

# MOLECULAR AND PHYSIOLOGICAL INSIGHTS INTO PLANT STRESS TOLERANCE AND APPLICATIONS IN AGRICULTURE

PART 2

Editor:  
**Jen-Tsung Chen**

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**Molecular and Physiological  
Insights into Plant Stress  
Tolerance and Applications in  
Agriculture**

*(Part 2)*

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**Molecular and Physiological Insights into Plant Stress  
Tolerance and Applications in Agriculture- Part 2**

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## FOREWORD

Stress tolerance is a continuing issue for researchers and professionals seeking to increase crop productivity. In the research field of plant science, stress physiology is an intensive topic for researchers, and tons of publications are reported per year to get increasing knowledge about stress tolerance when facing global climate change. In the meantime, the emerging knowledge of plant stress physiology should be applied to the practice of agriculture for sustainable agriculture as well as food security globally. Importantly, there is a high demand for the integration of current knowledge of plant stress physiology. Moreover, a systematic summary of methods in plant stress management also needs to be refined.

This book, "Molecular and Physiological Insights into Plant Stress Tolerance and Applications in Agriculture," collects the most recent original research and literature reviews for unraveling the physiology of plant stress tolerance. Divided into 21 chapters, it provides in-depth coverage of the recent advances by exploring the unique features of stress tolerance mechanisms, which are essential for better understanding and improving plant response, growth, and development under stress conditions, in particular by exploring knowledge that focuses on the application of plant growth regulators, advanced biotechnologies, high-throughput technologies, multi-omics, bioinformatics, systems biology, and artificial intelligence as well as beneficial microorganisms on the alleviation of plant stress.

The mechanisms covered in this book include the perception of stress, signal transduction, and the production of chemicals and proteins associated with the stress response. The book also offers critical knowledge of the gene networks involved in stress tolerance and how they are used in plant stress tolerance development. Modern genetic studies and useful breeding methods are also covered. It also presents the current challenges and further perspectives. Therefore, this book might largely benefit breeding programs as well as sustainable agricultural production in the future.

The editor, Pr. Jen-Tsung Chen has done an excellent job of bringing together specialists from diverse fields to present the most comprehensive view of current research findings and their implications for plant stress tolerance physiology. Therefore, this book, "Molecular and Physiological Insights into Plant Stress Tolerance and Applications in Agriculture," is an essential resource for academics and professionals working in agronomy, plant science, and horticulture. It is an essential resource for both novices and specialists. It can also be utilized as a resource for courses at the university level for students and Ph.D. students interested in the physiology of plant stress tolerance. I recommend it without reservation!

**Christophe Hano**  
University of Orleans  
France

## PREFACE

Part II of this book entitled "Plant Stress Physiology and Agricultural Biotechnology for Sustainable Agriculture" continues to summarize current findings, emerging technologies, and integrated strategies to mitigate stress responses and achieve sustainable agriculture through the understanding and application of integrated omics and molecular tools and the use of agricultural biotechnology and plant growth-promoting microorganisms and agents.

It first provides molecular aspects on the role of cytosine methylation and demethylation in plant stress responses and the importance of epigenetic genetics in regulating plant stress responses and the role of late embryogenesis abundant proteins in plant cellular stress tolerance with an emphasis on their molecular mechanisms and potential implications.

Several chapters focus on discussing the subtopics of beneficial microorganisms including rhizobacteria, endophytes, and mycorrhizal fungi, which are expected to be alternative fertilizers with the advantages of being cost-effective, toxin-free, and eco-friendly.

In the scenario of a rising world human population and consequently, increasing industrial activities, environmental pollutants continue to threaten human life globally. Fortunately, a range of plants have the ability to remediate such kind of environmental stress, and in part II of this book, several comprehensive reviews were provided to explore the role of medicinal plants in reducing the toxic and negative impacts of pollutants, and additionally, the stress responses induced by metal-nanoparticle were presented and discussed.

Pathogenic/biotic stresses are critical issues in agricultural production due to the resulting huge losses each year globally and certainly damage the goal of zero hunger in SDGs (Sustainable Development Goals). Part II of this book presents the potential use of endophytic bacteria for protecting crops against pathogens and an in-depth analysis of the molecular level to understand the impact of ATP-binding cassette transporters on plant defense mechanisms. Besides, a chapter discusses an interesting class of plant secondary metabolites, namely terpenoids and their precursors, terpenes, on their role in diverse growth and development, particularly with an emphasis on their effects on plant-microbial interaction and defense mechanisms and this knowledge can advance future utilization of these compounds through metabolic engineering or exogenous application as anti-pathogenic agents.

The content of Part II is an ideal reference for students and teachers in the research field of plant science, particularly the topics of plant stress physiology and plant-microbial interaction. It also provides advanced knowledge and valuable insights for experts in agricultural institutions and the R&D departments of agricultural corporations.

In the end, the editor is very grateful to the staff of the publisher for their guidance and assistance, and to all the chapter contributors for their efforts. Without their valuable works, this book will not be successfully organized.

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## CHAPTER 1

# Chemical Modifications Influence Genetic Information: The Role of Cytosine (De)Methylation in Plant Stress Responses

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**Abstract:** Genetic information is fundamental in biology. It is stored in all genomes, crucial to generating and maintaining a new organism. The biological importance of DNA lies in its role as a carrier of genetic information and how it is expressed under specific conditions. Among the different ways of controlling the manifestation of genomic information (or gene expression), epigenetic mechanisms have been highlighted. These mechanisms are diverse, multifunctional, and profoundly affect the plant's molecular physiology. Cytosine methylation and demethylation - one of the best-studied epigenetic mechanisms - is a dynamic process that influences, respectively, the down- and up-regulation of target genes. The referred chemical modifications occur in response to developmental processes and environmental variations, and have their biological value accentuated as they can be passed on to subsequent generations. This inheritance mechanism conducts 'states of gene expression' to new cells and even to the offspring, allowing them to be 'more adequate' to the changing environment. The possibility of inheriting such chemical modifications defies our understanding of the hereditary process, opening new perceptions and practical implications. This chapter aims to address the cytosine methylation and demethylation effects in plants. In the present review, we deal with how cytosine (de)methylation occurs in plant genomes, their participation in the biotic and abiotic stress responses, the recent studies for its use in crop breeding, and the epigenetic inheritance issue, which is a matter of intense debate.

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**Keywords:** Abiotic stress, Biotic stress, *De novo* methylation, DNA methyltransferase, DNA demethylase, Epigenetic inheritance, Gene expression, Methylation maintenance, Non-coding RNA, Plant epigenetics, Plant breeding, RdDM pathway, RISC complex.

## 1. INTRODUCTION

### 1.1. Epigenetics: Definition, Main Impacts, and Effects

Information is fundamental in Biology. It is stored in all genomes, crucial to generating and maintaining a new organism. The biological significance of DNA lies in the role it plays as a carrier of information and how it is expressed throughout the organism's life cycle. The control of the genetic information expression is *sine qua non* to the life maintenance.

To integrate and survive in a niche in which they are incorporated, plants constantly regulate their internal environment to external fluctuations, such as soil, climate and biological interactions. This regulation is controlled primarily by transcription modulation of specific genes (*i.e.*, genetic information). The gene expression in all organisms occurs through the action of protein effectors called transcription factors (TFs) and some RNA polymerases [1, 2]. TFs enable RNA polymerases to bind to the gene promoter region and initiate gene transcription [1]. These protein effectors' activity is indirectly influenced by chemical changes in DNA (for both eukaryotes and prokaryotes) and histone tails (for eukaryotes). The mentioned chemical alterations in chromatin structure affect the transcriptional machinery accessibility and act in signaling, engaging/inhibiting protein complexes that participate in the transcription processes (for a review, see Ferreira-Neto *et al.* [3]).

The aforementioned chemical mechanisms and their effects are part of the so-called Epigenetic phenomena. In terms of definition, an Epigenetic process is recognized as a '*structural adaptation of chromosomal regions to register, signal or perpetuate altered activity states*' [4]. Bird [5], in turn, adds inheritance-associated terms to its definition, to cite: '*Epigenetics is the study of mitotically and/or meiotically inheritable changes in gene function (expression) that cannot be explained by changes in DNA sequence*'. Admittedly, some epigenetic modifications can be passed on to cell generations and/or offspring [6]. The chromatin's chemical modifications inheritance affected the understanding of the heredity process in Mendelian terms: not only the parental DNA is inherited, but also chemical marks anchored in the chromatin structure.

The epigenetic modifications (also called epigenetic marks) are diverse, multifunctional, and profoundly affect the plant's molecular physiology. Chemical

changes in histone tails are numerous. They cover (de)methylation, (de)acetylation, (de)phosphorylation, (de)sumoylation, among others [7]. The pattern of histone modifications is called “histone code”. It influences transitions between chromatin states (permissive and not permissive to gene expression) and, consequently, the regulation of transcriptional activity [8]. Regarding the chemical modifications in DNA, these are represented by cytosine methylation and demethylation, which are the focus of the present work. This dynamic process influences, respectively, gene down- and up-regulation [9 - 11]. Plant cytosine methylation and demethylation have their biological value accentuated, as they can be passed on to subsequent filial generations (cell generations and offspring). This transgenerational inheritance allows transferring ‘*states of gene expression*’ to the progeny, allowing them to be ‘*more adequate*’ to the environment under the condition inducing such modification.

