affecting legumes and the biotechnological strategies employed for their mitigation. Focusing on diverse biotic stresses, including fungi, bacteria, and nematodes, the chapter underscores the complex interactions between legumes and microbial pathogens. The application of advanced biotechnological tools such as marker-assisted selection (MAS), quantitative trait loci (QTLs) mapping, and transgenic techniques has shown promising outcomes in bolstering resistance against these threats. Despite the considerable progress in understanding and managing legume pathogens through biotechnological interventions, crucial research gaps persist. The identified areas for future exploration include a deeper understanding of molecular mechanisms governing plant-pathogen interactions, continuous efforts to identify emerging or less-studied pathogens, ensuring long-term durability of resistance, integrating multi-omics approaches for a holistic understanding, and bridging the gap between laboratory findings and practical field applications. Addressing these research gaps will not only contribute to more effective and sustainable strategies for mitigating legume diseases but also play a pivotal role in ensuring global food security and agricultural sustainability.

Keywords: Fungus, GWAS, Legumes, Molecular markers, Pathogen, QTLs.

INTRODUCTION

Inadequate agricultural land, a growing population, and various environmental challenges pose obstacles to the agricultural and food production sectors. Meeting nutritional needs of an expanding global population are currently a significant challenge. Projections suggest that by 2050, the world population will exceed 10 billion, necessitating a 60-100% increase in food production [1]. India holds a prominent position as the top producer, consumer, and importer of legumes globally. To meet the expected demand for pulses, there is a requirement to

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elevate production from 755 kg/ha to 1.3-1.4 tonnes/ha, or alternatively, allocate 3-4 million hectares for pulse crop cultivation. Addressing post-harvest losses demands substantial efforts.

To fulfill the demand for 30 million tonnes of pulses by 2030, India must enhance its annual pulse output by 4.2%. This figure underscores the need for a thorough examination of production constraints and viable solutions. In addition to Cereals, legumes play a crucial role as a staple food. Legumes are part of the Fabaceae or Leguminosae family, which ranks as the third-largest angiosperm family. This family encompasses approximately 750 genera and 20,000 species, encompassing grains, forage, and economically significant legumes [2]. Cultivated legumes are categorized into two groups: grain and forage. Grain legumes are grown primarily for their seeds, commonly referred to as pulses. These seeds serve various purposes, such as human and animal consumption or the extraction of oils for industrial applications. Notable examples of grain legumes encompass beans, lentils, lupines, peas, and peanuts. Forage legumes, such as alfalfa, clover, and vetch, are planted in pastures where they are either grazed by livestock or harvested as hay.

Contributing 33% of human dietary protein, legumes are cultivated on 12 to 15% of the Earth's arable land and contribute to 27% of the world's primary crop production [3]. Common beans, peas, and soybeans offer humans and animals essential proteins, minerals, dietary fibers, and carbohydrates [4]. Furthermore, legumes contribute to soil enrichment by fixing atmospheric nitrogen and serve as feed for livestock [5]. Chickpeas, pigeon peas, mung beans, soybeans, common beans, and peanuts stand out as the key legume crops for addressing the dietary needs of individuals with nutritional deficiencies.

Despite this widespread cultivation, their yield faces limitations due to challenges in environmental adaptability and damage caused by pests and pathogens [6]. The changing climate and heightened instances of diseases and insect pressure have led to decreased yields and quality in current legume varieties [7]. Biotic stress significantly affects nearly all legumes, exerting negative influences on their growth, production, and overall development.

Major fungal diseases affecting legumes include rusts, mildews, root rots, wilts, blights, and anthracnose. Bacterial diseases are categorized as leaf blights, leaf spots, bacterial wilts, and a diverse group with symptoms like dwarfing and rots [8, 9]. Viral diseases, on the other hand, are attributed to Bean pod mottle virus, Soybean mosaic virus, Peanut stripe virus, and others. Among the devastating parasites of legumes are cysts and root-knot nematodes [8].

Understanding these basic aspects of plant-pathogen interactions in legumes is crucial for developing strategies to enhance crop resistance, improve agricultural practices, and mitigate the impact of plant diseases on legume crops. This book chapter attempts to navigate through the basics of plant-pathogen interaction with legume crops as the prime focus and the latest mitigation strategies undertaken in recent years to combat these threats for resourceful breeding.

FUNDAMENTALS OF PLANT-PATHOGEN INTERACTIONS IN LEGUMES

The fundamentals of plant-pathogen interactions in legumes involve complex processes that determine the outcome of the relationship between legume plants and various pathogens.

Plant-Fungal Interactions

Pathogenic fungi follow a systematic four-step process to invade plants, beginning with adhesion to the host surface, followed by the formation of infection structures, invasion of the host, and subsequent colonization and expansion within the host's tissues. Some pathogenic fungi are capable of producing toxic metabolites, serving as major contributors to plant diseases. The varied infection processes and metabolic regulation modes are governed by different pathogenic genes. Plant-fungus interactions are characterized by either incompatibility, leading to hyper-sensitive reactions and the formation of local necrotic spots, or affinity interactions where fungi exploit stomata or host trauma, using specialized hyphae to establish infection structures. Notably, infection cushion, appressorium, and haustorium play crucial roles in facilitating the invasion and establishment of parasitic relationships, resulting in plant infection.

