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Tariq Aftab *Editor*

New Frontiers in Plant-Environment Interactions

Innovative Technologies and Developments

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Editor

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ISSN 1863-5520 ISSN 1863-5539 (electronic)
Environmental Science and Engineering
ISBN 978-3-031-43728-1 ISBN 978-3-031-43729-8 (eBook)
https://doi.org/10.1007/978-3-031-43729-8

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Preface

Plants, as the lifeblood of our planet, have existed for millions of years, adapting and evolving to the ever-changing environment surrounding them. From the lush rainforests to the harsh deserts, they have demonstrated remarkable resilience and ingenuity. As we stand at the forefront of the twenty-first century, the urgency to understand and unravel the intricacies of plant–environment interactions has never been more pressing.

New Frontiers in Plant-Environment Interactions: *Innovative Technologies and Developments* is a collaborative effort that brings together a diverse array of research and expertise from scientists, scholars, and visionaries at the cutting edge of plant biology and environmental sciences. In this compendium, we embark on an exhilarating journey to explore the uncharted territories of plant responses to their environment, uncovering secrets that have remained concealed for centuries. The fascinating realm of plant environment interactions encompasses a vast spectrum of topics, ranging from the molecular level to entire ecosystems. In this volume, we delve into the intricate web of signaling pathways that enable plants to sense and adapt to environmental cues. We traverse the fascinating world of gasotransmitters, hormones, and secondary metabolites that act as messengers, orchestrating plant responses to biotic and abiotic stressors.

As we peer into the realm of epigenetics, we discover how environmental factors leave an indelible mark on the plant's genetic expression, shaping their adaptive strategies for generations to come. We delve into the symbiotic relationships between plants and beneficial microbes, unlocking novel avenues for sustainable agriculture and ecosystem restoration. The book also examines the ever-pressing challenges posed by climate change, pollution, and habitat loss, and how these global issues necessitate innovative strategies for conservation, restoration, and sustainable land management. We spotlight ground-breaking research on plant biotechnology, genetic engineering, and precision agriculture that hold the potential to revolutionize our ability to enhance crop productivity and adaptability.

Beyond the scientific realm, this book acknowledges the importance of interdisciplinary collaboration and communication. It encourages researchers, policymakers, and stakeholders from diverse backgrounds to unite in addressing the complex environmental challenges we face today. I hope this book will serve as a guiding light for current and future generations of plant scientists, environmentalists, and conservationists. Our understanding of the intricacies of plant environment interactions is vital to safeguarding the planet's biodiversity, ensuring food security, and mitigating the impacts of climate change.

I extend our heartfelt gratitude to all the authors who have contributed their expertise and passion to this volume. Their dedication to advancing knowledge in this field has made this endeavor possible. I hope the revelations within these chapters inspire fresh perspectives, foster innovative ideas, and catalyze transformative action in our quest to protect and cherish the precious bond between plants and their environment.

Lastly, thanks are also due to well-wishers, research students, and editor's family members for their moral support, blessings, and inspiration in the compilation of this book. I also thank the Springer-Nature team for their generous cooperation at every stage of the book production.

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About the Editor

Dr. Tariq Aftab received his Ph.D. in the Department of Botany at Aligarh Muslim University, India, and is currently an Assistant Professor there. He is the recipient of a prestigious Leibniz-DAAD fellowship from Germany, Raman Fellowship from the Government of India, and Young Scientist Awards from the State Government of Uttar Pradesh (India) and Government of India. After completing his doctorate, he has worked as a Research Fellow at the National Bureau of Plant Genetic Resources, New Delhi, and as a Postdoctorate Fellow at Jamia Hamdard, New Delhi, India. He also worked as a Visiting Scientist at Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben, Germany, and in the Department of Plant Biology, Michigan State University, USA. He is a member of various scientific associations from India and abroad.

He has edited 20 books with international publishers, including Elsevier Inc., Springer Nature, and CRC Press (Taylor & Francis Group), co-authored several book chapters, and published over 80 research papers in peer-reviewed international journals. His research interests include physiological, proteomic, and molecular studies on medicinal and crop plants.

Chapter 1
Plant-Environment Interactions: The Dynamics of the Skill and Beyond

Misbah Naz and Muhammad Rahil Afzal

Abstract Plant's dynamic phenotypes are shaped by the interactions between the plant and its environment. To advance the study of plants and their environmental interactions, including crop breeding and management, it is crucial to have a comprehensive understanding of plant activities throughout their lifespan in dynamic settings. The plant research community faces the challenge of accurately analyzing a range of traits in an increasing number of plants to aid in adapting to resource-limited situations and low-input agriculture. This chapter explores the evolution of plant phenotyping as a field that draws on various academic disciplines. Technological advancements that enabled the formation of phenotyping centers are discussed, as well as the obstacles that need to be addressed for plant phenotyping to progress further, particularly with regard to data collection consistency and reusability. The emergence of the plant phenotyping community is described as the final step in integrating the community and leveraging synergies.

Keywords Agricultural production · Environmental interactions · Technological advancements · Fundamental plant biology · Plant phenotyping

1.1 Introduction

Plant-environment interactions are crucial for the growth, development, and survival of plants. These interactions are influenced by a variety of factors, including temperature, light, moisture, nutrients, and other biotic and abiotic factors (Orcutt and Nilsen 2000). Understanding these interactions is important for agricultural production, ecological restoration, and conservation efforts. In the context of municipal landscaping, plant-environment interactions play a critical role in ensuring that plants

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_1

thrive in urban environments (Yuan et al. 2023). Urban environments are often characterized by high levels of pollution, heat, and limited space, which can create challenging conditions for plant growth. However, by selecting plant species that are adapted to these conditions, and by implementing appropriate management practices, it is possible to create beautiful and functional green spaces that enhance the quality of life for urban residents (Wingfors et al. 2011). Beyond municipal landscaping, plant-environment interactions are also critical for understanding how plants respond to global environmental changes such as climate change, land-use change, and habitat fragmentation (Bestelmeyer et al. 2015). Through studying these interactions, we can better predict how plant communities will respond to these changes and develop effective conservation strategies to protect plant biodiversity. Overall, understanding plant-environment interactions is critical for addressing a wide range of environmental challenges, from urban landscaping to global environmental change (Caujape-Castells et al. 2010).

In order to address and comprehend how plants and their environments interact, crop management approaches, the impacts of biostimulants, microbial communities, etc. may all benefit from using plant phenotyping (Walter et al. 2017; Walter and Schurr 2005) One of the main phenotyping applications in use today is plant breeding, and many advancements in plant phenotyping are controlled by breeding aims (Furbank and Tester 2011). In this situation, emerging methods must provide benefits in terms of throughput, field usability (across a wide range of weather conditions), and, in particular, the utility of the breeding process itself and the heritability of the derived characteristics (Rouphael et al. 2018). Over the past few decades, there has been a significant increase in plant phenotyping, providing several opportunities to fulfill various phenotyping requirements.

However, the progress in this field is still rapidly advancing. To ensure seamless integration of new technologies into academic and breeding workflows, generate more capacity, and facilitate data exchange and information acquisition across different experiments, locations, and facilities, it is crucial to establish appropriate access opportunities and data management systems (Kumar et al. 2015). Simultaneously with the continuous integration of state-of-the-art technology, it is imperative to address the remaining challenges and take advantage of opportunities in plant phenotyping, despite the progress made in this field (Mir et al. 2019). To effectively leverage the existing synergies in plant phenotyping, several national infrastructures for plant phenotyping have been established to facilitate interaction and critical mass (Li et al. 2020b).