In another context, epigenetic marks help improve plant fitness under stress within the same generation. Since environmental perturbations may occur frequently, it is advantageous to plants to ‘remember’ past incidents and to use this ‘experience’ to adapt to new threats. This ‘memory’ system is called ‘priming’ (or somatic memory [12]). Plant priming allows the plant to perform a more rapid and robust response to pathogen attack, or abiotic stresses, in the second round of stress, compared with the first one. Therefore, plant priming increases the plant's chances of survival/adaptation. The duration of that ‘priming’ can vary from the range of days to weeks [13, 14]. Some scientific evidence supports the link between priming and epigenetic marks (for a review, see Turgut-Kara *et al.* [15]).

This chapter will focus on plant cytosine methylation and the demethylation process. In higher plants, cytosine nucleotides of the nuclear genome are often extensively methylated [16]. DNA methylation has been implicated in a series of critical biological responses, and errors in the mentioned process may have severe functional consequences. Here, it is argued how these epigenetic marks occur, their effects on plant tolerance/resistance to (a)biotic stresses, their inheritance mechanism, and how epigenetics can be used in plant breeding.

## 2. THE CYTOSINE METHYLATION MECHANISM

### 2.1. How Does This Mechanism Occur?

The cytosine nucleotides can be methylated by two different strategies, considering the novelty of the mark (*i.e.*, methylation of a cytosine not yet methylated; also called *de novo* methylation) or the maintenance of the mark (also called methylation inheritance; transfer of the cytosine methylation pattern to a newly synthesized DNA molecule, during mitotic or meiotic division).

## Microbial Dynamics within Rhizosphere: An Aspect to Agricultural Sustainability

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**Abstract:** Numerous anthropogenic activities, such as novel agricultural practices, coal mining, industrial pollution, *etc.*, pose a negative impact on the environment. Such factors cause the accumulation of different pollutants within the ecosystem, ultimately hampering the plants as well as animals. However, plants possess a series of physiological as well as molecular mechanisms for defense and resistance. The global population has posed a significant food challenge, therefore, to ensure food security, soil nutrition, agricultural productivity as well as fertility, different sustainable aspects should be kept in mind. Chemical fertilizers dilapidate the ecological balance along with human health, henceforth the microflora present in the rhizosphere acts as quintessential elements. Microbes such as plant growth-promoting rhizobacteria and mycorrhizae have been formulated as biofertilizers in agriculture that enhance their nutrient uptake as well as yield, along with providing resistance against different stressors. Biofertilizers have been shown to provide a positive outcome for plants, therefore, an array of microbial strains have been selected and formulated to be used in the agricultural sector. These are based on rhizobacterial species, endophytes, and mycorrhizae. Regardless of the challenges observed in the production, usage, and application, these have been proven to be the exclusive alternatives for chemical-based fertilizers. Therefore, their elaborate understanding will offer new approaches to sustainable agriculture. Biofertilizers not only boost crop yield and soil fertility but also interact with plants to trigger their immune systems, physiological processes, growth, and development. They also enable solubilization of essential nutrients such as nitrogen, phosphorous, zinc, potassium, and silica that promote plant growth. Most importantly, they are cost-effective, toxin-free, eco-friendly, and serve as the best alternative for chemical fertilizers. In this chapter, we have highlighted the microbial

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dynamics within the rhizospheric zone and its significance in agriculture by its usage as biofertilizers for sustainable crop production.

**Keywords:** Biofertilizers, Formulation, Microbiome, Mycorrhizae, Rhizosphere, Rhizobacteria.

## 1. INTRODUCTION

As per the Food and Agriculture Organisation of the United Nations, the world populace has been exceedingly growing at an exasperating rate, and by 2050, it is expected to be increased by more than nine billion by that time. Therefore, to feed such a massive population, it is necessary to enhance agricultural production by maintaining rhizospheric activities [1]. Alongside, certain factors such as proper environmental conditions, soil fertility, beneficial microbial communities, *etc.*, play a major role [2]. Since traditional times, chemical fertilizers have been prominently used for agriculture to provide an adequate quantity of nutrients to plants. Approximately 54 billion tons of NPK-fertilizers have been used for this purpose and to enhance crop productivity [3]. However, only a certain amount of these nutrients are taken up by the plants, and the majority of them are precipitated through metal cations present in the soil. Further, the extensive usage of these chemicals also causes environmental hazards causing a major concern for farmers, therefore causing a critical concern to develop sustainable agricultural practices [4]. Researchers have initiated their interest in designing methods to ensure agrarian sustainability with the aid of microflora existing in the soil as a replacement for chemical pesticides and fertilizers (Fasusi *et al.*, 2021).

Rhizosphere management is defined as the process to improve the nutrient abilities within the soil for fertility, growth, and development with the help of microflora residing in this zone [5]. Microbes stimulate the rhizosphere through their multi-dimensional roles in the form of producing siderophores, lytic acid, organic acids, hydrogen cyanide, and indole-3-acetic acid [6]. Besides, they also perform specific functions for plants in the form of nitrogen fixation, phosphate solubilization, and potassium mobilization. These mechanisms play a critical role in enhancing soil fertility, growth, productivity, and yield. Several microbes have been isolated for their ability to regulate the rhizosphere for inducing plant growth and development [5]. Biotechnological applications in root microbiomes enable the establishment of agricultural sustainability along with food security. Presently, fungal and bacterial strains are being explored by researchers to ensure their commercial value as well as ensure nutrient bioavailability to stimulate the growth and yield of the plant. Therefore, the applicability of biofertilizers is seeking more attention due to their environment-friendly nature and cost-effectiveness with the role in increasing productivity as well as the fertility of soils [6]. Microbial

biofertilizers comprise viable cells of microbes with the ability to promote growth and interact with the rhizospheric and endosphere zone of plants, alongside improving their yield, soil fertility, and nutrient uptake [7]. These microbiological tools in the form of biofertilizers and biocontrol agents have provided an essential outcome for plant growth and development for decades. Biofertilizers are defined as a product containing living microbes and are applied to soil, plant roots, seeds, *etc.*, for rhizosphere colonization and penetration into plant tissues to induce plant growth. Biofertilizers undoubtedly reduce the cost of chemical-based fertilizers and pesticides and promote the global demand for green technology in the agriculture sector [8]. Additionally, microbial inoculants are most effective in terms of replacing pesticides, thereby forming appropriate biocontrol agents against various plant diseases. The biocontrol potential of biofertilizers results from their ability to synthesize antibiotics, lytic enzymes, toxins, *etc.*, along with the induced systemic resistance mechanisms [9]. Antibiotic synthesis is the common mechanism of action with biocontrol potential. Along with this, numerous microbes possess the ability to produce antifungal enzymes, for instance, chitinases,  $\beta$ -1,3-glucanases, lipases, and proteases that lyse the pathogenic cells. Moreover, siderophore biosynthesis near root sites also enables the chelation of iron in soil for the inhibition of fungal pathogens [10]. This chapter mainly focuses on rhizosphere management and studying the microbial dynamics within the rhizosphere for stress management. Moreover, we have also presented in detail the elaborated role of applying beneficial microbes for crop production in the form of biofertilizers as sustainable means of agriculture.

## **2. RHIZOSPHERE: A COMPLEX ZONE OF INTER-COMMUNICATIONS**

The rhizosphere is a soil zone that encompasses the immediate vicinity of plant roots with some major microbiota [11]. The rhizosphere is a zone with high microbial diversity and nutrient turnover, wherein abiotic and biotic variables are heavily regulated by one another [12]. Plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi (AMF) are among the most common microbiota that can be found in the rhizospheric region. The microbial community present in the rhizospheric zone is influenced by the diversification and the amount of organic matter released in root branching order and root architecture. Moreover, this microbial community is utilized by the members of the biotic community, including plants as well [13 - 15].

Plants recruit microbes with the potential of growth-promoting properties to live in the rhizospheric region. The microbial diversity of the rhizosphere is improved *via* the generation of extravasation of particular chemicals that suppresses the growth of specific microorganisms, such as sesquiterpene and pyrone [16]. Root

## CHAPTER 3

## The Role of Terpenoids in Plant Development and Stress Tolerance

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**Abstract:** Plant terpenoids and their precursors, terpenes, are among the most important classes of plant secondary metabolites that have provoked increased interest regarding their application in the medical field to treat different health issues. Additionally, terpenoids are known to play a crucial role in many different plant processes, such as photosynthesis, root growth, flower production, fruit set, and plant interaction with the environment. A plant can produce different kinds of terpenoids with diverse structures and functions. These compounds are usually liberated in the atmosphere in the form of flavors or fragrance compounds or stored in plant organs, such as glandular trichomes. Due to increased water scarcity, salt stress, mineral deficit, temperature level, and pathogens resistance, it has become difficult to provide natural conditions for the development of some plant species, which has led to a shortage in levels of some naturally occurring compounds, such as terpenoids. So, to reduce the alteration of terpenoid production, some strategies have been recently applied, like metabolic engineering and applying biofertilizers. Thus, this chapter will define the different classes of terpenoids produced by plants, their metabolic pathways, and their roles in plant development and physiology, nodule formation, mycorrhizal symbiosis, wounding healing, and plant defense as well as recent advances regarding the increase in the accumulation of terpenoids through metabolic engineering and exogenous application of natural substances.

**Keywords:** Mycorrhiza, Metabolic engineering, Nodulation, Plant growth, Phytohormones, Terpenoids.

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## 1. INTRODUCTION

Nature contains a large number of molecules of industrial and medical importance. Some of them can be used as flavors, colors, and spices, while others can be used as medicine. In the distant past, several medicines were produced, based on natural ingredients, such as terpenoids extracted from animals, plants, and microbes, to treat various human diseases. Terpenoids also referred to as terpenes, are a metabolite family that has antibacterial and pharmacological activities and the ability to remedy skin inflammation and lung disorder [1]. In 2002, the global sales of terpenoid-based medications were about USD 12 billion [2].