The plant's innate immune system responds through two main mechanisms: nonspecific defence (Pattern-Triggered Immunity – PTI) and specific defence (Effector-Triggered Immunity – ETI). Pattern recognition receptors (PRRs) in plants identify pathogen-associated molecular patterns (PAMPs), such as flagella and polysaccharides, activating signal transduction pathways that induce PTI to limit the invasion of pathogenic microorganisms. Concurrently, pathogenic microorganisms have evolved effector proteins to counteract PTI. In response, plants have evolved Resistance (R) genes to monitor and identify effectors, triggering Effector-Triggered Immunity (ETI). This specific defence mechanism, characterized by a hypersensitive response (HR), serves to restrict the invasion of pathogens and enhance the plant's resistance against infection.

The genetic flexibility and plasticity of fungi make them formidable plant pathogens, as they can rapidly adapt to changing environments [10]. Significant

CHAPTER 6

Molecular Perspectives of Host-Pathogen Interaction in *Fusarium*-Wilt in Pigeonpea

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Abstract: Pigeonpea (*Cajanus cajan* (L.) Millspaugh) is the seventh most economically important legume crop in the world, cultivated on 6.09 million hectares of land across the world with 5.01 million tonnes of global productivity. *Fusarium udum* Butler is responsible for vascular wilt, the most devastating pigeon pea disease throughout the world. Management of *Fusarium*-wilt through cultural practices is not effective enough, and chemical control methods cause the killing of non-target beneficial soil microorganisms. Biological practices using various antagonistic fungi or microorganisms are found to be more effective than other practices. Expression analysis and molecular characterization of various biotic and abiotic stress-related molecular factors have been established in order to understand the host defense response mechanism. Development of disease-resistant cultivars through marker-assisted breeding programs is restricted due to insufficient genome resources, pathogenic variability, and location-specific occurrence and behavior of pathogenic isolates. Marker-assisted breeding through the introgression of resistance (R) genes is difficult to achieve in pigeon pea, as mapping of R genes was not completed in the recent past. Therefore, understanding molecular factors and signaling pathways associated with disease resistance or susceptibility is supposed to be helpful in finding out future directions for wilt management. Whole genome sequencing, transcriptome profiling through cDNA, AFLP and NGS, *etc.*, are convenient methods to recognize the mechanism of host defense and defense regulatory pathways during *Fusarium*-wilt. The recent availability of pigeonpea whole genome sequence and transcriptome-wide marker resources and molecular characterization of disease-responsive molecular factors can efficiently be utilized for accelerating resistant breeding programs.

Keywords: *Fusarium*-wilt, Fungal invasion, Genetic variability, Genomic assisted breeding, Marker-assisted selection, Pathogenesis, Pigeonpea, Pathogenicity, Resistant cultivar.

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INTRODUCTION

Pigeonpea (*Cajanus cajan* (L.) Millspaugh) is the seventh most economically important pulse crop and is cultivated predominantly in arid and semi-arid regions of tropical countries of Asia, Africa, the Caribbean region, Latin America, and Australia [1]. This perennial short-lived pulse is also referred to as arhar, tur, guand, gandul, red gram, congo bean, *etc.* In more than 80 nations worldwide, pigeonpea is primarily farmed as a field crop and also as a garden crop [2]. It is a vegetable protein-rich legume (20-22%) and its productivity is nearly 5.32 million tones, worldwide. The crop is grown on 5.62 million hectares of land globally and India is responsible for 75% of the total production worldwide [3]. This pulse serves various functions, being utilized for food, fodder, and fuel. It caters an important role in ensuring food security, fostering a well-rounded diet, supporting subsistence agriculture, and contributing to poverty alleviation [4 - 6]. Particularly in rural communities, pigeonpea proves to be a valuable addition to cereal-based diets. The fresh pigeonpea is consumed as a vegetable, while the grain is cooked and eaten as 'dal.' Pigeonpea seeds serve as a significant source of edible protein, constituting 20–22% of dietary intake, and are rich in essential amino acids like phenylalanine, methionine, lysine, and tryptophan. Furthermore, the seeds contain carbohydrates (65-70%), fiber, and a diverse array of minerals [7]. Pigeonpea also ensures a robust supply of vitamin B, carotene, and ascorbic acid in vegetarian diets, addressing deficiencies typically found in cereals [8]. It also aids in replenishing soil fertility by capturing atmospheric nitrogen, contributing up to 40 kg ha^{-1} in a single cropping season. Additionally, it possesses the capability to dissolve soil-bound phosphorus, enhancing its accessibility for plant growth [9]. The extensive and deep root system not only imparts drought tolerance to pigeonpea but also helps mitigate soil erosion. However, it is important to note that this plant is highly vulnerable to water logging stress. *Fusarium udum* is a soil-borne fungus characterized by its mitosporic and necrotrophic nature, lacking identifiable sexual stages in its life cycle [10]. The fungus exhibits the production of three distinct types of asexual spores: robust chlamydospores, 2-6 celled macroconidia, and 1-2 celled microconidia. Notably, microconidia, the most frequently generated spores, are found within the vascular system of the infested host. On the surface of infected and deceased host plants, macroconidia form groupings resembling sporodochia. Macroconidia manifest in clusters resembling sporodochia on the surface of afflicted plants. Chlamydospores are generated either internally or at the tips of mature mycelium or within macroconidia. While all spore varieties are generated in both culture and soil, only chlamydospores exhibit the ability to endure extended periods in the soil [10]. The fungus can persist on contaminated plant remains in the soil for duration of up to 10 years or even more [1, 11, 12].