Plant activities such as growth, photosynthesis, and yield generation sustain the foundation of life on our planet, supporting the current population of 7 billion people. To meet the increasing demand for food and non-food items from plants while minimizing environmental impact, including land and water usage, these processes need to be further enhanced FAO, (WHO 2018). Over ten thousand years ago, humans began domesticating plants, initiating the purposeful alteration of plant traits such as yield (Fuller et al. 2014).

The selection of food plants with desirable traits and their exploitation as seed sources for subsequent generations led to the accumulation of these traits over time, serving as the foundation of breeding and significantly impacting human history (Smýkal et al. 2018). Initially, phenotyping was the only available method for selecting plants based on experience since the fundamentals of genetics had not yet been established. However, the discovery of Mendel's heredity principles over a century ago contributed to the development of genetics, which is now the cornerstone of modern plant breeding (Stenseth et al. 2022). Various techniques, including visual observation, hand measurements, and invasive methods, have been employed to assess plant qualities such as structure and function. In the nineteenth century, pioneers in plant science, such as Pfeffer (1887), developed the first sensors and instruments to evaluate plant attributes in response to external stimuli. Hare (2011) compiled an overview of the historical techniques used to examine various plant features (Hare 2011).

1.2 Examining the Characteristics of Plants

The chance to create predictive models is offered by the quantitative fields of physics and chemistry, which have been instrumental in numerous breakthroughs throughout the last century and continue to significantly impact our daily existence (Pieruschka and Schurr 2019). These developments were the driving force behind many of the advancements that have occurred in the last century (e.g., (Nelson and Nelson 2002). In the field of biology, the advancement of sequencing technology has made it possible to conduct an analysis of the genome. The genome is what gives an organism the fundamental tools it needs to thrive and reproduce in the ever-changing environment in which it exists during its entire existence (Khew et al. 2022). To the understanding of biology has undergone a remarkable transformation over the past two decades (Jiao and Schneeberger 2017) The availability of sequencing technology and the ability to analyze genome data has played a significant role in this development.

The requirement for a comprehensive understanding of the mechanical interplay between a plant and its surrounding environment presents further challenges (Ball and Wietschel 2009). To assess the dynamic nature of adaptation to the surrounding environment, it may be imperative to utilize deep phenotyping methodologies that offer a highly precise analysis of specific features, such as the carbon allocation dynamics to different plant organs, with a high spatial and temporal resolution (Jahnke et al. 2009) or patterns of root and shoot development (Walter and Schurr 2005). Nearly all components and entire plant structures can generate phenotypes that capture the attention of scientists, as they provide valuable insights into the underlying mechanisms that influence plant performance. Furthermore, phenotypes offer practical applications in breeding, crop management, and the processing of harvested crop parts (Olsen and Wendel 2013). Phenotyping technologies and procedures are essential tools for analyzing the form and function of various plant parts, such as seeds, roots, root systems, above and below ground storage organs, leaves, complete canopies, fruits, and flowers (Li et al. 2020b). Accuracy, sensitivity, and throughput pose significant challenges in this regard. To address the primary bottleneck of a specific application, trade-offs are often inevitable (Li et al. 2020b; Reynolds et al. 2021).

1.2.1 Fundamental Plant Science and the Cultivation of Crops

There is a pressing need to gain a comprehensive understanding of basic plant biology and to expedite crop development (Begum et al. 2019). Genome editing tools have been utilized to generate novel phenotypic characteristics in crops, such as increased tomato fruit production, enhanced oils, and resistance to powdery mildew disease (Zhu et al. 2020). The analysis and delineation of plant-associated microbiomes have the potential to generate probiotics that enhance plant performance (Verstraete et al. 2022). The use of model organisms such as Arabidopsis and rice has facilitated a profound understanding of plant growth, immunity, and metabolic processes, which can be applied to benefit any crop species (Trivedi et al. 2020). Currently, the fields of basic and applied plant biology are experiencing some of the most fascinating advancements in history, and the significance of plant research has never been more paramount (Way and Van Emden 2000).

1.2.2 Physiological Outputs of Plants that Hold Significance in Agriculture

Plant physiological outputs that have a significant influence on agriculture, such as transitions between developmental phases or responses to stress, are tightly regulated by sophisticated regulatory networks; nevertheless, our power to intervene in these networks is presently quite restricted (Urquidi Camacho et al. 2020). The field of bioengineering offers exciting opportunities for equipping plants with synthetic signaling circuits that can interact with biological networks (Cheng and Lu 2012). This presents a challenging task, but also holds the potential for numerous applications in agriculture, medicine, and environmental science. By developing synthetic signaling circuits, it may be possible to engineer plants to respond to specific environmental cues, such as drought, disease, or pests (Tucker and Zilinskas 2006).

Additionally, synthetic signaling circuits could be designed to regulate plant growth and development, leading to improved crop yields. Moreover, plants equipped with synthetic signaling circuits could also serve as biosensors for monitoring environmental pollutants, toxic chemicals, and other harmful agents (Yang et al. 2022). This could have significant implications for environmental monitoring and protection. Synthetic circuits would allow us to take control of important natural processes such as flowering time, temperature, and drought responses; they would also allow us to switch newly engineered programs such as synthetic defense mechanisms or added-value metabolic pathways (Brooks and Alper 2021), which would allow us to avoid the harmful effects of constitutive activation In order to make progress in this direction, new sensors will need to be engineered (Habash et al. 2009).

1.3 Novel Implements

To safely utilize these new technologies in the field, it is important to develop sensors that can detect environmentally-friendly agrochemicals or optogenetic inputs (Leydon et al. 2020). These sensors will need to be based on protein or *RNA* receptors. To achieve the desired result, orthogonal genetic processors must transduce signals, which will then be deployed to genetic actuators (Pieruschka and Schurr 2019). These actuators will likely be programmable transcriptional regulators based on the *CRISPR/Cas9* architecture, and will connect to endogenous factors (Selma et al. 2019). The latest observations in the modification of microbial systems indicate that the most efficient path forward in the emerging field of green bioengineering is through the application of synthetic biology techniques (Farsad et al. 2016). This entails creating modular elements that can be interchanged and undergoing repeated cycles of design, construction, and testing using readily assessable biological systems (Xu et al. 2020). The synthetic biology approach allows for interchangeable modular elements that can be easily screened, making it a more effective solution (Andrianantoandro et al. 2006).

1.3.1 Plant Engineering

“Plant engineering” may help generate highly productive and environmentally robust crop cultivars for future food security, say plant experts (Tester and Langridge 2010). Conventional breeding based on line crossover and phenotypic selection is inefficient and mostly relied on experience (Watson and Preedy 2015). With DNA-sequencing, most crops and economic plants have reference genomes. Resequencing important agricultural germplasms reveals their genetic diversity (Li et al. 2020a). SNPs, haplotypes, gene presence/absence variations, and cryptic structural variants have been linked to phenotypes (Alonge et al. 2020). Together with plant functional genomics, these developments are unleashing a new age of plant engineering: breeding by design. The biggest problem is using “incomplete” information at many loci to efficiently improve several complicated features (Karaca and Ince 2019). Strong phenotypic selection for abiotic stress tolerances in segregating plant populations may induce genome-wide loss of heterozygosity or alleles. This technique contradicts Mendelian genetics and is poorly understood, yet it may reduce genome-based breeding cycles (Judelson 1997).