To date, more than 64,000 terpenoid compounds have been identified, and they have several structures in linear or carboxylic forms [3]. These molecules can have different roles in plant systems, especially root growth and photosynthesis, and can be used as bio-pesticides and attenuators of stress in plants.

Thus, the present chapter will show an overview of terpenoids produced by plants, their different classes, their biosynthesis pathways, and their effects on plant development in normal and stressful conditions as well as their metabolic engineering strategies for increasing the stress tolerance of plants.

## 2. DIFFERENT CLASSES OF TERPENOIDS AND THEIR BIOSYNTHESIS PATHWAYS

Terpenoids are a group of secondary metabolites produced by plants, animals, aquatic organisms, insects, and microbes [4, 5]. These compounds are characterized by their high volatility, which therefore induces the aroma of flowers and plant products [6]. Plants that bear flowers exhibit a variety of terpenoids compared to other organisms [7]. These compounds are considered signaling molecules that have an essential role in establishing a way for plants to be in touch with the closest plants and beneficial microorganisms, attract pollinators, and alleviate biotic and abiotic stresses. In addition, the consumption of foods rich in terpenoids can reduce the effect of free radicals, the growth of tumor cells, and the infection of human cells by bacteria and fungi [8].

Terpenoids can be divided into eight classes based on their structure and the number of carbon atoms in their skeletons: isoprene ( $C_5$ ), monoterpenoids ( $C_{10}$ ), sesquiterpenoids ( $C_{15}$ ), diterpenoids ( $C_{20}$ ), sesterterpenoids ( $C_{25}$ ), triterpenoids ( $C_{30}$ ), tetraterpenoids ( $C_{40}$ ), and polyterpenoids ( $C$  is higher than 40) [3]. Also, they can be subdivided into different sub-classes such as lactones, hydrocarbons, aldehydes, alcohols, oxygenated molecules, and esters [9], which are produced by either woody plants (*i.e.*, *Anvillea garcinii*), or herbaceous plants (*i.e.*, *Tanacetum*



*cinerariifolium*), or plants that live in harsh conditions such as cacti (*i.e.*, *Lemaireocereus stellatus*) [10 - 12].

### 2.1. Isoprene

Isoprene, a lipophilic hydrocarbon molecule, consists of 5 carbon atoms, produced by photosynthetic organs and liberated into the atmosphere [13]. Isoprene can also be called hemiterpenes [14]. The emission rate of isoprene by plants is similar to that of methane from all sources [15]. Isoprene is synthesized by two pathways: one of them is called the methylerythritol phosphate pathway (MEP), which occurs in the chloroplast, while the other one is called the mevalonate pathway (MVA), which takes place in the cytosol and peroxisome [16, 17] (Fig. 1).

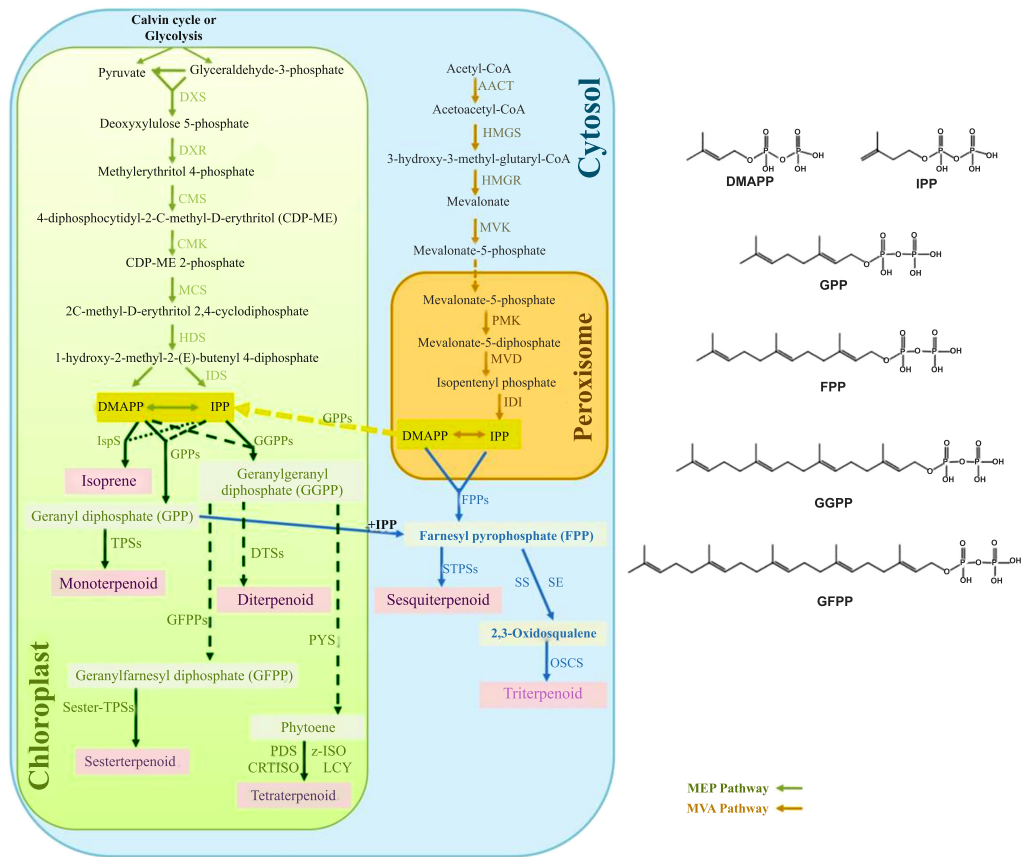


Fig. (1). Terpenoids biosynthesis pathways.

Regarding the MEP pathway, three steps are required for the biosynthesis of isoprene (Fig. 1). The first step is the production of methylerythritol 4-phosphate

## CHAPTER 4

## Phytoremediation Potential of Medicinal Plants to Relieve Pollutant Stress

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**Abstract:** With the rise in rampant anthropogenic activities, the contamination of the environment due to heavy metals is increasing at an alarming rate. This poses a serious threat to both the plant and animal world, including poor human health and disturbed crop physiology and yield. Heavy metal pollution commonly leads to oxidative stress in sensitive plants, thereby altering the entire homeostasis within the plant system. Therefore, plants have evolved certain regulatory circuits for combating the resulting stress ensuing from the excess concentration of heavy metals in the soil. Certain plants have the immense potential to accumulate such heavy metals, followed by their detoxification *via* a range of mechanisms, inherent to the plant system. This process is commonly referred to as phytoremediation, which is an efficient, cost-effective and sustainable approach for the rejuvenation of contaminated soil. In present times, medicinal plants are not only exploited as a source of different traditionally available medicines, but have also displayed the immense capacity of cleaning up heavy metal-contaminated soil and serve as sinks for the toxic effects of heavy metals to clean up the environment. The present chapter, therefore, focuses on medicinal plants as potential phytoremediation agents.

**Keywords:** Anthropogenic activities, Heavy metal, Medicinal plants, Oxidative stress, Phytoremediation.

### 1. INTRODUCTION

The process of phytoremediation refers to the natural cleaning up of pollutants, mainly heavy metals from the environment, *via* plant roots and their associated microbiota [1]. Several plant species harbor the capacity of develop newer adaptive mechanisms, which aid them to thrive even in a severely polluted environment. The plant that can survive in a heavy metal-polluted environment,

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even after high concentrations of toxic heavy metals within their system, are commonly called hyper-accumulators [2, 3]. Moreover, plants often display certain essential therapeutic properties, which have been considered one of the most prominent medicinal sources for decades. The medicinal properties inherent to various plants come from the secondary metabolites produced within the plant system, rendering widespread protection against myriads of environmental stressors [4, 5]. Therefore, medicinal plants can potentially serve as excellent phytoremediation agents, although such applications need to be judiciously explored.

Due to ever-increasing anthropogenic activities, the release of toxic pollutants into the environment has progressively increased [6]. Certain heavy metals like arsenic, mercury, lead, nickel, cadmium, aluminium, manganese, copper, *etc.*, in excessive doses, tend to interfere with crucial plant enzymatic reactions and metabolic cascades. However, some of these toxic metals can even serve as essential cofactors and components of important plant proteins and enzymes mediating plant growth and development, and photosynthetic and respiratory pathways, when present in optimal concentrations [7]. Several plant nutritional studies indicate that plants need a very minute yet optimum dose of these trace elements, but they respond in an altered fashion to a lower or higher supply of these elements. Heavy metal pollution, marked by a progressive rise in toxic metal concentration in the environment, is laid down *via* industrial outlets and other wastes and has become a serious global issue [8]. Most of these heavy metals act as systemic toxins, and display widespread nephrotoxic, neurotoxic, teratogenic and fetotoxic effects. These toxic metals can severely affect human neurological and mental functions, leading to altered human behavior. Moreover, they can also turn out to be detrimental for foetal and child neural, mental and overall development, as they can pass across the placental barrier and even accumulate in breast milk [9]. Organic pollutants like crude oil, PAHs (polyaromatic hydrocarbons), organic solvents, *etc.* are of global environmental concern since these compounds can trigger severe human disorders like cancer and inflammatory diseases. Certain plants can remove these pollutants from nature. However, the biochemistry, physiology, molecular biology, and cell biology governing such stress response mechanisms in plants have not been elucidated [10]. Hence, phytoremediation has gained huge importance in the past few years and has been considered an alternate strategy to ensure the successful removal of metal pollutants from contaminated soil. Phytoremediation is one of the cheapest, most effective, and environment-friendly methods. This technique particularly utilises the capacity of plants to carry out pollutant removal or render them harmless. Therefore, remediation of the heavy metal-contaminated environment *via* hyperaccumulator species tends to serve as a promising alternative strategy as compared to other existing methodologies [11]. This

review particularly aims at the role of various medicinal plants in phytoremediation and management of heavy metal and other organic pollutant toxicity in plants.