Fusarium-wilt of pigeonpea, a destructive disease, primarily manifests its impact during the flowering and fruiting growth stages, with the potential to inflict damage even at the seedling stage [13]. The initial manifestation of wilt becomes apparent through the observation of patches of dead plants within the field, serving as an early warning sign [5]. The insidious nature of this disease involves the fungus gaining entry into the host vascular system at vulnerable root tips, exploiting wounds or invasions made by nematodes. Once inside, the fungus establishes its presence by clogging xylem vessels in both stems and roots with mycelia, spores, and polysaccharides it produces. This intrusive activity extends to the stimulation of xylem parenchyma cell division, resulting in a consequential reduction in vessel diameter or complete collapse [10]. Furthermore, the pathogen's impact extends beyond the vascular system. Pathogen-secreted toxins are transported to the photosynthetic tissues, where they interfere with chlorophyll synthesis and disrupt the permeability of leaf cell membranes. This disruption impairs the plant's regulation on respirational water loss, giving rise to visible symptoms such as wilting, interveinal necrosis, and yellowing. Ultimately, these detrimental effects culminate in the death of the infected plant [10]. *Fusarium*-wilt thus poses a multifaceted threat, affecting various growth stages and vital physiological processes in pigeonpea plants. Effectively managing wilt is imperative to maintain a stable pigeonpea production. Various approaches, including crop rotation, seed treatment with chemicals, fungicide application, and the use of biocontrol agents, have been employed for wilt management. While these practices can contribute to reducing disease incidence, they come with certain drawbacks, particularly in terms of cost and commercial viability. Crop rotation, a commonly used strategy, involves alternating the cultivation of pigeonpea with other crops to disrupt the life cycle of the pathogen and reduce soilborne pathogens. Seed treatment with chemicals is another method, aiming to protect seeds from infection before planting. Additionally, the application of fungicides is a common practice to control the spread of the pathogen. However, fungicides can be expensive and may not be environmentally friendly, and often do not provide complete protection.

The use of biocontrol agents represents a more sustainable approach, leveraging natural enemies of the pathogen to suppress its growth. However, despite being environmentally friendly, the commercial viability of biocontrol agents can also be a challenge. Despite the identification of a few resistant cultivars of pigeonpea, the breeding of resistant varieties faces substantial challenges. The primary obstacle stems from the pathogenic variability present among natural populations, coupled with the location-specific occurrence of distinct pathogenic races. This variability poses a significant hurdle as resistant cultivars may gradually lose their resistance over time and successive generations due to the evolving nature of the pathogen.

CHAPTER 7

Plant-Microbe Interaction: Tomato as a Case Study

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Abstract: Tomato is a nutrient-rich vegetable crop plant consumed worldwide. Tomato is a fruit-bearing crop plant of the Solanaceae family. This plant harbors diverse microbes in its rhizosphere, phyllosphere, and endosphere, of which, beneficial microbes can promote their growth, and harmful pathogens can cause various diseases and play a crucial role in determining their overall growth, development, and fitness. Since the plant is being colonized by both beneficial and harmful microbes, the tomato has become an excellent model system for the study of plant-microbe interactions. Besides, their yield is limited due to several pathogen attacks. Therefore, it is crucial to understand both the disease biology and the interaction of beneficial microbes with the tomato plant to obtain extensive knowledge which would ultimately help to find out the possible mechanisms for controlling diseases in tomatoes as well as other Solanaceae crops like potatoes, eggplant, *etc.* for sustainable agriculture. Here in this chapter, we will discuss the details of the biology of the interaction of both the beneficial and harmful microbes with the tomato plant.

Keywords: Beneficial microbes, Bacterial leaf spot, Biocontrol, Causative agent, Endophytes, Leaf mold, Microbiomes, Pathogen, Rot, Tomato yellow leaf curl, Wilt.

INTRODUCTION

The tomato (*Solanum lycopersicum*) is one of the commercially important vegetable crops cultivated worldwide. It is a rich source of nutrients such as lycopene, potassium, iron, folate, vitamins, fiber, and a dietary source of antioxidants such as beta-carotene, and phenolic compounds, such as flavonoids, hydroxycinnamic acid, chlorogenic, homovanillic acid, and ferulic acid [1]. Today, tomato is the second most consumed and widely grown horticultural

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vegetable crop in the world after potato. In 2022, the global production of tomatoes was 187 million tons (https://www.fao.org/faostat/en/#data/QCL/visualize).

Tomato is a member of the nightshade or Solanaceae family and is extensively used as a model system for studies on fruit development and functional genomics [2, 3]. Moreover, this plant is attacked by a variety of pathogens and insect pests, resulting in significant yield losses worldwide. Thus tomatoes become a model system for stress biology analysis as well [3]. To develop disease-resistant tomato plants, several transgenic varieties like tomato leaf curl virus-resistant transgenic tomatoes, insect-resistant transgenic tomatoes, *etc.* have been developed [4 - 6]. Analysis of tomato microbiome suggests that several beneficial microbes remain associated with this plant resulting in better growth, development, and stress tolerance where microbes get their food or habitat from the plant. Here in this chapter, different aspects of interactions of tomato plants with microbes, both pathogen and beneficial interactions have been discussed in detail.