Major advances in fundamental biology, medicine, and biotechnology will result from the simple and precise manipulation of genomic DNA in cells and animals. Self-splicing introns, zinc-finger nucleases, TAL effector nucleases, and other genome-editing methods are discussed by Doudna and Charpentier (Voellmy and Linding 2017). These technologies depend on endogenous repair and recombination processes to accomplish the intended alterations. They go on to explain how scientists found that clustered regularly interspaced palindromic repeats (*CRISPR*s) and their associated (Cas) nucleases make up an adaptive immune system in bacteria (Yamato et al. 2019).

These studies record the evolution of the *CRISPR*-Cas system into the powerful but simple genome engineering tool that is reshaping the field of molecular biology Fig. 1.1. Since the discovery of the DNA double helix, improvements in biology have been made possible by the advent of technologies for producing and manipulating DNA (Xu and Qi 2019). However, methods for making targeted changes to cellular and organismal genomes remained difficult. Many of the first methods relied on oligonucleotides, tiny compounds, or self-splicing introns to recognise particular sequences of DNA. Recently, the concepts of DNA–protein recognition have been used to the development of site-directed zinc finger nucleases (ZFNs) and Transcription activator-like effector nucleases (TALENs), (Childs-Disney et al. 2022). While these designed nucleases have shown promise, they have not yet been widely used due to the challenges of protein design, manufacturing, and validation. Integrating new technologies from a variety of fields and reviving the overall throughput of gene discovery are crucial steps toward meeting the problem of global food security via crop breeding (Cho 2007).

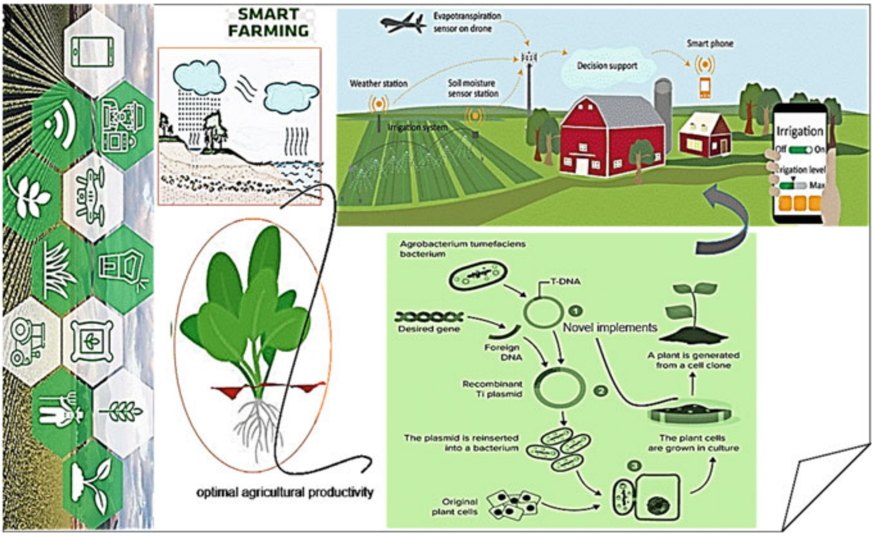

Fig. 1.1 One potential setup for a precision agriculture system integrated with a smartphone

This brief overview aims to outline recent developments in two important fields, multi-omics analysis and plant phenomics technology, with an eye on the promise of the life-course approach for tracking plant and agricultural health through time (Yang et al. 2021). Here, we detail the recent developments in analytical technologies for tracking plant health, such as multi-omics-based approaches to tracking physiological status (highlighting strategies to integrate heterogeneous datasets from multiple omics areas) and phenomics methods for tracking plant growth without causing any harm to the plant (highlighting emerging technologies in spectroscopy, implantable sensors and affordable devices) (Cao et al. 2022). Tools for plant phenotyping and the coupling of multi-omics analysis with life-course analysis are two significant topics that are set to increase our knowledge of plant-environment interactions in tandem. Plant science, sensor technology, nanotechnology, data science, and Internet of Things (IoT) technologies must all work together to assure sustainable agricultural output in order to fulfil the growing worldwide need for food (Großkinsky et al. 2018). To better use the potential of genetic variety within a crop species and plant phenotypic data to aid breeding efforts, high-throughput sequencing methods have opened up new paths, such as Genebank-scale genomics (Tardieu et al. 2017).

It is possible that long-term continuous monitoring of plant condition with high spatiotemporal precision made possible by nanotechnology-based implanted sensors would shed new light on plant-environment interactions in ways that imaging-based phenotyping alone cannot (Mochida et al. 2020).The widespread availability of SBCs has hastened the development of low-cost do-it-yourself sensors for plant phenotyping, and SBCs equipped for deep learning may allow the use of AI-based edge computing to diagnosis crop status based on continually recorded biomarkers. Multi-omics and phenome studies generate high-dimensional datasets, which have created difficulties in interpretation and necessitated the creation of appropriate dimensionality reduction methods (Lemaire et al. 2008).

Recently, for instance, Perlikowski et al. (2020) Through comprehensive time-series analytics, including analyses of root architecture, phytohormones, proteome, primary metabolome, and lipidome under progressive stress conditions, integrated features potentially related to a trait for drought-avoidance strategy were demonstrated in *Festuca arundinacea*. These analytical advancements will facilitate the digitization of data on plant-environment interactions and the monitoring of plant health, leading to advancements in crop breeding, precision agriculture, and smart farming on the path to global food sufficiency (Kashyap and Kumar 2021).

1.4 Atmospheric Carbon Dioxide

The primary driver of climate change, which endangers food security and quality for a growing global population, is the rapid increase in the quantity of CO_2 in the atmosphere. Plants require CO_2 for photosynthesis, which enters through stomatal holes in leaves (Myers et al. 2017). However, more than 90 percent of a plant's water is lost via evapotranspiration when these pores are open. For every single carbon atom fixed during photosynthesis, hundreds of water molecules are lost (Mooney et al. 1987). Additionally, a higher level of CO_2 in leaves during nighttime respiration signals stomatal closure. As a result, the rising levels of atmospheric CO_2 are causing various plants and crops worldwide to reduce stomatal apertures to varying and sub-optimal degrees (Brito et al. 2019).

The concentration of CO_2 in the atmosphere is now 50% more than before the industrial revolution, making it the primary cause of climate change that threatens food security. One theory suggests that plants could significantly reduce water loss without reducing carbon fixation by enhancing the stomatal CO_2 response (Brevik 2013). Experiments on the plant Arabidopsis thaliana have shown an increase in plant water usage efficiency of more than 40% by upregulating stomatal conductance. However, there is still limited understanding of the machinery involved in stomatal CO_2 signal transduction Fig. 1.2. Furthermore, molecular engineering and breeding in various crops will determine which plants will benefit most from modifying the stomatal CO_2 response to improve water usage efficiency in drought-prone agricultural areas (Engineer et al. 2016). Alternatively, decreasing the stomatal CO_2 response, coupled with other improvements, may also prove beneficial in increasing carbon intake and yields in habitats with abundant water (Polley 1997).

1.4.1 Advances in Organismal Biology—The Next Steps

Organismal biology has long been challenged with understanding how complex creatures operate as cohesive entities. It offers valuable insights into the overarching principles governing the organization of physiological systems and behavior, which is particularly useful for understanding multicellular species (Turnbull et al. 2018). The study of individual variability and its role in preserving evolutionary diversity is also a major area of focus. However, genetic diversity alone cannot explain the wide range of physiological and behavioral characteristics seen in complex species. To fully understand emergent features, genetic data must be considered alongside a renewed focus on the context and life-history dependence of individual phenotypes (Nevo 2001).