### 1.1. Properties of Plants Capable of Phytoremediation

Apart from the traditional values, most medicinal plants display essential economic uses, particularly in industrial sectors, *viz.* cosmetics, food, ornaments, and pharmaceuticals. Medicinal plants harbor certain therapeutic properties, through some inherent bioactive agents like terpenoids, phenolics and other crucial nitrogen and sulfur-containing compounds [12]. Phenolic compounds are mainly released in the form of plant root exudates, and contain organic acids like acetate, lactate, *etc.*, which aid in metal chelation and solubilisation [13 - 15]. Moreover, these compounds, along with terpenoids, aid in the bioremediation of metal pollutants under optimal temperature, soil conditions and pH. In addition, the entire mechanism involving the uptake and accumulation of pollutants in plants largely depends on the type of tissue associated. The root system as well as the aerial plant parts (mainly leaves), mediate pollutant uptake followed by storage or oxidation within particular cellular sub-compartments (like vacuoles). Plants trigger the production of toxic reactive oxygen species (ROS) in response to the administration of stressors, including heavy metals [16]; thereby leading to the upregulation of protective antioxidant levels, to nullify the detrimental effects of heavy metal-induced oxidative stress [17, 18]. Fig. (1) summarises the properties inherent to plants capable of phytoremediation.

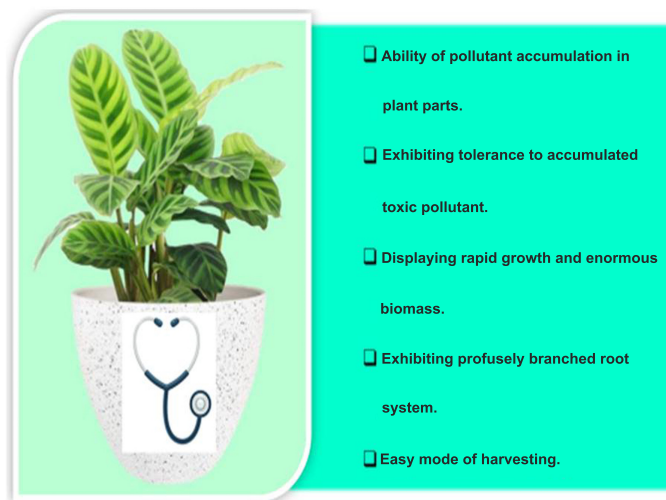


Fig. (1). Common properties of plants capable of phytoremediation.

## LEA Proteins in Plant Cellular Stress Tolerance: Insights and Implications

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**Abstract:** Plants, throughout their life cycle, are exposed to vagaries of biotic and abiotic stresses. To alleviate the stresses, plants have developed different molecular response systems. One such response is the high-level accumulation of Late Embryogenesis Abundant (LEA) proteins, a group of hydrophilic proteins encoded by a set of genes during seed dehydration, at the late stage of embryogenesis. These proteins are reported not just in plants, but also in algae, bacteria, and nematodes. LEA proteins are reported to play a versatile role in stress tolerance. This chapter discusses the classification, distribution, characterization, and functions of LEA proteins and their implications for plant stress tolerance.

**Keywords:** Drought, Late Embryogenesis Abundant proteins, Plant stress, Salinity.

### 1. INTRODUCTION

Plants have a lifetime of exposure to diverse biotic and abiotic stresses. Biotic stresses like pest and disease outbreaks and abiotic stresses like low and high temperatures, osmotic stress, drought, submergence, cold, salinity, and heavy metal pollution are among the major limiting factors that affect plant growth, and development and productivity. To overcome these stresses and survive under unfavorable conditions, plants have developed an array of responses at biochemical, molecular, and physiological levels. Unraveling the underlying molecular mechanisms of stress tolerance through multiple omic approaches greatly aids to increase plant growth, development, and productivity. Salinity,

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high temperature and drought are indirectly associated with water loss or limitation due to the accumulation of salt molecules and transpiration, which affects the plant's normal metabolism and results in adopting the new process for its survival. High temperature can cause irreversible damage including enhanced fluidity of membrane lipids that disrupts the cell membrane integrity, inhibits photosynthesis and aggregation and degradation of protein, and inhibition at transcription and translational levels [1]. The extreme low temperature or cold stress disturbs the cellular plasma membrane. It increases the production of antioxidants and changes in gene expression and protein levels [2], which causes inactivation of the enzyme activity and ROS generation leading to DNA damage and activation of programmed cell death (PCD).

### 1.1. Late Embryogenesis Abundant (LEA) Proteins

Late embryogenesis abundant (LEA) proteins are small, low molecular weight, hydrophilic in nature, that have a higher accumulation rate in the later stages of seed maturation as they acquire desiccation tolerance and constitute 4% of cellular proteins and in various other vegetative parts of the plant. LEA proteins are also known as ‘molecular shields’, which are strongly expressed when the organism experiences various kinds of stresses. LEA proteins were first reported by Leon Dure [3] and have also been reported in wheat (*Triticum aestivum* L.) and cotton (*Gossypium hirsutum* L.) at the late seed developing phase, mainly during the embryonic stage. LEA proteins are part of the extended family of osmotic stress-tolerant proteins known as hydrophilins. This is an essential protein with more than 6% Gly residues and a hydrophilicity index greater than 1 [4].

In higher plants, LEA proteins are replete with repeating hydrophilic amino acids, which help to form a highly hydrophilic structure with high thermal stability and help acquire a random winding profile in an aqueous state. This property paves the way for the description of “intrinsically disordered” proteins (IDPs) that are involved in the adaptation of plants to a new environment and the advantage of carrying out more than one function called ‘moonlighting’ activity [5]. Various investigations on LEA proteins divulge that in addition to having a very crucial biological in seeds and vegetative tissues, LEA proteins play a major role in different stress tolerance mechanisms when plants are subjected to environmental constraints.

### 1.2. Distribution of LEA Proteins In Various Organisms

It can be seen that members of the LEA protein family are pervasive in the plant kingdom. It is recognized that these proteins are not only found in angiosperms and gymnosperms [6] but also in seedless vascular plants and bryophytes, pteridophytes, and even algae [7]. The LEA proteins are primarily distributed in

the seeds of higher plants, however, it is also reported in various other plant parts such as root tips, root vascular system, stems, leaves, and flowers, whereas other protein groups accumulate in specific types of plant cells such as root meristematic cells, pollen sacs and guard cells [8]. Apart from the plants, the existence of LEA proteins in plants is reported in certain invertebrates and some bacterial species like *Deinococcus radiodurans* [9], *Haemophilus influenzae* [10], *Bacillus subtilis* in response to dehydration state, and even in anhydrobiotic organisms such as the nematode *Steinernema feltiae* [11], *Aphelencus avenae* [12], *Polypedilum vanderplanki* [13] and *Megaphorura arctica* [14], *Caenorhabditis elegans* (*CeLEA-1*) [15], and *Saccharomyces cerevisiae* [16]. Intriguingly, LEA protein can protect the human hepatoma cell during acute desiccation [17], and the presence of this protein in *Drosophila melanogaster* cells was reported to improve tolerance to salt and water stresses [18].

Embryonic axes of mung beans revealed the presence of a low relative molecular mass storage protein nearly similar to albumin [19]. Protein encoding cDNA was sequenced and characterized based on sequence homology studies and reported to be an Early Methionine (EM) labeled protein. A more in-depth analysis of the sequence of the mung bean LEA genes revealed that they function as a DNA-binding protein and are inherently hydrophilic, sharing characteristic features of Group 1 LEA proteins [20].

### 1.3. Classification of LEA Proteins

In higher plants, several proteins get accumulate under various physiological conditions. Many members of the LEA family have been identified and studied at the genome level. The LEA proteins belong to the largest gene family with well-known examples of rapeseed with 108 members [21], 79 members in cucumber [22], 60 in Grapes [23], 51 in Arabidopsis [24], 27 in tomato [25] and 12 in *Klebsormidium crenulatum* [26].