TOMATO MICROBIOME

The soil microbiome serves as a major inoculum for microbes associated with plants. Studies on rhizosphere microbiomes have been published by several groups [7, 8]. Rhizosphere microbiota is primarily determined by the type of soil and cultivar of the plant. In the tomato microbiome, we can find Proteobacteria, Bacteroidetes, and Acidobacteria as the most prominent phyla. In wild tomatoes like *S. pimpinellifolium*, *Acidovorax, Massilia*, and *Rhizobium* are most abundant whereas the domesticated variety is found to be rich in pseudomonas [9, 10]. The microbes associated with the host play an essential role in the maintenance of the plant's overall health and fitness. While some microbes can cause diseases that can result in significant losses in yield, some microbes also play an important role in enhancing the efficiency of nutrient uptake, providing tolerance against biotic and abiotic stresses, and, therefore, improving plant survival [11, 12].

Several plant organs of *S. lycopersicum* were found to exhibit different bacterial community compositions. There is evidence that microbiomes may contribute to plant health by their probiotic effect [13, 14]. Comparative analysis of leaf microbiomes between various tomato cultivars by Toju *et al.*, 2019 has demonstrated that the bacterial and fungal community compositions remained almost consistent [15]. A rhizosphere microbiome transplant of *S. lycopersicum* cultivar Hawaii 7996 to susceptible cultivar “Moneymaker” conferred resistance to *Ralstonia solanacearum* [16, 17, 12].

TOMATO-PATHOGEN INTERACTION

Bacterial Diseases in Tomato

Bacterial Stem and Fruit Canker

Causative Agent and Disease Biology

Bacterial canker caused by the gram-positive actinobacterium *Clavibacter michiganensis* is a detrimental disease of tomato [18, 19, 20]. During infection, the pathogen colonizes the fluid environment of the xylem, which consists of living parenchyma cells, dead tracheary elements, and xylem fibers [21, 22, 20]. The constant flow of Xylem sap containing low concentrations of metabolites, sugars, proteins, *etc.* is utilized as the source of nutrients by the pathogens [18, 23]. In some cases, the composition of xylem sap is altered by the pathogen activity itself to create a more favorable medium for colonization [24, 23]. *C. michiganensis* NCPPB382 strains contain adhesin-like genes and two operons with tight adhesion (Tad) pili encoding genes whose products are used for surface sensing, aggregation, and biofilm formation [25, 26].

During the early stages of the infection cycle, the pathogen prefers to colonize in the narrower protoxylem vessels [21, 27]. With the progression of wilt symptoms, *C. michiganensis* can macerate the pit membrane and spread into metaxylem and parenchyma cells [21, 28, 29]. In tolerant wild tomatoes, *C. michiganensis*, colonization is confined only in protoxylem vessels but not in metaxylem or parenchyma tissue [28].

The symptom includes unilateral wilt, stem cankers, and necrosis in the marginal leaf, which ultimately leads to plant death. During the early stage of the disease symptom development, typically 8 to 12 days post inoculation [dpi], the pathogen can spread systemically. As a result, there would be the activation of basal defense response in the host cell, which includes an increase in pathogenesis-related [PR] proteins, reactive oxygen species generation, and elevated levels of ethylene production, *etc*. [19, 27, 30]. Ethylene plays a crucial role in symptom development by inducing the production of tyloses and pectin that physically block the spread of pathogens [31]. This blockage can cause hydraulic dysfunction, leading to cavitation in the xylem vessel and embolism, which contribute to wilt disease symptom development [32, 33]. Inoculation of ethylene synthesis mutants and insensitive *Nr* plants with *C. michiganensis* showed a delay in the onset of symptoms development and the disease severity was also less as compared to wild-type plants [30] (Fig. **1**).

CHAPTER 8

Nitrogen-Fixing Bacteria: The Friends in Need

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Abstract: Nitrogen is one of the most abundantly available elements in the atmosphere, but it is not available in a biologically utilizable form. In nature, lightning storms and biological nitrogen fixation (BNF) by prokaryotes are responsible for converting the inorganic atmospheric nitrogen into forms that can be utilized by biological systems. The process of BNF occurs only in prokaryotes expressing the enzyme nitrogenase. Some plants, like legumes and a few non-legumes, can form symbiotic relationships with specific nitrogen-fixing bacteria, forming a specialized organ called nodules. Low oxygen content inside the nodules and easy access to sugars from the host plant help the bacteria in expressing nitrogenase. The host plant in turn benefits by utilizing the fixed nitrogen. Most of the staple food crops do not have the capacity to form nodules for harbouring nitrogen-fixing microbes; further, the increase in population has compounded the intensity of cultivation across agroecosystems. Hence, nitrogen becomes limiting for crop plants and it becomes imperative to encourage sustainable methods like BNF for providing N. Synthetic fertilizers used presently by the farmers, are a major cause of pollution. In such a scenario, the associative, endophytic, and free-living nitrogen fixers or biotechnological interventions hold the key to providing pollution-free nitrogen to these crop plants. In this chapter, we will discuss the diversity of nitrogen-fixing systems and the methods of assessing and utilizing these microbes for crop benefit.