In recent decades, biology has shifted its emphasis from studying organisms to studying genes, resulting in the development of population and quantitative genetics, as well as reductionist experimental approaches based on DNA technologies (Van Dijk et al. 2014). While these paradigm shifts have enabled the investigation of the processes that govern phenotypic diversity, they have displaced the organism as biology's fundamental building block (Gawad et al. 2016). To better understand how the phenotypes of complex organisms evolve, it is crucial to study individual organisms within the context of their environments and life experiences (Moreno et al. 2011). This requires cross-disciplinary education, effective communication, and biological databases that integrate genotype and phenotype data (Table 1.1).

A greater focus on integrating various facets of whole-organism biology and the development of new technologies will allow for a deeper understanding of the biology

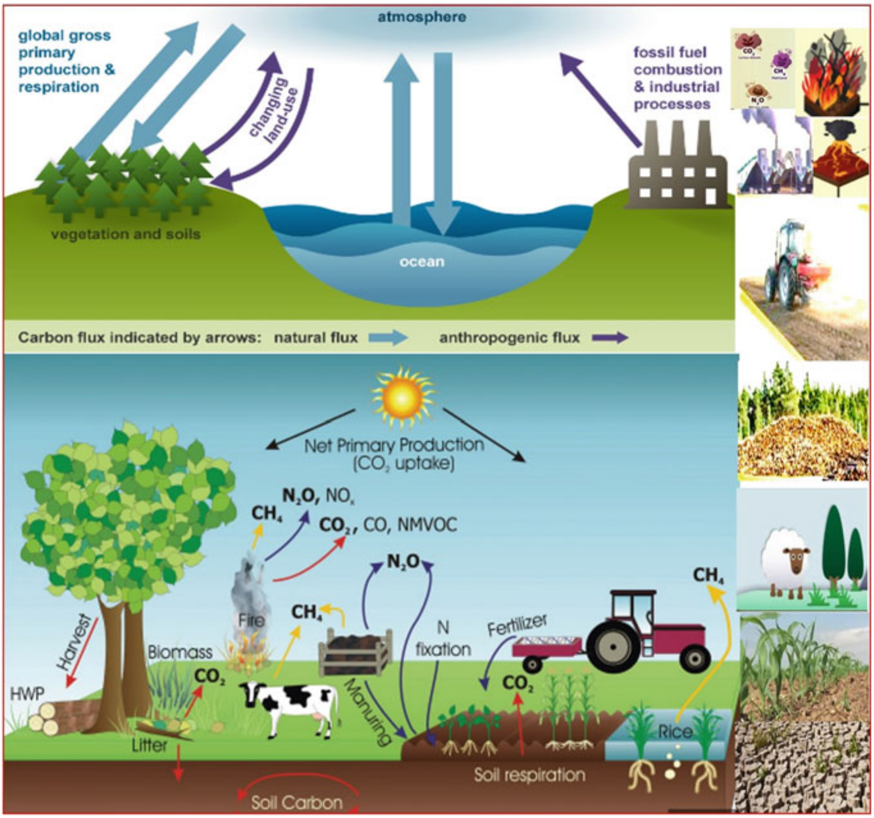

Fig. 1.2 The presence of carbon dioxide in the atmosphere can have an impact on climate change and agricultural practices

of complex creatures. Despite promising discoveries, further efforts are needed to reach a new level of advancement in this field (Kültz et al. 2013).

Precision agriculture, a farming approach that seeks to maximize crop yield while minimizing the use of expensive resources, could be facilitated by these sensors. It is important to ensure that such technologies are affordable and accessible to both large and small-scale farmers, as both are critical in achieving optimal agricultural productivity (Bramley 2009).

Table 1.1 A brief introduction to and the usage of in vivo plant sensors

Category	Method	Plant condition/ disease of interest	Target	References
Synthetic biology	Tomatoes were transformed using reporter genes fused to synthetic promoters for plant defense	General plant stress	Plant defense hormones,	Mazarei et al. (2008)
nIR fluorescent imaging and functionalized SWCNT	Single-walled carbon nanotubes (SWCNTs) were functionalized for the detection of H_2O2	General plant stress	H_2O_2	Wu et al. (2020)
Electronic	A sensor consisting of microneedles was inserted into the stem of a tomato	Plant response to light, humidity, and soil water content	Sap flow	Baek et al. (2018)
Electronic	An organic electrochemical transistor (OECT) sensor was inserted through the stem of a tomato	Drought	Ion concentration (Na^+, K^+, Mg^{2+}, Ca^{2+})	Janni et al. (2019)
Electronic	Organic electrochemical transistor (OECT) sensors were inserted into the xylem of aspen trees	Photosynthesis	Sucrose and glucose	Diacci et al. (2021)

1.5 Conclusion

To meet the growing demand for food security resulting from population growth and urbanization, it is essential to combine emerging technologies from various disciplines to accelerate gene discovery and crop breeding throughput. Since many agronomic traits only become apparent in the later stages of plant growth, decoding the interactions between plants and their environment requires identifying the genetic and environmental factors, timing, and pathways that affect complex end-point agronomic traits such as yield. The life-course approach to monitoring crop and plant health has the potential to increase yields by revealing connections between plants and their environments that were previously hidden. This chapter discusses recent advances in multi-omics analysis and methodologies for integrating diverse datasets from different omics fields, with a focus on their application to plant health monitoring. We also highlight new developments in phenomics, which will enable continuous, non-destructive monitoring of plant development in three dimensions, including at the root level, using implantable/injectable sensors, and at a low cost. Finally, we provide a comprehensive assessment of analytical tools and applications for monitoring plant growth, drawing on various fields such as plant science, data science, sensors, and Internet-of-Things technologies, with the ultimate goal of increasing plant production.

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Chapter 2
Plant-Environment Interactions: Proteomics, Metabolomics and Genetic Engineering Perspective

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Abstract Proteomics research has been used to shed light on the molecular processes underpinning plants' reactions to diverse environmental stimuli, offering useful insights into how plants interact with their environment. An introduction to proteomics and how it may be used to study how plants interact with their environment is given in this chapter. It examines the many proteomics study types, including metabolomic, differential, targeted, global, time-course, and phosphoproteomic investigations, as well as their advantages and disadvantages. Abiotic stress responses, interactions between plants and microbes, plant hormone signalling, and plant pathways of metabolism are some of the other major topics of plant-environment interaction study that are highlighted in this chapter. The chapter finishes with a consideration of possible future proteomics technologies, including developments in mass spectrometry-based proteomics, spatial proteomics, post-translational modification studies, and proteogenomics, all of which show potential for furthering the understanding of plant-environment interactions. Overall,

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_2

proteomics research provides useful insights into the intricate molecular mechanisms that regulate plant-environment interaction and may lead to improved crop management and sustainability.

Keywords Biotic and abiotic stress · Environment-plant interactions · Plant proteomics

2.1 Introduction

2.1.1 Implementation of Proteomics Studies to Understand Plant–Environment Interactions

2.1.1.1 Overview of Proteomics

Water, temperature, light, nutrients, and pathogens are just some of the environmental stressor that plant experience. These elements have a substantial impact on plant growth, development, and adaptation, making them critical for plant survival.

Researchers use cutting-edge approaches such as genomics, transcriptomics, metabolomics, phenotyping, and plant physiology to better understand plant-environment interactions. By integrating multiple methodologies, researchers can get extensive insights into how plants respond to their surroundings.

Proteomics studies are one such effective strategy for shedding insight on the molecular mechanisms underlying plant-environment interactions. Researchers can find possible targets for increasing plant growth and stress tolerance by examining changes in protein expression that occur in response to various environmental factors.