The classification of LEA proteins in cytoplasmic and nuclear regions is primarily dependent upon the amino acid sequence and homology of RNA. Traditionally, the classification of the LEA protein group has been based primarily on two categories, namely, amino acid sequence or conserved motifs and protein or oligonucleotide probability profile (POPP) [27]. According to the nomenclature of the different LEA protein groups in the Pfam database based on bioinformatics analysis, the pattern retained is those belonging to protein families (PF04927, PF00257, PF03760, PF03168, PF03242, PF02987, PF00477, and PF10714) [28]. Most studies have suggested that the versatile LEA proteins are categorized into eight domains, namely, LEA-1, LEA-2, LEA-3, LEA-4, LEA-5, LEA-6,

**CHAPTER 6****Insights into Physiological and Molecular Responses of Plants under Metal-Nanoparticle Stresses****Sneha Tripathi<sup>1</sup>, Samarth Sharma<sup>1</sup>, Shubhangi Suri<sup>1</sup>, Kavita Tiwari<sup>1</sup>, Durgesh Kumar Tripathi<sup>1</sup> and Shivesh Sharma<sup>1,\*</sup>**<sup>1</sup> *Department of Biotechnology, Motilal Nehru National Institute of Technology, Allahabad, Prayagraj, India*

**Abstract:** In a natural system, plants are experienced adverse effects of continuously changing climatic conditions and various types of stress throughout their life in which abiotic stresses are the major constraints that affect the growth and development of plants. Metal-based nanoparticles are emerging as a new pollutant of concern because of their widespread application in consumer products, which pose new challenges to the environment due to their complex interaction and possible toxic effects on plants. Plants absorb these metal nanoparticles (MNPs) from the soil along with other minerals and nutrients. Nanoparticles cause phytotoxicity by adversely affecting plants at the morphological, biochemical, physiological, and molecular levels. Various MNPs alter growth, yield, photosynthesis, and mineral nutrient uptake and induce oxidative stress, cytotoxicity, and genotoxicity in plants. Although plants have evolved various mechanisms to cope with nanoparticles-induced stress. Coordinated activities of antioxidants, some key regulatory genes and proteins regulate cellular function under stress conditions. Understanding the interaction of MNPs with plants and elucidating the behavior of genes and proteins in response to NPs stressors could lead to the development of novel approaches to mitigate stress which will support agricultural production. In this chapter, nanoparticle-induced physiological and molecular responses and tolerance mechanisms in plants against the mechanistic action of nanoparticles were described.

**Keywords:** Abiotic stress, Antioxidant, Genotoxicity, Nanoparticles, Phytotoxicity.

**1. INTRODUCTION**

In the current scenario, continuous climate change and soil contaminants cause a dramatic change in the environment and agricultural system. Among these, abiotic

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stress is the major cause of extensive loss in agricultural production worldwide [1]. Along that, intervention in nanotechnological sectors also threatens the environment because of their complex interaction with biological systems [2]. MNPs are extensively used in paints, medicals, fabrics, agriculture, the health industry personal care products like cosmetics [3 - 6]. Hence, through several ways, MNPs finally end up in the soil where it appears to be persistent and immobile and therefore does not break down in the environment. Subsequently, the movement of MNPs in the soil interacts with plants and impose devastating effect that is reported to limit the productivity of several crops *via* inducing physiological, biochemical and molecular perturbation [7 - 9]. Interaction of nanoparticles with plants induces chemical changes, such as the production of reactive oxygen species [10], membrane ionic leakage and altered permeability [11], lipid peroxidation [12], oxidative stress [13], and physiological alteration like decreased photosynthetic efficiency [14], mitochondrial disruption [15], change in stomatal opening [16]. Any kind of stress in a plant evokes a plant basal defense mechanism steering to the activation of a complex signaling cascade of defensive response. In the case of nanoparticle exposure, antioxidant and non-antioxidant enzymes are activated, and reprogramming of related gene expression provides adequate tolerance to minimize cellular damage caused by nanoparticle stress. Several studies on plant- nanoparticle interaction have uncovered the toxic behavior of metal NPs in plants; only a few reports supported nanoparticles induce plant growth promotion and tolerance against stress. Recently, some researchers have been performed to mitigate the phytotoxicity of nanoparticles by exogenous addition of some alleviators like nitric oxide, hydrogen peroxide, silicon, soil beneficial microbes, *etc.* [17, 18]. Managing the risk of nanoparticles in crop plants by inducing tolerance is a sustainable solution for stress management. In this context, to address concerns, we need to understand multiple tolerance mechanisms developed by plants to evade phytotoxicity due to MNPs. Therefore, a study of OMICS-based approaches helps to uncover the potential toxicity MNPs and their effect on stress-responsive genes in plants. This book chapter summarizes the various MNPs-induced morphological, physiological and molecular responses that affect overall plant growth and development. In addition, the chapter also summarizes the various strategies to alleviate MNPs stress to develop novel varieties with high attributes of the crop- plants.

## **2. METAL NANOPARTICLES' PHYSICOCHEMICAL PROPERTIES, SOURCES AND PRODUCTION**

Nanoparticles are materials having <100nm diameter at least in one dimension [19]. Metal-based nanoparticles have a central metallic core that may cover with inorganic, organic, or metal oxides [20]. MNPs have unique physicochemical properties compared to their native bulk material and gained significant interest in

product development because of their small size, high surface area and unique physiochemical characteristics [21]. Nanotechnology is considered a rapidly growing field with diverse applications in industrial sectors. Metal nanoparticles have good electrical conductivity, optical properties, thermal, and mechanical properties, catalytic and antimicrobial activities [19, 20]. The physiochemical properties of MNPs may govern by their atomic number, size and metallic nature. Due to the high intrinsic properties obtained from nanosized, the global production rate of nanoparticles is increased by 2.5 billion in 2021, and it is estimated to be over 6% by 2028. Some widely used metal-based nanoparticles are gold, silver, aluminum oxide, zinc oxide, cerium, titanium dioxide and iron oxide. They have diverse applications in various sectors like  $\text{Al}_2\text{O}_3$  as a fuel additive, Au in cellular imaging, Si as electrical and thermal insulators, Ag as an antimicrobial and catalyst [22], Ce as a photocatalyst, Ti and Zn used in sunscreen and cosmetics [23, 24], Fe in magnetic imaging and battery [25]. Due to the wide application of MNPs in various industries, MNPs enter into environmental matrices by various pathways. The source of MNPs is complex; it includes both point and non-point sources. Point sources of MNPs are direct application NPs such as in remediation and nanofertilizers in soil. The indirect or nonpoint source includes accidental spills during industrial production and transport [26]. The main source of NPs deposition in the terrestrial system is through the landfills and sewage sludge where NPs come from a consumer product in wastewater streams; for example, it is reported that  $\text{TiO}_2$  NPs easily enter into the water stream *via* washing and end-of-self-life of consumer products and 99% entered  $\text{TiO}_2$  retain in sludge phase [27]. Similarly reported concentration of silver nanoparticles in waste water treatment effluent was 1.8 to  $>100 \mu\text{g/L}$  [28].

### 3. MNPs UPTAKE, TRANSLOCATION AND ACCUMULATION IN PLANTS

To understand the impact of MNPs on plants, there is a need to determine how MNPs enter into plant tissue and, once entered, how their translocation and active accumulation occur inside the plants. Plants have a complex structure that acts as a barrier to the entry of NPs [29]. First of all, the interaction of nanoparticles in soil takes place on the root surface of plants. After attaching to the root surface, a complex array of mechanisms occurs, which depends upon various plant-related factors (Su *et al.*, 2019). Plant root and leaf differ morphologically, which impact the entry and transport of NPs for example, after entering in root system NPs move through the apoplastic and symplastic pathway and reach the endodermis. However, the Casperian strip permits only a symplastic pathway in passage cells for the movement of MNPs. Most of the MNPs are not held up by plant roots in the soil-drenching method. On the other hand, plants have a larger pore size in the stomata of leaves, which efficiently permits MNPs entry in foliar application.

# Inoculation of Plant Growth-Promoting Bacteria Aiming to Improve Rice Tolerance to Abiotic Stressful Conditions

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**Abstract:** Rice is one of the most important cereals, as it feeds over half of the world's population. Rice production is limited by different abiotic stresses, which would probably worsen with climate change. Also, we must expect a rapid increase in food demand. Therefore, there is an urgent need for innovative agricultural technologies able to increase cereal amounts without increasing arable lands. The inoculation of plant growth-promoting bacteria (PGPB) from paddy soil can improve plant response to abiotic stresses; however, the mechanisms involved in such protective response are largely unknown. The current chapter comprehensively analyses and presents the state-of-the-art inoculation of selected PGPB aiming to improve rice tolerance to abiotic stress conditions. Different plant responses at the molecular, biochemical, physiological, and agronomical levels will also be appraised. This summary can stimulate the producers to inoculate rice plants, contributing to rice production in abiotic stress-impacted regions.

**Keywords:** Cold, Drought, Heat, Heavy metal, Inoculation, Nutrient starvation, Rhizobacteria, Rice, Salinity, Tolerance.

## 1. INTRODUCTION

Rice (*Oryza sativa* L.) is probably the most important crop globally since it feeds over half the world's population [1, 2]. To meet the upcoming global food security needs, food amount must substantially increase, while the producers' environmental footprint must decrease. To meet the ever-increasing demand for food, global rice production must double by 2030 [3]. Therefore, the improvement

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of rice crops is of utmost importance [4]. However, plants are always under different abiotic stress conditions that decrease plant performance and productivity [4, 5]. In addition, climate change is predicted to increase the periodicity and severity of these impacts on plant performance [6].

The most common abiotic stresses that impact rice development and yield around the world are salinity, drought, cold, heat, and minerals [7]. Recent studies in different areas, such as omic analyses with the dissection of stress regulation networks, have been performed in rice plants, enabling a broad platform for rice research [4]. Several stress-tolerance genes/proteins/molecules have been identified/characterized and could be used as biological markers. Based on these data, several strategies have been used to improve or generate rice tolerance to different abiotic stresses, such as searching for genetic diversity in wild species [8 - 11], QTL mapping and genome-assisted breeding [12 - 15], modulation of key stress-related genes by transgenic approaches [16 - 19], and genome editing by CRISPR/Cas9 technology [20 - 23].