Keywords: Biological nitrogen fixation, Diazotroph, Endophytic nitrogen fixation, Free-living nitrogen fixation, Legumes, Microbiome, Non-legumes, Nitrogen cycle, Symbiotic nitrogen fixation, Rhizosphere.

INTRODUCTION

The atmosphere is composed of approximately 78% nitrogen. This nitrogen is present in the form of dinitrogen (N_2) with a triple bond that is not available in the biological system. Lightning storms create enough temperature and pressure to break this bond and form NO_3 & NO_2, which can be utilized by microbes and plants to be incorporated into the biological systems. Another natural process that

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helps in breaking the triple bond of dinitrogen is the presence of nitrogen-fixing microbes that can convert inorganic N_2 into NH_3, an alternative form of biologically active nitrogen. This process, called Biological Nitrogen Fixation (BNF), occurs only in prokaryotes that can express the enzyme nitrogenase [1]. In the prehuman world, the relative loss and acquisition of nitrogen in the terrestrial system may have been equal [2]. However, with the boom in population, the increase in deforestation, industrialization, and intensive exploitation of agricultural soil; the loss in organic N from the soil increased more than the input creating an imbalance, especially in the agroecosystems [2 - 4]. This gap between demand and availability of biologically utilizable forms of nitrogen by crop plants will only keep escalating with the increase in population [5]. A substantial portion of the input of inorganic N in the ecosystem comes from industrially produced nitrogenous fertilizers. Synthetic nitrogenous fertilizer is produced by using the Haber-Bosch process. This process requires high amounts of fossil fuels to create the temperature and pressures required to break the triple bond of dinitrogen. The application of synthetic fertilizer has an intrinsic drawback due to the pollution caused by the unutilized portion [6]. Synthetic nitrogenous fertilizers are usually applied as highly active forms of nitrates, urea, or ammonium. These can either volatilize very quickly or leach into the groundwater, causing pollution [2]. The loss due to leaching, volatilization, denitrification, handling of synthetic fertilizers, *etc.* is responsible for most of the pollution from the agroecosystem. This is especially true for non-leguminous crops, which require high inputs of synthetic fertilizers [6]. Hence, encouraging BNF during crop growth by replacing or reducing the use of synthetic fertilizers becomes essential.

DIVERSITY OF NITROGENASE

The first report that legumes could fix their nitrogen was by Jean-Baptiste Boussingault in 1838. However, it was only in 1880 that Hermann Hellriegel and Hermann Wilfarth concluded, after conducting a series of experiments, that microbes present in the rhizosphere fix nitrogen and not the plants [5]. The process of BNF occurs only in prokaryotes expressing the enzyme nitrogenase. The Fe-Mo nitrogenase is a heteromeric enzyme with two subunits: the homodimeric subunit containing Fe and a heterotetrameric subunit containing the MoFe active center. The Fe subunit, also known as the dinitrogenase reductase, is encoded by *nifH,* and the MoFe subunit, called the dinitrogenase, is encoded by *nifD* and *nifK*. From several studies and the Last Universal Common Ancestor (LUCA) hypothesis, it was inferred that loss, gene duplication, and horizontal gene transfer have played a dominant role in the evolution of nitrogenase [7 - 9]. The presence of nitrogenase has been detected across the bacterial and archaeal domains and as we go higher up the evolutionary tree, the genes of nitrogenase seem to have been lost. From phylogenetic studies, it is hypothesized that the distribution of nitrogenase in bacteria and archaea is paraphyletic, having several independent points of origin [8, 10]. Based on full genome studies, nitrogenase present in different bacteria and archaea can be divided into three categories: NifI, NifII, and alternative nitrogenase [10]. Nitrogenase with Mo-Fe metal centres is known as NifI (earlier named clade I). Nitrogenase of this clade is found in aerobic and facultative anaerobic bacteria. NifII or nitrogenase containing Mo-Fe centres is present in anaerobic and facultative anaerobes bacteria or archaea clusters (earlier known as clade II). The third category of nitrogenases replaces Mo in the metal centre with V (VFe nitrogenase) or Fe (FeFe nitrogenase) (earlier called clade III) [8, 10]. To date, VFe and FeFe nitrogenases are only found in cells that also possess the MoFe nitrogenase. NifI, NifII, and alternative nitrogenases are homologous, but genetically distinct [10]. Based on sequence similarities, three clades of uncharacterised nitrogenases were identified: Mb-Mc, F-Mc, and Clfx. The Mb-Mc nitrogenases form a monophyletic clade and have sequence similarities with the alternative nitrogenases and are found in archaeal hydrogenotrophic methanogens from the Methanobacteria and Methanococci class [11 - 13]. The F-Mc and Clfx nitrogenases have primarily been identified from thermophilic bacteria. Microbes containing F-Mc lack *nifN* and bacteria possessing the Clfx nitrogenase lack both *nifE* and *nifN* genes. Hence, the less characterised F-Mc and Clfx possessing microbes may not be able to synthesise nitrogenase. However, *Methanocaldococcus* sp. FS406 and another anaerobic methane-oxidizing archaeon, possessing the F-Mc nitrogenase, have been reported to assimilate isotopically labelled nitrogen [14, 15]. Hence, it is not so improbable that as more genome sequences of uncultivable microbes become available divergent nitrogenases from nature may also be discovered.