Using techniques like mass spectrometry and RNA sequencing, proteomics studies can measure the presence of proteins and examine plant transcriptomes under different environmental conditions. This information is critical for understanding the complex interaction between plants and their environment, as well as developing ways to help plants thrive in challenging environments.

2.1.2 Types of Proteomics Studies

Different types of proteomics studies have their strength and also limitations. The choice is depending on the research purpose. It can also be integrated with other approaches, such as metabolomics or transcriptomics, to provide a more comprehensive view of plant-environment interactions.

Several types of analysis, including, metabolomic (Bernardo et al. 2019; Skoneczny et al. 2018), differential proteomics (Sheng et al. 2022; Tan et al. 2019), targeted proteomics (Allwood et al. 2021; Kasthuri et al. 2022), global proteomics

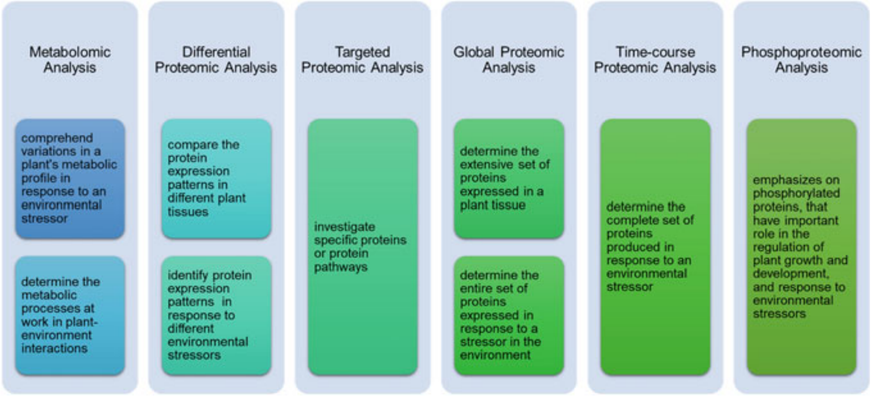

Fig. 2.1 Proteomics studies implemented to understand plant-environment interaction

(Fiorilli et al. 2018; Liu et al. 2022), time-course proteomics (Pinheiro 2021; Prinsi and Espen 2018), and phosphoproteomic (Hamzelou et al. 2021; Pongprayoon et al. 2022; Shao et al. 2021). Figure 2.1 summarizes the type of proteomics studies applied according to the research purpose.

2.2 Common and Widely Studied Areas in Plant–Environment Interaction

Proteomics studies can provide significant insights into the molecular mechanisms underlying plant-environment interactions, which can then be exploited to develop new approaches to improve plants' tolerance towards stress and food security. Stress conditions, for example, drought, salinity, heavy metal toxicity, and high-temperature, are some of the interactions that have been extensively researched using proteomics approaches. The main purpose of stress studies is to comprehend the molecular mechanisms and pathways that respond to stress (Al-Obaidi et al. 2017).

The plant-environment interaction study is broad and involves a variety of areas. Among highly researched plant responses to abiotic stress are (Canales et al. 2023; Zhu et al. 2023), plant–microbe interactions (Bastías et al. 2022; Ge et al. 2023; Gul et al. 2023; Xu et al. 2023; Al-Obaidi et al. 2017), plant hormone signalling (Khan et al. 2023; Xiao and Zhou 2023), and plant metabolic pathways (Parvathi et al. 2022; Silva et al. 2023).

Changes in water uptake and photosynthesis are also investigated in drought stress research. In salinity stress studies, it involves changes in ion transport and osmoprotectant. Whereas, in heavy metal toxicity studies, changes in metal uptake, and detoxification, are among the area of interest. High-temperature stress studies, on the other hand, look at changes in heat shock proteins and photosynthesis (dos Santos et al. 2022).

2.2.1 *Current Trends and Emerging Opportunities for Proteomics Studies*

The current trends in proteomics studies include the integration of other omics techniques. For example, transcriptomics has become increasingly popular. Transcriptome studies might elucidate how plants acclimate the abiotic stressors for survival (Wang et al. 2020b).

Plants can control their own physiological, and cellular processes. They can alter the transcriptome and stress tolerance pathways. Hence, metal ion toxicity, drought stress, severe temperatures, salt, and other abiotic stressors are adaptable (Hussain et al. 2020).

Research done on adaptation at the transcriptional level helps a better understanding of the ability of plant adaptation. It can be done by focusing on the expressed functional genes in plants under stress sources and intensity. Following that, researchers will look into the association between critical functional genes and resistance.

The second example is using targeted proteomics. It uses selected reaction monitoring (SRM), and parallel reaction monitoring (PRM). It allows the quantification of specific proteins with high accuracy and sensitivity.

There is a wide range of volatility and polarity in metabolites, diverse combinations of cells of plant cells and pathogens, and rapid metabolite turnover. Hence, defensive and protective chemicals, secondary messengers, phytohormones, and signalling compounds monitoring are required to unravel the plants' systematic biochemical responses to individuals or combined stressors (Allwood et al. 2021). This necessitates the use of both targeted and untargeted metabolomics methods.

The third trend example is high-throughput proteomics. It enables protein analyses faster and with greater accuracy. This method has been used to investigate tomatoes as a plant-pathogen system (Campos et al. 2021). High-throughput proteomics elevates the understanding of the molecular mechanisms, therefore leading to the improvement of tomatoes. The advent of next-generation sequencing (NGS) technology allows for the characterization of tomato transcriptome responses to various disease challenges. The RNA-seq data allows the understanding of the molecular mechanism in tomato infection resistance.

Technological advancement has opened a wider potential for understanding the interaction of the plant-environment. This provides the potential for significant advances to understand more complex interactions.

Recent developments in proteomics technology, including improved mass spectrometry techniques and new data analysis software tools, have enhanced the sensitivity and accuracy of proteome research. Integrating proteome data with other omics data, such as transcriptomic and metabolomic data, might help researchers gain more complete knowledge of plant-environment interactions. Transcriptomics, proteomics, and metabolomics, for example, can offer a comprehensive overview of the biological processes involved in plant-environment interactions (Manzoni et al. 2016).

2.2.2 The Most Commonly Used Methodologies

The appropriate selection of methodologies in proteomics studies depends on the research questions, the type of plant material, the type of environmental stressor, and the type of plant-environment interaction. Among the methods are, Two-Dimensional Polyacrylamide Gel Electrophoresis or 2D-PAGE, Sodium Dodecyl Sulfate Polyacrylamide Gel Electrophoresis or SDS-PAGE, Liquid Chromatography-Tandem Mass Spectrometry or LC-MS/MS, Isoelectric focusing (IEF) and gel-free techniques.

Gel-free techniques are increasingly being used in plan-environment interaction studies. For example, a study was done to understand how soybean plants induced by Sneb183 respond. An iTRAQ (isobaric tag for relative and absolute quantitation)-based proteomics was applied to determine the proteomic changes (Wang et al. 2017, 2020c).

Another gel-free method is a stable isotope labelling by amino acids in cell culture (SILAC). SILAC distinguishes variances in protein abundance among samples using non-radioactive isotopic labelling (Balotf et al. 2022; Das et al. 2021; Demir et al. 2018; Yan et al. 2022). Cells are grown in SILAC media that contain either “light” or “heavy” isotopes of specific amino acids, such as lysine and arginine. These isotopes are integrated into newly synthesized proteins, producing “light” and “heavy” variants of the same protein.

SILAC is used to detect the differentially expressed proteins in the shoot tips of two alfalfa cultivars with different flowering periods (Sun et al. 2019). A total of 62 proteins were found to be differentially expressed. These proteins were shown to be involved in a variety of biological activities, such as photosynthesis, stress response, and carbohydrate metabolism. They concluded that protein expression patterns differ among the two cultivars may cause their distinct florescence features.