Another available biotechnological strategy to improve plant tolerance to abiotic stress conditions is the rational modification of rhizospheric microbial communities through inoculation practices [24 - 26]. It is widely known that soil microbial communities can stimulate plant development [27] and induce beneficial outcomes in plants submitted to stressful conditions [28]. Therefore, we can modify the relative abundance of specific microbial groups in stressed environments [29]. Inoculation of plant growth-promoting bacteria (PGPB) can be used to engineer the plant-microbe interaction and help induce plant tolerance to adverse environmental conditions [28]. Thus, inoculation of selected microbes can be a powerful option to sustain plant growth under non-optimal conditions [30] and improve plant tolerance [31].

Most of the studies indicate that the beneficial effects detected in plants inoculated with selected microorganisms under non-optimal conditions are related to the production of phytohormones, such as indoleacetic acid (IAA) and gibberellin (GA) [32, 33], siderophores [34], phosphorus solubilization [35], biological nitrogen fixation [36], and increased potassium uptake, maintaining the photosynthetic apparatus efficiency and contributing to water use efficiency [37]. These microorganisms can also maintain the osmotic potential inside the cell [30], reduce oxidative stress indicators and increase antioxidant levels [38], avoiding cellular damages caused by stressful conditions.

It is important to highlight that under abiotic stress conditions, ethylene synthesis is activated to modulate signaling pathways that will in turn protect the stressed plants from deleterious effects. However, the activation of ethylene synthesis at

greater levels can also be deleterious to the plants, inhibiting root and shoot proliferation and accelerating leaf senescence, and therefore limiting plant growth and development [39]. Therefore, the use of PGPB with aminocyclopropane--carboxylate (ACC) deaminase activity to decrease stress-induced ethylene synthesis has been carried out in different plant species to avoid the detrimental effects of stress-induced ethylene and maintain plant development even under abiotic stressful situations [40, 41].

In this chapter, we summarize the studies involving the inoculation of selected plant growth-promoting bacteria (PGPB) aiming to improve rice tolerance to the major abiotic stressful conditions: salinity, drought, heavy metal, and extreme temperatures. We also briefly discuss different plant responses at the molecular, biochemical, physiological, and agronomical levels, and the prospects/future challenges associated with this biotechnological and ecofriendly approach.

## 2. RICE TOLERANCE TO SALINITY

Approximately 20% of the arable lands around the world are saline, substantially reducing the growth and yield of cereals [42]. Therefore, salt stress is a major worldwide environmental concern causing cultivable land area decreases, given that drastic reductions in root size and weight are observed, leading to decreased crop productivity [43, 44]. Reduction in photosynthesis rates and increased intracellular NaCl levels, which are the main responsible for plant growth limitation under salt stress conditions, can affect different physiological processes [45, 46]. Salinity also interferes with water transportation and nutrient uptake and transport in plants, thereby leading to osmotic deregulation and nutrient discrepancy [47, 48]. Long exposures to salinity enhance ionic stress in plants, leading to early foliar senescence, yellowing, and grain distortions [49].

A feasible strategy to diminish the plant injury induced by high salinity conditions is the inoculation of halotolerant PGPB [50]. Therefore, the aim of using salt-tolerant PGPB is to increase plant performance (growth and yield) under salt conditions [44]. Several studies listed in Table (1) reported the use of PGPB to improve salinity-induced damages in rice plants. The most common bacterial genus used in these inoculation strategies (ten out of 24) was *Bacillus* spp., while other genera such as *Brevibacterium*, *Enterobacter*, *Streptomyces*, and *Achromobacter* have been used in two strategies. *Bacillus* is abundantly found in soil samples due to its ability to survive even under different and harsh environmental conditions [51]. This functionally versatile genus is one of the most commercially exploited bacteria in the agrobiotechnology industry [52]. As a general response, most studies reported several beneficial effects when salt-stressed plants were inoculated with the selected bacteria. Such beneficial effects

**CHAPTER 8****Plant Growth-Promoting Rhizobacteria (PGPR): A Credible Tool for Sustainable Agriculture**

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**Abstract:** Modern agricultural practices rely on the excessive use of chemical fertilizers to increase crop yields to meet the growing population's demand. It has exploited the inherent biological potential of soil and plant systems. Sustainable agricultural practices focus on equal attention to soil and plant health. Plant growth-promoting rhizobacteria (PGPR) serve the plants by combating abiotic and biotic stressors in the environment. These microorganisms aid plants in multiple ways by colonizing the plant roots. They work effectively as biofertilizers and as biocontrol agents and help in fostering plant growth through either direct (potassium and phosphorous solubilization, siderophore production, nitrogen fixation) or indirect (production of VOCs, antibiotics, lytic enzymes) mechanisms. To upgrade their application to agro-ecosystems, modern technologies are being worked out. These aim at improving the efficacy of PGPR and uplifting agricultural sustainability. Therefore, in this book chapter, the role and mechanism of PGPR as soil health boosters and plant growth enhancers were discussed. Further, it sheds light on recent developments made to strongly present PGPR as a potent candidate for green agriculture.

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**Keywords:** Biofertilizer, Plant growth-promoting rhizobacteria (PGPR), Green agriculture, Crop yield, Biocontrol agents.

## 1. INTRODUCTION

Food is one of the primary needs of humans that play a critical role in a nation's growth. The issues of hunger, poverty, food insecurity and malnutrition pose a major risk to the health and development of a society. As per information from the Food and Agriculture Organization of the United Nations (FAO), the count of undernourished people in the world is rising and has 21% of the African population (256 million people) and 11.4% in Asia (515 million people) in 2017 (FAO, IFAD – International Fund for Agricultural Development, UNICEF – United Nations Children's Fund, WFP – World Food Programme, WHO – World Health Organization, 2018). Modern agricultural practices can fulfill the requirement but with the excessive utilization of fertilizers [1].

The unfair application of synthetic agrochemicals is precarious to the environment and human health as it results in harmful effects such as (1) a drop in soil fertility and microbial diversity; (2) improved emergence of resistance among phytopathogens and insects; and (3) pollution and degeneration of soil and the environment [2]. Conventional agricultural practices are toxic as their excess use makes the soil acidic & also leads to the formation of dead zones with reduced oxygen levels for marine flora and fauna [3]. Both infants and humans suffer from several disorders, such as vector-borne diseases, stomach cancer, and methemoglobinemia, due to bioaccumulation and biomagnification of toxic heavy metals such as mercury, cadmium and lead [4]. Furthermore, industrial production of fertilizers depends on nonsustainable assets, *e.g.*, coal and natural gas, which leads to the production of greenhouse gases (*e.g.*, CO<sub>2</sub> and NO<sub>2</sub>) that contribute to global warming [5].

Towards the vision of a healthy environment and sustainable agriculture, the challenge is to produce crops adorned with qualities such as salt tolerance, heavy metal stress tolerance, disease resistance, and better nutritional value. The latest techniques involved in sustainable agriculture are agricultural intensification, eco-friendly management practices [6], use of genetically engineered crops [7], use of microbes or genetically engineered microbes to stimulate plant growth [8] and use of biofertilizers.

Soil is the dynamic and valuable natural resource that supports diverse microbial communities, being a reservoir of reduced carbon components, thus maintaining global nutrient balance and ecosystem function [9]. Indigenous eco-friendly microorganisms enhance soil-plant environmental sustainability by influencing physiological processes like cell turgor maintenance, photosynthesis

enhancement, nitrogen uptake, enzyme activation, transportation of sugars and starches, increased disease resistance and stress tolerance [10]. In the early 20th century, microbial-based agricultural inputs started with the use of broad-scale rhizobial inoculation of legumes [11]. Plant growth-promoting rhizobacteria (PGPR) is used for microorganisms that benefit plants in diverse sectors such as yield, growth and disease tolerance. It mainly includes abundant forms of bacteria such as *Pseudomonas*, *Bacillus*, *Rhizobia*, *Bradyrhizobium*, *Mesorhizobium*, *Azotobacter*, *Acinetobacter*, *Enterobacter*, *Burkholderia*, *Klebsiella*, *Variovorax*, *Azospirillum*, *Serratia*, etc. They settle as symbionts, closely with the plant's root system, or as free-living forms. PGPR can colonize, survive and divide in microhabitats in association with the root surface in return for promoting plant growth [12]. They can possibly minimize the use of synthetic fertilizers and agrochemicals in the field. The application of PGPR has promising results regarding increased plant biomass production [13]. PGPR improves soil health through different mechanisms like nitrogen fixation, phosphate solubilization, decomposition of crop residues, heavy metal sequestering, quorum sensing, phytohormone production, mineralization of soil organic matter, and suppression of phytopathogens, etc. [14]. PGPR also produces growth hormones, exopolysaccharides, siderophores and enzymes like 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, antioxidants and volatile compounds. It supports plants by stimulating their stress resistance mechanisms. They also induce systemic resistance (ISR) and act as antagonists of plant pathogens by producing antifungal and antibacterial compounds in soil [15]. PGPR perceives the host plant by specific molecules which have conserved chemical structures/patterns termed microbe-associated molecular patterns (MAMPs). They are detected by members of a large family of plant pattern recognition receptors (PRRs). These PRRs stimulate signaling cascades and turn on the first line of plant defense, called MAMP-triggered immunity (MTI). They are categorized as biofertilizers, biopesticides, phytostimulators and rhizoremediators [16]. Effective utilization of PGPR by thoroughly understanding the mechanisms through which they influence soil health is the key to ensuring sustainability in agriculture [17].

## **2. THE PGPR DIVERSITY IN THE RHIZOSPHERE**

The rhizosphere is a playground for microbial activities, particularly an arena surrounded by plant roots where interactions take place. These interactions may be collegial or uncooperative [18]. Two components, namely rhizosphere and rhizoplane, surround the roots where microbial colonization occurs, and these interactions are crucial for plants as well as microbes [19].