DIVERSITY OF NITROGEN-FIXING MICROBES

The ability to fix nitrogen is present in many bacterial and archeal phyla. The best-known and most studied nitrogen fixers are from *α*-proteobacteria and *β*-proteobacteria bacteria. Rhizobiaceae, an α-proteobacteria, and *Paraburkhoderia* (Burkholderiaceae), a *β*-proteobacteria, can form symbiotic relations with legumes. Bacteria from the family Frankiaceae (actinobacteria) can form mutualistic relations with angiosperms. Another phylum of bacteria, the Cyanobacteria from the Nostocaceae family can form symbiotic relations with hosts from different kingdoms of life. Most other bacteria with the ability of nitrogen fixation are free-living. As a matter of fact, free-living nitrogen fixation may be more important than symbiotic nitrogen fixation [3]. By an estimate, BNF fixes 30-50% of the N required by crops [16].

Nitrogen-fixing bacteria have been isolated from the depth of hydrothermal sea vents, deserts and high altitudes. However, an understanding of the global

CHAPTER 9

Role of Rhizosphere Microbes in Nutrient Bioavailability for Plants

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Abstract: In natural ecosystems, macronutrients and micronutrients are present as complexes with organic or inorganic molecules in soil, and hence bio-availability of both is low. Plants depend on microbes to improve the availability of nutrients. Microorganisms increase nutrient uptake by plants through siderophore production or mineralization or solubilization activity. Microbes depolymerize and mineralize complexes using their metabolic pathways. Subsequently, these minerals are released into the soil in soluble form. Mycorrhizal fungi, bacteria, fungi present in the rhizosphere soil, and bacterial and fungal endophytes contribute to plant nutrient acquisition and are referred to as plant microbiomes. Research on plant-microbe interactions has shown that plant-associated microbes are recruited by plants and are influenced by soil type and plant genome. Conversely, microorganisms show adaptations to survive in the rhizosphere of a particular plant. This chapter focuses on plant-microbe interactions and mechanisms underlying the nutritional benefits that plants receive from the rhizosphere microbiome.

Keywords: Acidolysis, Ammonia, Arbuscular mycorrhizal fungi, Chelators, Ectomycorrhizal fungi, Endophyte, Gluconic acid, Mineral mobilization, Mineral nutrient, Mineral transporters, Phosphate-solubilizing bacteria, Potassium-solubilizing bacteria.

INTRODUCTION

Plants associate with a wide range of endophytic and epiphytic microorganisms and reap benefits from their metabolic diversity. Arbuscular mycorrhizal fungi (AMF), ectomycorrhizal fungi, endophytic, epiphytic bacteria, and rhizosphere microbiome, all boost plant health by [1]: manipulating growth-promoting molecules [2], activating defense/outcompeting pathogens and [3] improving nutrient bioavailability in soil (Fig. **1**). Initially, studies were conducted to characterize nutritional benefits received by certain plants *via* association with

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particular symbiotic mycorrhiza and nodulating bacteria. However, development in sequencing technologies has enabled researchers to link plant nutrition to entire microbiomes; and to document abundance and diversity of microorganisms through metagenomics. Multidisciplinary approaches combining plant and microbial genomics, transcriptomics with metabolic modeling have enhanced our mechanistic understanding of the interactions between plants and microbes. This chapter focuses on the role of plant microbiome in the uptake of key soil nutrients by plant roots. This chapter summarizes current progress in understanding plant-microbe interactions relevant to mineral nutrition.

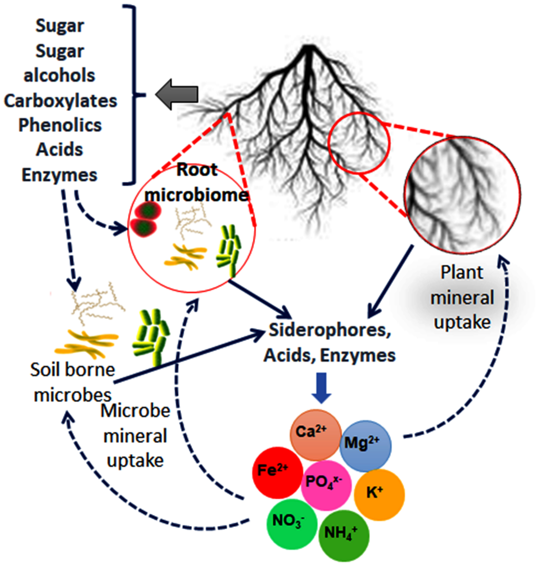

Fig. (1). Interactions between plant root, rhizosphere microbiome, and soil-borne microbes. Plant root exudates are up-taken by microbes, plant roots and microbes secret siderophores, acids, and enzymes to solubilize minerals that may be up-taken by plants and microbes. Solid arrows denote secretion and dotted arrows denote up-take.