2.2.3 Planning a Proteomics Study

Proteomics studies necessitate careful planning and execution, as well as a thorough understanding of proteomics procedures, and data analysis tools. It involves several general key steps as in Fig. 2.2.

The first step in conducting a proteome study is to acquire samples from plants and the environment. To reduce artifactual alterations and preserve protein integrity, careful sample collection, storage, and preparation are essential. The validity of the

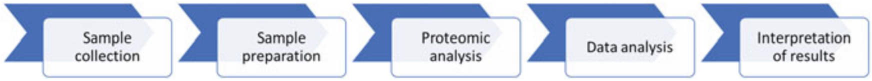

Fig. 2.2 General steps to implement in a proteomics study

data produced might be considerably influenced by the quality of the plant samples utilized in the proteomics analysis. Protein extraction is followed by quantification, normalization, and digestion of the proteins. The sample preparation methods used will be determined by the type of study, type of samples, and aim of the research.

The basic proteomics analysis includes identifying and quantifying proteins using proteomics techniques such as mass spectrometry, 2D gel electrophoresis or liquid chromatography. The advance or integration of proteomics methods used will be determined by the research objectives.

It is important to use advanced analytical tools and bioinformatics methodologies to reliably identify and quantify proteins and determine their significance in the plant-environment interaction when interpreting proteomics data. Data analysis may include, among other things, statistical analysis, network analysis, and pathway analysis.

The final step in implementing proteomics studies is the interpretation of the results to understand the plant-environment interactions. This includes the identification of key proteins involved in plant-environment interactions and the assessment of their roles and functions.

However, it is critical to establish quality control procedures and evaluate the proteomics results of the study to confirm that the information is accurate and reliable. This can include employing positive and negative controls, repeating experiments, and validating results with additional techniques.

2.2.4 Advantages of Proteomics Studies to Understanding Plant–Environment Interactions

All methodologies have advantages and limitations. Despite the limitation such as the complexity and variability of the proteome, proteomics studies are still dependable in advancing the knowledge of the molecular mechanisms of plant-environment interactions.

The main reason why proteomics studies are still been widely used is their sensitivity. Proteomics studies have a substantially lower detection threshold than other techniques, allowing for the detection of small changes in response to environmental factors. Hence, allowing researchers to obtain a better understanding of the molecular mechanisms driving plant-environment interactions.

The second reason is functional and dynamic information. This study provides functional information about the proteins associated with plant-environment interactions, such as their biological roles and the pathways they participate in. It can also detect changes in protein abundance in real-time, offering a dynamic picture of plants' biological responses to their surroundings.

The ability to integrate with other omics data is another reason why proteomics studies are preferred. Data from transcriptomics and metabolomics can be easily integrated which will provide a more comprehensive view of plants' molecular reactions to their surroundings.

2.2.5 Disadvantages of Proteomics Studies to Understanding Plant–Environment Interactions

Among the major issues in implementing proteomics studies are cost, technical limitations, limitation of protein function understanding, sample preparation, data analysis, and environmental variability. The new technologies are expected to innovate reliable and accurate proteomics results in the future.

Data interpretation can be challenging, as changes in protein abundance can result from factors such as protein stability and post-translational modification. Environmental factors may impact the results.

For example, temperature, nutrients, and water contribute to the environmental context, which will influence the data interpretation. As a result, it necessitates integration with other data as well as sophisticated computational tools and bioinformatics methodologies to reliably identify and measure proteins as well as analyze their significance in the plant-environment interaction (Ong et al. 2016).

If the data are not accurately evaluated and utilized, proteomics studies may have unforeseen consequences. For example, the discovery of important proteins involved in stress response or pathogen defence could be utilized to design crops that are more resistant to environmental stresses or diseases. If transgenic crops are exploited in ways that damage natural ecosystems or promote the creation of new pests, they may have unforeseen environmental consequences.

Furthermore, the use of proteomics data in plant breeding and genetic engineering may create ethical considerations, such as the possibility of intellectual property disputes over the use of proprietary information or gene and protein patenting. To guarantee the accuracy and dependability of the data generated, it is crucial to carefully weigh these concerns, use the best practices, and implement the necessary controls (Rimmer 2008).

2.2.6 Future Proteomics Technology on Plant–Environment Interaction Studies

Proteomics is a rapidly evolving field, with a promising future for technologies on plant-environment interactions. Proteomics technology is predicted to become more sensitive, selective, and high-throughput. New tools and methodologies will be created to enable researchers to analyze more proteins in less time and with greater precision.

One area of advancement is mass spectrometry-based proteomics, which is projected to grow more sensitive and specific. Advanced mass spectrometers should have higher resolution and accuracy, allowing for more precise protein identification and measurement. Furthermore, approaches like parallel reaction monitoring (PRM) and data-independent acquisition (DIA) are projected to enhance the number of proteins that may be studied in a single experiment (Elmore et al. 2021; Janssen et al. 2022).

Spatial proteomics can be used to locate protein locations inside plant tissues (Al-Obaidi et al. 2016). This method helps to uncover new targets for genetic alteration. It also provides insights into the cellular mechanisms of adaptability to environmental challenges (Naik et al. 2023).

The interactions between plants and their environment can be significantly influenced by the modification in post-translational, for example, phosphorylation, ubiquitination, and glycosylation. Future proteomics technologies could emphasize identifying and quantifying post-translational modifications in response to environmental stressors. Identifying PTM patterns under various stress circumstances and determining functional consequences may provide insights into how plants adapt to adversity (Muleya et al. 2022).

Another potential future development is in proteogenomics. It integrates proteomics and genomics data to improve plant genome identification. This method can be used to discover new genes and proteins involved in plant-environment interactions, as well as to provide some insight into the development of stress responses in plants (Al-Mohanna et al. 2019; Sinha et al. 2021). It is important to plan a statistical analysis using reliable bioinformatics tools that can help provide functional interpretation in the research.

2.2.7 Conclusion

In conclusion, a proteomics study is necessary in elucidating the intricate molecular processes underpinning plant- environment interactions. This line of inquiry offers a complete and highly sensitive perspective of the complex cellular responses of plants to their surroundings. Hence, this will afford researchers new insights into the dynamic interactions between plants and their environment.

Proteomics studies provide critical functional information on the proteins involved in plant- environment interactions and the pathways in which they operate, by examining modifications in protein abundance in response to environmental factors. This essential data allows researchers to obtain a better knowledge of the molecular mechanisms underlying these interactions, allowing for the creation of innovative approaches to addressing the issues provided by environmental stressors.

The exceptional capabilities of proteomics studies in establishing a highly sensitive, comprehensive, and functional perspective of the molecular underpinnings of plant- environment interactions make them a potent tool in advancing our knowledge of this field of study. Researchers can construct new strategies to enhance plant adaptability and boost yields, ultimately contributing to the sustainable management of our world's natural resources.

In summary, proteomics research is an essential pillar of our understanding of plant- environment interactions, providing invaluable data on the functional dynamics of these complex systems. Its sophisticated capabilities offer a potent tool for advancing our knowledge of this field and devising innovative approaches to enhance plant productivity, sustainability, and adaptability.

2.3 Decoding Plant–Environment Interactions Genetic Engineering that Affects Crop Management

2.3.1 Introduction

Plant–environment interactions refer to the interplay between a plant's environment's physical and biological conditions and its growth, development, and survival (Chand et al. 2021). This includes factors such as temperature, water availability, light, soil composition, and other environmental factors that affect the plant's ability to grow, produce yield, and respond to environmental changes (Smith and Chitwood 2020). These interactions are critical for crop management, as they significantly impact the yield, quality, and resilience of crops, and therefore, understanding and managing these interactions is crucial for optimising crop performance (Chand et al. 2021).