This micro-environment exhibit higher microbial activity, and by root exudation, roots control soil microbes in its vicinity, respond towards herbivory attack,



## CHAPTER 9

# ATP Binding Cassette (ABC) Transporters in Plant Development and Defense

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**Abstract:** ABC transporters (ATP-binding cassette transporters) are dynamic proteins found in both types of organisms, prokaryotes and eukaryotes. They play pivotal roles in the transportation of various substances along cellular membranes by utilizing ATPs. ABC transporters consist of four domains: two NBDs with highly conserved motifs and two TMDs. They have a large diverse family, which is grouped into 8 subfamilies (A, B, C, D, E, F, G, H, I), though the H subfamily is not found in plants. ABC transporters are well-defined for transporting xenobiotic compounds, secondary metabolites, phytohormones, toxic heavy metal ions, chlorophyll catabolites, lipids, and drugs across cellular membranes. Importantly, several kinds of ABC transporters investigation discovered their functions in plant growth, development, and defense. Commonly localized on plasma membranes, they are also found on the membranes of vacuoles and various cellular organelles. Under stress, these are known to contribute to various physiological, developmental, and metabolic processes by helping plants adapt. Initially, they were recognized as tonoplast intrinsic transporters, but now they are well-known in cellular detoxification mechanisms which protect plants and maintain homeostasis. This chapter presents a comprehensive account of the roles of ABC transporters with insights into molecular and physiological leading to stress tolerance.

**Keywords:** ABC transporter, Detoxification, Heavy metal, Phytoremediation.

## 1. INTRODUCTION

ATP-binding cassette (ABC) transporters are functional proteins that transport various biomolecules and solutes across cellular membranes [1, 2]. They are present in all living phyla, from prokaryotic cells to human beings [3, 4]. They consist of four domains, *i.e.*, two transmembrane domains (TMDs) and two cytoplasmic-nucleotide binding domains (NBDs). The binding of ATP is utilized by NBDs which are then hydrolyzed and used for substrates translocation [5]. Across several different biological membranes, ABC transporters transport the

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substrates such as lipids, phytochemicals, secondary metabolites, xenobiotics, carboxylates, toxic metals, and chlorophyll compounds [6, 7].

There are three types of ABC transporters, *i.e.*, type I and type II ABC importers with ABC exporters. All these transporters were found in prokaryotes except ABC exporters which were only found in eukaryotes. These two ABC importers transport various micro-nutrients, essential metal ions, vitamins, and biosynthetic precursors, but ABC exporters export metabolites like lipids, sterols, and drugs [8].

### 1.1. ABC Family

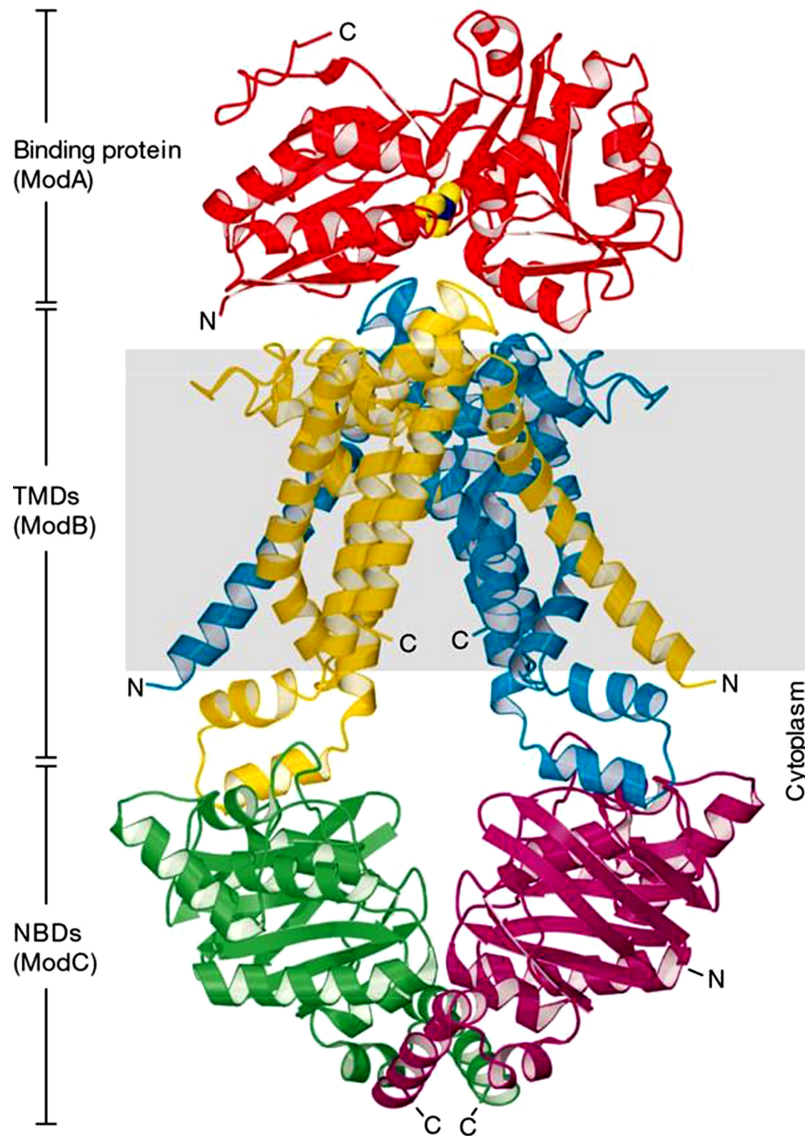
ABC transporter proteins are arranged systematically into groups of eight subfamilies like ABCA, ABCB, ABCC, ABCD, ABCE, ABCF, ABCG, ABCH, and ABCI subfamilies, however, the ABCH subfamily does not exist in plants [9, 10]. Plant ABC transporters subfamily B (ABCB)/Multidrug-resistant (MDR) homologs, were categorized by their plasma membrane localization and are known as the largest subfamily of plants, commonly called P-glycoproteins have 22 members and are overall known as the second major ABC subfamily. This vast family of ABC transporters in plants was associated with their terrestrial lifestyle, which makes them predominantly open to biotic and abiotic stresses [11].

### 1.2. Structure

ABC transporters are termed as ‘full (complete)’ and half transporters. Essentially, all functional ABC transporters comprise two transmembrane domains (TMDs) and two nucleotide-binding domains (NBDs). These domains are synthesized independently and, therefore constitute a full ABC transporter of four domains (2 TMDs and 2 NBDs) and half transporter of two domains (1 TMD and 1 NBD). Subsequently, to get functional, half transporters dimerize in pairs to create virtually full transporters. The third category of ABC transporters has only two NBDs. The transmembrane domain (TMD) provides transport selection and substrate recognition. It extends throughout the lipid bilayer, which consists of 4-6 alpha-helices [12]. Substrates transportation depends upon the adjacent association between TMD and NBD (Fig. 1).

In the ABCC subfamily, an additional N-terminal TMD (TMD0) has also been characterized. Several basic conserved motifs like Walker A, switch H-loop, Q-loop, Walker B, signature motif and D-loop were set up in NBD. D-loop held dimers together, the P-loop consisted of Walker A-B motifs that bound to ATP. The H-loop switch interacted with TMD, and finally, crucial residues of both the loops Q and H network with ATP  $\gamma$ -phosphate [12]. ABC proteins are distinguished from other ATPases by signature motif (LSGGQ), which was

completely established in all ABC transporters. In the physiological environment, ABC works in only one track, but LmrA, which is the drug efflux pump, had also been reversed in some situations, and for this, P-type ATPases have a transmembrane domain that interchanges in inward and outward-facing conformation proposed by Jardetzky [13 - 15].



**Fig. (1).** Demonstration of the overall structure of ABC transporter in ribbon depiction, with ModA, ModB and ModC subunits (Adopted from Hollenstein *et al.* 2007).

## How can Endophytic Bacteria Benefit Agronomically Important Plants by Protecting Against Pathogens?

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**Abstract:** The use of endophytic bacteria is an emerging trend in agriculture since they can promote plant growth under normal conditions and abiotic and biotic stresses. In this regard, endophytic bacteria have been used to deal with the consequences of the climate crisis in global crops, as alternatives to ecologically unsustainable chemical pesticides and fertilizers. These bacteria can benefit plant growth by direct mechanisms, such as hormone production and nutrient solubilization, and indirect mechanisms, which involve protecting the plant against pathogens and suppressing disease. Thus, this chapter aims to present the main mechanisms of plant growth promotion by endophytic bacteria, focusing on the genetic and physiological processes of biocontrol of pathogen growth and induction of systemic plant resistance. Genome sequencing data from endophytic bacteria provide information about genes involved in the synthesis of enzymes and antimicrobial compounds, such as siderophores and hydrocyanic acid, among others. Furthermore, genetic pathways involved in plant response induction were characterized using sequencing experiments and differential RNA expression analysis. Jasmonic acid and salicylic acid biosynthesis genes are differentially expressed in response to plant interaction with endophytic bacteria. Therefore, data from the most current methodologies of genetic and molecular analysis will be condensed here to provide an overview to respond to the question that heads the chapter.

**Keywords:** Biotic stress, Bioinoculants, Endophytic bacteria.

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## 1. INTRODUCTION

Endophytic organisms (from the Greek endon = inside, phyton = plant) are microbial symbionts that colonize plant tissues for most of their life cycle without any harmful impact on the host [1 - 3]. Strictly speaking, endophytes are commensal symbionts, but they can range from latent or saprotrophic pathogens to mutualistic associations [2, 3].