Phosphate Uptake

Plants' roots absorb phosphate in the form of inorganic orthophosphate (Pi), however, roots are unable to absorb phosphate complexed with cations or organic molecules [1]. Apart from direct uptake, plants also acquire Pi indirectly through symbiotic pathways [2]. Roots acquire Pi through H+/Pi symporters, PHOSPHATE TRANSPORTER1 (PHT1), on the epidermis [3, 4]. This assimilated Pi is then loaded into the xylem *via* PHO1 transporters [5, 6]. AMF are ubiquitous symbionts well known for their role in Pi acquisition. AMF acquires Pi by H+/Pi or Na^+/Pi symporters of the AMF extraradical hyphae [7, 8]. The assimilated Pi is then imported into the tonoplast *via* the vacuolar transporter chaperone complex [9] and is translocated as polyphosphates to the intraradical mycelium [10]. AMF supplies assimilated Pi to the plant in exchange for fixed carbon or stores it in vesicles. It releases phosphate from arbuscules to plant cortical cells, which is then transported by plant PHT1 symporters across the peri-arbuscular membrane into cortical cells [11]. The mycorrhiza-specific Pht1 family genes are known to be specifically induced in cortical cells during AMF symbiosis [12, 13]. AMF can also mobilize organic Phosphate (Po) by secreting acid phosphatases [14]. Studies have shown AMF also allows plants to take advantage of phosphate solubilising bacteria; the AMF-associated bacteria secrete acid phosphatases to solubilise Po for uptake by AMF [15].

Ectomycorrhizal fungi (EcM) form a sheath around roots and their hyphae extend between the epidermis and cortex of plant roots to form a Hartig net. They are also known to increase plant phosphorous uptake [16]. Several H^+/Pi transporter genes have been identified in EcM [17, 18]. These have also been found to be upregulated during phosphorous-limiting conditions *i.e.* HcPT1.1 and HcPT2 genes of *Hebeloma cylindrosporum* [19]. Similarly, H^+/Pi transporters in *Tricholoma* spp [20], *Boletus edulis* [21], *Rhizopogon luteolus* [22], and *Leucocortinarius bulbiger* [22] are known to be induced under low phosphate availability. Plant taxa-specific mycorrhizal associations *i.e.* Orchid mycorrhiza [23], and Ericoid mycorrhizal (ERM) [24, 25], are also known to enhance Phosphate absorption.

Soil bacteria also improve phosphate mobilization. Several species of *Azotobacter*, *Bacillus*, *Burkholderia*, *Pseudomonas*, and *Rhizobium* genera are known to secrete organic acids that mobilize organic and inorganic phosphate to soluble orthophosphate by lowering soil pH and/or solubilizing phosphate from its iron oxides, hydroxides, and calcium salts [26, 27]. Phosphate-solubilizing bacteria (PSB) release phosphate from insoluble sources by acidification, chelation, exchange reactions, and formation of exopolysaccharide (EPS)or the release of protons [26]. EPS acts synergically with organic acids for P solubilization [26]. *Azospirillum brasilense* strains Cd and 8-I and *Azospirillum lipoferum* JA4 secrete gluconic acid for P solubilisation from calcium phosphate resulting in a reduction of pH of medium [27]. Similarly, *Rahnella aquatilis*, a hydroxyapatite solubilizing bacterium, decreases media pH and is known to secrete gluconic acid. In PSB, gluconic acid is formed from glucose by glucose dehydrogenase (GDH), a membrane-bound enzyme involved in the direct oxidative pathway of glucose catabolism [28, 29]. Several studies have shown that glucose dehydrogenase enzyme activity is vital for phosphate solubilization [30]. Studies have also shown that bacteria and mycorrhiza work synergistically to facilitate mineral absorption. Bacteria associated with extraradical AM hyphae are known to secrete phosphatases [31] and phytase [32] to solubilize organic phosphate.

CHAPTER 10

Halotolerant Plant Growth Promoting Rhizobacteria: The Hidden Gem

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Abstract: Soil salinization results in the continuous reduction of agricultural land worldwide. Salinity, a major abiotic stressor, adversely affects plant growth and development by interfering with various physiological, biochemical, and molecular processes. These processes include nutrient imbalance, osmotic stress, ionic stress, oxidative stress, membrane destabilization, reduced photosynthetic capacity, protein synthesis, energy and lipid metabolism, DNA replication, protein metabolism, and cell division. Despite the rapid increase in the global population, food production is not sufficient to meet the challenges posed by such growth. In this context, salt-tolerant plant growth-promoting rhizobacteria (ST-PGPR) may play a crucial role in sustainable agriculture to meet the ever-increasing demand for food. ST-PGPR can enhance plant growth, development, and productivity by producing phytohormones, 1-aminocyclopropane-1-carboxylate deaminase (ACC) activity, phosphate solubilization, exopolysaccharide (EPS) production, siderophore production, biological nitrogen fixation, and the synthesis of compatible solutes, among other mechanisms. The generation of reactive oxygen species (ROS) at low concentrations is a natural phenomenon, but at elevated levels, they can cause oxidative damage. Salinity-induced osmotic stress and ionic stress lead to the overproduction of ROS, which, at severe levels, can result in cell and plant death. ST-PGPR can mitigate the overproduction of ROS under saline stress, thereby protecting the plant from oxidative damage. In this discussion, we shed some light on salt stress sensitivity, the impact of salinity, the role of salt-tolerant PGPR, and their mechanisms in promoting plant growth, antioxidant defense, osmotolerance, and ion homeostasis under saline conditions, enabling plants to mitigate salt stress.