Plants and the environment are closely associated with a wide range of abiotic and biotic environmental agents interacting with plants. They might only develop and become reproductively mature under particular climatic conditions, depend on pollinators for reproduction, build advantageous mutualisms with microbial partners, or both (Baucom et al. 2020). In addition, plants must endure a variety of environmental difficulties, including herbivore damage, inadequate nutrition levels, and drought conditions (Mochida et al. 2020). Plants must deal with these issues in the present since they cannot move quickly over a geographic expanse like mammals can. Plants interact in a variety of nuanced and complex ways with environmental inputs and impacts, and doing so is essential for both survival and reproduction. Therefore, interactions between plants and their environment, as well as potential stressors, are part of any efforts to understand plant evolution, growth, reproduction, distribution, and community structure (Smith and Chitwood 2020). Numerous environmental pressures caused by humans, such as fire, pesticides, agriculture, and deforestation, can also affect plants. From germination to reproduction, a single plant takes into account various environmental factors while deciding whether to grow, root, branch, blossom, defend, or senesce (Temesgen et al. 2021). These environmental factors shape the plant phenotype genetically over geologic timescales through evolutionary mechanisms (Smith and Chitwood 2020). Plants have been changing to adapt to their rapidly shifting environments for millions of years. They do this by encouraging beneficial interactions with other organisms, taking advantage of novel physical conditions, and developing defence mechanisms against pathogens, pests, and adverse environmental conditions (Li and Lam 2022). The majority of the information needed for a plant to adapt to its environment is found in its DNA. However, to ensure successful interactions, creatures that interact with plants have also evolved unique sets of genetic components (Li and Lam 2022). The basic mechanisms of genetic controls of plant-environment interactions have been revealed by recent developments in genome biology.

2.3.2 Factors that Affect Plant–Environment Interactions

Complex interactions between plants and their surroundings are influenced by several factors. To create efficient crop management strategies that maximise plant growth, production, and quality, understanding the variables that influence plant-environment interactions is crucial. Several elements that may have an impact on how plants and the environment interact include:

1. Temperature: Extreme temperatures can be harmful to plants since temperature impacts how they grow and develop. Heat stress brought on by high temperatures can limit photosynthesis, plant growth, and yield. Cold stress brought on by low temperatures might result in decreased enzyme activity and sluggish development.
2. Water availability: Water is necessary for plant growth, and its availability has a big impact on how plants interact with their surroundings. Plant wilting, reduced plant growth, and yield loss can all be caused by drought stress. On the other side, too much moisture can produce waterlogging, which can impair plant growth by causing an oxygen shortage, root rot, and decay.
3. Light: Photosynthesis, the process through which plants make food, depends on light. Plant development, growth, and yield can all be impacted by the type, intensity, and duration of light. For instance, insufficient light can cause photosynthesis to be inhibited, growth to be sluggish, and yield loss.
4. Soil composition: Essential nutrients and support for plant growth are provided by soil. Plant development, growth, and yield can all be impacted by soil composition. For instance, nutrient lack or toxin exposure can result in stunted growth and decreased yield. Plants' ability to absorb water and nutrients can also be impacted by soil structure.
5. Atmospheric gases: Carbon dioxide (CO_2) is needed for photosynthesis and plant growth. CO_2 concentrations in the atmosphere can be increased to promote photosynthesis and plant development. However, other pollutants with high quantities, such as ozone, can injure plants and reduce output.

6. Biotic factors: Biotic factors, such as pests and diseases, can affect plant-environment interactions. Pests and diseases can reduce plant growth, development, and yield. Plant pathogens can also affect plant-environment interactions by altering soil composition and nutrient availability.

2.3.3 Importance of Plant–Environment Interactions in Crop Management

Plants that may be widely cultivated, grown in one location, and harvested for food or profit are considered to be a crop (Tanveer et al. 2017). Most plants are grown in hydroponic systems or through agriculture and the majority of crops are collected for human consumption or as animal feed (Tanveer et al. 2017). Crop plant study has long attempted to increase crop productivity, resistance to biotic and abiotic stress, and food nutritional levels to increase food security (Abdul Aziz et al. 2022). Breeders have created better types of crops thanks to conventional breeding techniques; hybrid grain crops, for instance, have significantly higher yields (Sciences 1984). Crop plant improvement has been carried through using increasingly sophisticated tools over time. For example, new types of plants adapted to certain conditions or requirements have been developed using contemporary plant breeding techniques, such as crops that are easier to harvest or are disease-resistant (Sciences 1984). Chemical technology has been used to improve these breeding techniques (Tian et al. 2021b). To protect crops from insect infestations, pesticides are increasingly often employed (Sciences 1984). Herbicides have mostly supplanted mechanical cultivation as a weed-control strategy, and the nutrients lost from the soil are regularly replaced with fertiliser (Esse et al. 2019). The current high level of agricultural output is a result of these breeding techniques, agricultural chemicals, and enhanced cropping techniques (Vincelli 2016). Despite these achievements, crops continue to be lost to pests, illnesses, and extreme weather (Esse et al. 2019). A growing portion of agriculture spending is now going toward fertiliser and other chemicals (Tanveer et al. 2017). Concern over how these chemicals affect the environment is also developing at the same time. Given the continually growing population in the Third World, agricultural issues are particularly severe (Datta 2013). The demand for food is anticipated to exceed the supply without advancements in agricultural technologies. These and other agricultural demands can be met using new technologies provided by genetic engineering (Abdul Aziz et al. 2022).

Additionally, population expansion has certain effects on the climate, environment, and amount of arable land. These factors will eventually impact crop output (Tian et al. 2021b). Although the primary issue of eating is no longer a problem in some places, hidden hunger—defined as the body's insufficient intake of critical nutrients and trace elements—remains a secondary issue (Zhu et al. 2017). By 2050, it is predicted that there will be 10 billion people on the planet (Cucina and Regni 2021). Deliberate thought should therefore be given to the difficulty of achieving the crop output and quality requirements of 10 billion people (Cucina and Regni 2021).

2.3.4 How Genetic Engineering Can Affects Crop Management

Molecular biologists are studying the ability to introduce foreign genes into plant cells, better known as genetic engineering (Bauer-Panskus et al. 2020). Genetic engineering is the process of altering recipient cells' genetic makeup by utilising contemporary biological tools to change their genomic DNA at the molecular level (Lanigan et al. 2020). The era of plant genetic engineering began in 1983 when herbicide-resistant tobacco was created using the first plant genetic engineering technique (Herrera-Estrella et al. 1983). The first batch of transgenic crops was successfully grown commercially in 1996 (Mackelprang and Lemaux 2020), and genetically modified crops started to appear on the market. Since that time, quickly advancing genetic engineering technologies have significantly improved crop yields and quality (Carl 2002). This technology combines genes in novel ways to produce superior crops, just as plant breeders have done with complete plants for decades (Kalendar et al. 2022). Instead of using entire plants, working with single genes has various benefits (Datta 2013). Specificity is one of the benefits (Datta 2013). Traditional breeding introduces genes that make crop improvement more difficult (Sedeek et al. 2019). Even though the breeder may be attempting to convey a trait regulated by a single gene, the whole genomes of two plants are joined during a sexual cross (Ye et al. 2022). It takes many years to develop an improved variety since it requires numerous backcrossing to get rid of unwanted genes (Ye et al. 2022). A gene can be removed from one plant and spliced into another using molecular techniques in a single experiment (Lanigan et al. 2020). More importantly, crop development can now take advantage of a new source of genetic variety made possible by genetic engineering. The promise of genetic engineering, on the other hand, is the ability to choose desirable features from any creature, such as the transmission of genes for nitrogen fixation from bacteria to plants as well as transferring herbicide resistance genes from weeds to crop plants (Kalendar et al. 2022).