Fungi, bacteria, protozoa and archaea can be considered endophytes [4, 5]. In bacteria, which will be the focus of this chapter, the most representative phyla are Proteobacteria, Actinobacteria, Firmicutes and Bacteroidetes [4 - 6].

The interaction between host plants and the community of endophytic bacteria involves a long process of co-evolution guided by tissue colonization dynamics and plant genotype [1, 7]. Soil provides the initial inoculum and the necessary conditions for the occupation of the plant rhizosphere [7, 8]. Then, root exudates and photosynthates select the endophytes by chemotaxis [9, 10]. Finally, endophytes respond to host stimuli through quorum sensing, guiding the colonization process [11, 12].

Endophytic bacteria colonize specific regions or systemically throughout the plant body, including the root cortex, stem, leaves and inflorescences [13, 14]. Within tissues, they can be found in inter- or intracellular spaces and transmitted vertically to the next generation by seeds [15].

The most optimistic researchers believe that bacterial endophytes evolved at least 60 million years ago and, even at the beginning of the association, played an important role in terrestrial ecosystems, benefiting both partners in the interaction [16, 17]. Evolutionarily, Hallmann, *et al.* (1997) suggest that endophytic bacteria may be intermediate between saprophytic and pathogenic bacteria, with a chance that endophytic bacteria are more evolved than the pathogenic ones, as they feed on the host without causing damage. An opposing hypothesis suggests that endophytic bacteria emerge as antagonists [18], but the direction taken from the ultimate symbiotic relationship to antagonism or mutualism will rely on the genotype, tissue, health and nutrition of the host plant [18, 19].

Bacterial endophytes that can establish mutualistic relationships with their hosts are called plant-growth-promoting bacteria (PGPB) [20, 21]. They play an indispensable role in plants' health, as they can produce hormones, facilitate nutrient uptake, and protect and prepare the plant against abiotic and biotic stresses, in addition to increasing plant growth and biomass [21 - 24].

PGPB have great biotechnological potential when inoculated into agronomic crops. They can be used to alleviate the impacts of climate change on agricultural fields by promoting plant growth under drought and heat stress [25, 26]. They are also incorporated in the bioremediation of soils contaminated by metals because of predatory anthropogenic activities [24, 27]. Finally, PGPB have emerged as an ecological alternative to the application of chemical fertilizers and pesticides used in the fight against various phytopathology, given that they can control pathogen growth and plant disease without harming the environment [28, 29].

New genetic sequencing technologies have provided important data not only on genes and secondary metabolites produced by endophytic bacteria, but also on how plants interact with endophytes, and which pathways and which genes are activated in this interaction [30]. These data provide a dynamic panel of information about the host/endophyte relationship and its implications for plant species of agronomic application.

Based on these studies and data obtained over the last decades, it is possible to explain how endophytic bacteria manage to promote growth and mitigate plant stress, which is the main goal of this chapter.

In the first part of the chapter, we will focus on the general mechanisms of growth promotion, like hormone production and nutrient solubilization. We will analyze studies that correlate the inoculation of endophytic bacteria with traits for plant resistance to biotic and abiotic stresses. Finally, we will consider the role of endophytes in controlling pathogens and plant disease and in inducing systemic resistance to plant pathologies.

## **2. GENERAL MECHANISMS OF PLANT GROWTH PROMOTION BY ENDOPHYTIC BACTERIA**

Endophytes can benefit plants directly or indirectly. The direct pathways involve nutrient solubilization and phytohormone production. Indirectly, endophytic bacteria favor host plants through phytopathogen biocontrol and disease mitigation. Endophyte biocontrol involves the production of antibiotics and lytic enzymes, competitive exclusion by nutrients and induction of systemic plant defense [13, 29]. In this initial moment, we will focus on the direct mechanisms of growth promotion.

### **2.1. Phytohormone Modulation**

Plant hormones are a diverse group of chemical molecules involved in regulating the plant's genetic program in response to environmental signals and variations [30]. Phytohormones play an important role in plant development under normal

## CHAPTER 11

# Sustainability of Agriculture and Global Food Supply Using Advanced Molecular Tools and Integrated Multi-omics and Gene Functions

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**Abstract:** Food security has become the biggest challenge today due to the burgeoning population and environmental impacts on crops. The agriculture system needs to meet the food demand by using appropriate sustainable approaches while exerting minimum impact on the ecosystem. Multiomics is one of the successful sustainable technologies that contribute toward crop improvement and acceleration in food production. Progressive development in next-generation sequencing for various omics like genomics, transcriptomics, proteomics, metabolomics, ionomics and phenomics have provided desired genetic resources for crop improvement. With the development of molecular technology, new breeding tools are used for the transfer of genes from one species to another. Biotic and abiotic stress-resistant traits are incorporated in cultivating varieties to make them superior and produce a good yield. This chapter solely summarizes the development of new traits with the help of new breeding tools such as TALENs and CRISPR in plant breeding. The high throughput multi-omics techniques are not only applicable for enhancing agricultural growth and yield but also helpful in refining food security.

**Keywords:** Breeding tools, Cultivation, Multi-omics, Sustainability.

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## 1. INTRODUCTION

Currently, the global population is approaching 7.9 billion and, by 2050, is expected to surpass about 9.7 billion; such a rapid surge in population is creating a great challenge for food supply (<https://www.worldometers.info/world-population/#>). The crop quality and yield are needed to improve to meet the demands of the rising population. Another great challenge that interferes with better food production is climate change which affects plant growth. Increased atmospheric temperature directly disrupts the photosynthetic apparatus, respiratory chain, and nitrogen use efficiency of harvested plants [1]. So this necessitates plants to adapt and be tolerant to various biotic and abiotic stresses. The transformation from conventional agricultural practices to genomics-assisted breeding is the need to meet the challenges in agriculture caused by climate change.

Many breeding strategies are developed for sustainable agriculture in which different crop varieties are grown with high yield potential, high nutrition value, grain superiority, good produce, resistance to disease, and use of a very low amount of fertilizers. Many omics tools may be worked independently or in an integrated way to elucidate the biological function on a genetic basis. Over the last few years, multi-omics techniques are exploring the genetic origin of the plant system through the changes in DNA, RNA, proteins, and metabolites against adverse environmental conditions [2]. Various omics techniques such as genomics, transcriptomics, proteomics, metabolomics, phenomics and ionomics have evidenced each genetic and molecular aspect interspersed with plant systems [2 - 6]. These high-throughput technologies are not only recognizing the gene functions but also facilitate to recognition of the novelty of valuable genes more than that of wild varieties of existing crops. These technologies also help to enhance the yield of primary crops such as maize, wheat, and rice [7]. Vigor cultivars with desirable traits have been selected by advanced genotyping systems, and the germplasm collection of several species characterizes the diversity and potential of the whole genome to resequence [8]. In this chapter, we discuss the integration of various omics technologies such as genomics, transcriptomics, proteomics, metabolomics, ionomics and phenomics, gene editing tools for enhancing crop productivity, and various breeding methods for enhancing disease resistance by introgression of R genes from wild species in plants.

## 2. MULTIOMICS TECHNOLOGIES FOR SUSTAINABLE AGRICULTURE

The crop quality and yield are enhanced by integrated multi-omics techniques, and such biofortified produce provides safety against malnutrition. Progression in



next-generation sequencing (NGS) has revolutionized plant breeding and whole-sequenced genomes by targeting genomic areas. Fundamental breeding traits are observed by mapping genomic regions with high-density markers. Collection and characterization of propagated and wild germplasm are utilized by germplasm approaches to understanding morphological and molecular changes in useful characters [9]. Omics-tools also comprehended the plant disease ecology by identifying pathogenesis through the observation of plant and microbial physiognomies along the genotype-phenotype spectrum [10].

Gene editing technology, along with omics technologies, can aid to develop new varieties for sustainable agriculture. Genes can be knockout by inducing insertions or deletions frequently at non-homologous end joining (NHEJ) through gene-editing techniques resulting in framing error-producing premature stop codons. Double-strand break is induced by CRISPR/Cas9, and this genetic manipulation method depends on the DNA repair mechanism of the cell to repair the breaks. The introgression of genes responsible for high nitrogen use efficiency in some agricultural varieties is advantageous for sustainable crop development [11]. So the expression of semi-dwarf varieties can be improved by modifying the genes using versatile and precise CRISPR/Cas9 technology that can not only enhance crop productivity but also reduce the use of nitrogen fertilizers and protect the environment from these chemicals.

## **2.1. Genomics**

Genomics is the well-known study of genes and genomes. It becomes involved in finding out the hereditary changes that include performing better and improving breeding competence, all in all causing genetic enhancement of plant species. Among different types of genomics, structural genomics involves the whole genome construction, organization of chromosomes, and also sequence polymorphisms; this leads to the production of high-resolution genetic as well as physical maps for categorizing different genomic areas and managing the desirable traits. However, functional genomics describes the various roles of a gene that contribute to a particular trait of interest. It is well known that DNA forms chromatin in organization with histone proteins, and these basic proteins are very sensitive to going through epigenetic changes such as DNA methylation, adjustment of histones and sRNA-facilitated methylation. This whole phenomenon at the genome level is delineated as epigenomics.

### **2.1.1. Structural Genomics**

Structural genomics relies on molecular markers such as amplified fragment length polymorphism (AFLP), restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), SRAP (sequence-related), and

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