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Keywords: Antioxidant enzyme, Crop, Exopolysaccharide, Ionic stress, Nitrogen fixation, Osmotic stress, Osmoprotectant, Oxidative stress, PGPR, Phosphate, Phytohormone, Rhizosphere, ROS, Salinization, Salt tolerant, Saline stress, Siderophore.

INTRODUCTION

One of the main abiotic environmental stresses that limit plant growth and development is soil salinity [1]. According to the Food and Agriculture Organization (FAO), Land and Plant Nutrition Management Service, over 6% of the world's land is salt-affected, and the salinization of arable land will result in 50% land loss by the year 2050 [2 - 5]. Worldwide, salinity stress affects more than 20% of cultivable soil, and each year, 1%-2% of arable land becomes reduced due to elevated salinity [6]. Crop production and plant growth are negatively impacted by salinity in cultivated areas. High salinity has negative impacts on every stage of the plant life cycle, from germination to the last stages of growth [7, 8].

Salinity interferes with many mechanisms, including nutrient imbalance, osmotic stress, ionic stress, oxidative stress, partial stomata closure, membrane destabilization, reduced photosynthetic capacity, chlorosis, protein synthesis, energy, and lipid metabolism, total nitrogen contents, DNA replication, protein metabolism, reduces cell division, regulation of roots and shoots, *etc.*, in plants, which significantly reduces plant growth and productivity in saline soils [7, 9 - 12]. The yield of significant crops like wheat, maize, rice, and barley has decreased by up to 70% as a result of salinity [8, 10]. Osmotic stress is caused by a water shortage that is mediated by an increased cell water efflux from root cells [9]. Ionic stress results from an imbalanced inflow of Na^+ ions through the root cell, upsetting the Na^+/K^+ and Na^+/Ca^{2+} balances, leading to elevated concentrations of Na^+, reduced concentrations of K^+, and Ca^{2+} causing inhibition of normal cell function. Subsequently, Reactive oxygen species (ROS) are overproduced in the mitochondria, chloroplast, and cytosol, which is harmful to cells because it breaks down membranes, modifies DNA, and destroys proteins, lipids, and pigments involved in photosynthetic processes [8, 11 - 13].

Therefore, to improve plant growth under saline stress conditions, and for sustainable crop production, it is necessary to improve salt stress tolerance in crops [14]. Salt-tolerant plant growth-promoting rhizobacteria (PGPR) can improve plant growth and crop productivity of the plants under saline conditions [8, 10, 12, 15, 16]. Excessive salinity makes plants more vulnerable to a range of phytopathogens and fosters the growth and survival of certain fungal soil-borne diseases [17]. Nonetheless, salt-tolerant PGPRs have the ability to modify plant host immunity *via* several ingenious mechanisms like hydrogen cyanide (HCN) production, ammonia production, siderophore production, chitinase production, *etc.*, and also through induced systemic resistance [10, 12, 18].

A major challenge for the 21st century is producing enough food due to the alarming rate of the world's population increase [15]. Furthermore, using chemical fertilizers in agricultural fields to increase crop productivity poses significant risks to the environment and human health [15]. In recent times, attention towards PGPR for sustainable agriculture has increased tremendously in various parts of the world as they have been investigated as potential substitutes for chemical fertilizers [12] due to their multifunctional properties ranging from plant growth promotion to soil nutrient recycling [10, 14], and in the context of international concern for food security and environmental quality.

SOIL SALINIZATION: GLOBAL PERSPECTIVE

Global agriculture is confronting significant challenges due to salinity, a problem expected to be exacerbated in the coming decades [19]. According to The Food and Agriculture Organization of the United Nations [5], soil salinization is diminishing arable land by 1-2% annually, with arid and semi-arid regions bearing the brunt. In arid, warm climates, evapotranspiration brings salt to the surface, where it accumulates at harmful concentrations [6, 20]. Additionally, water from irrigation systems can infiltrate mineral reserves, dissolve salts, and then transport them to the surface through plant uptake and water evaporation [21]. These circumstances lead to secondary soil salinization, affecting 20% of irrigated land [22], and 50% of cropland [19] worldwide, resulting in an estimated annual loss of arable land area of approximately 16,000 km^2 [23, 24]. As global climate change progresses, there may be heightened concerns regarding secondary salinization due to the necessity of irrigating larger areas, thereby increasing the potential for salinization [25].

Based on a model relying on the FAO's 2002 estimate for secondary salinized soil covering 397 Mha, it was found that 17% of the organic matter in the soil in these areas was lost as the soil became saline [26]. Salinity-induced soil carbon loss may also adversely affect climate feedback mechanisms [25]. Throughout the world, naturally salted soils coexist with anthropogenic soil salinity [27]. Recent estimates indicate a total of 1128 Mha of naturally salt-affected areas globally, predominantly located in the Middle East, Australia, North Africa, and the former Soviet Union [27]. Efforts are underway to develop satellite-based methods for measuring soil salinity [28]. The economic and social impact of salt stress on farmers is negative, with an estimated potential annual decrease in farmers' income of $11 billion as a result of salinity problems [29].

SUBJECT INDEX

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