Genetic engineering is a powerful tool in the field of agriculture and has the potential to revolutionise crop management practices (Lanigan et al. 2020). By modifying the genetic makeup of crops, scientists can enhance their resistance to environmental stressors, improve their yield and quality, and increase their overall performance (Datta 2013). Scientists can modify the genes that regulate the plant's ability to conserve water, which can enhance its tolerance to drought (Dong and Ronald 2019). This can lead to increased crop yields and reduced crop failure in areas affected by water scarcity. Another area of genetic engineering that affects crop management is the improvement of nutrient utilisation efficiency (Sedeek et al. 2019). By engineering crops to absorb nutrients more efficiently, farmers can reduce the number of fertiliser inputs, leading to cost savings and a more sustainable agriculture system (Sedeek et al. 2019).

2.3.5 Techniques Used in Genetic Engineering that Can Affect Crop Management

Introducing novel traits into crops, can be used to enhance agricultural management by enhancing crop performance, yield, and quality. Crop managers can increase the sustainability of agriculture and help to feed a growing population by carefully choosing and engineering crops that are well-adapted to local environmental circumstances. Several genetic engineering methods (Ye et al. 2022; Tian et al. 2021b; Sedeek et al. 2019; Datta 2013; Carl 2002; Dong and Ronald 2019) have been applied to enhance crop management, including:

1. Gene editing: A potent genetic engineering technology called gene editing can be used to precisely alter the DNA of crops to add desirable features or remove undesirable traits. CRISPR/Cas9 is one of the most popular methods for editing genes because it enables precise targeting of particular genes for modification. There are various ways that gene editing can be utilised to enhance crop management. For instance, disease resistance, drought tolerance, improve nutrient uptake, and increased yield.
2. Transgenic modification: Transgenic modification involves introducing a gene from one species into the genome of another species. This technique can be used to introduce desirable traits into crops, such as increased resistance to environmental stress or improved yield.
3. RNA interference: RNA interference is a technique that involves using small RNA molecules to silence specific genes. This technique can be used to silence genes that are responsible for negative traits in crops, such as susceptibility to pests and diseases. RNAi can be used to improve crop management in several ways, including pest control, disease resistance, improve nutrient uptake and abiotic stress tolerance.
4. Synthetic biology: Synthetic biology involves the design and construction of new biological systems. One of the advantages of synthetic biology is that it allows for the design and construction of biological systems with precise control over their functions, which can lead to more efficient and sustainable crop management practices. Synthetic biology can be used to improve crop management in several ways, including:

    - Biosensors: Synthetic biology can be used to develop biosensors that can detect and respond to environmental changes in crops. For example, biosensors can be used to monitor soil moisture levels, nutrient concentrations, and pest infestations, allowing farmers to make informed decisions about crop management.
    - Bioremediation: Synthetic biology can also be used to develop crops that can remediate contaminated soil and water. For example, scientists have engineered plants that can absorb and break down toxic pollutants, such as heavy metals and pesticides, thereby reducing the environmental pollution.

- Biofuel production: Synthetic biology can be used to develop crops that are optimised for biofuel production. For example, scientists have engineered plants that produce high levels of sugars, which can be converted into biofuels such as ethanol and butanol.
- Crop improvement: Synthetic biology can be used to develop new crop varieties that are optimised for specific environmental conditions, such as drought, heat, and salt stress. For example, scientists have engineered crops that produce higher yields under drought conditions by optimising water use efficiency.

2.3.6 Benefits of Improving Plant–Environment Interactions Through Genetic Engineering on Crop Management

When compared to traditional breeding, genetic engineering, which is the direct modification of an organism's genetic code using biotechnology, offers several benefits. First off, it permits the addition, deletion, modification, or fine-tuning of particular genes of interest with the least amount of undesirable modifications to the crop genome (Barrangou and Doudna 2016). As a result, compared to conventional breeding, crops displaying desired agronomic qualities can be produced in fewer generations (Christou 2013). Second, interspecies genetic material exchange is made possible through genetic engineering (Lorence and Verpoorte 2004). As a result, the genetic raw materials that can be used for this process are not limited to the genes present in the species (Barrangou and Doudna 2016). Third, genetic engineering allows for the insertion of novel genes into vegetatively propagated crops like potatoes and bananas (Dong and Ronald 2019). The majority of plant genetic engineering examples use more current genome-editing tools or traditional transgenic techniques (Dong and Ronald 2019). In traditional transgenic techniques, plant transformation is used to introduce genes encoding desirable agronomic features into the genome at random sites (Zhu et al. 2017). Using these techniques often produces plants with foreign DNA (Carl 2002). In contrast, genome editing enables modifications to the endogenous DNA of plants, such as DNA substitutions, insertions, and deletions at specific sites (Barrangou and Doudna 2016). The amount of foreign DNA in the final result will depend on the type of edits used (Datta 2013). Despite variations in regulatory practises in different parts of the world, traditional transgenic methods and genome editing remain effective tools for crop development.

2.3.7 Impact of Plant–Environment Interactions Genetic Engineering on Crop Management

Plant-environment interactions are essential to crop management to achieve optimal crop output (Sedeek et al. 2019). Crop management is incredibly important since plant-environment interactions are a major factor in influencing a crop's yield, quality, resilience, sustainability, and profitability (Chand et al. 2021). Crop managers can improve crop production and boost agricultural sustainability by carefully monitoring and regulating these interactions (Egea-Gilabert et al. 2021). Understanding and managing these interactions is essential for a variety of reasons (Abdul Aziz et al. 2022; Datta 2013; Egea-Gilabert et al. 2021; Mochida et al. 2020; Raman 2017; Sedeek et al. 2019; Tian et al. 2021b; Ye et al. 2022), including:

First: Yield and quality: Crop output can be impacted by environmental factors like temperature, water availability, and light. Loss of yield can be brought on by extreme temperatures, drought stress, or insufficient light. On the other hand, ideal environmental circumstances can result in a higher yield. Farmers and growers may improve environmental conditions to enhance production by understanding how plants and their environments interact. Interactions between plants and their surroundings can impact crop quality. For instance, the flavour and colour of fruits and vegetables can be influenced by temperature and light. Fruits and vegetables can ripen too quickly in high temperatures, resulting in diminished flavour and quality (Chin et al. 2019). Crop nutrition can also be impacted by the type and intensity of light. Crop quality can be improved by farmers and producers by better understanding these connections. Crop productivity and quality are significantly influenced by genetics in addition to environmental factors. Crops may be modified through the application of genetic engineering techniques to improve how they interact with their surroundings. Transgenic crops, for instance, can be developed to be more resilient to drought or extremely high temperatures. Crop management can be enhanced to maximise production and quality by comprehending and changing plant-environment interactions.

Second: Crop resilience: Crop resilience, or the capacity of crops to survive environmental challenges including drought, disease, and pests, can also be impacted by plant-environment interactions. More resilient crops are better able to withstand environmental shocks and are more likely to deliver crops of higher yield and higher quality. For instance, in regions with scarce water resources, crops that can withstand drought are better equipped to endure and yield a strong crop. By altering the DNA of the plant to better survive environmental challenges, genetic engineering techniques can be utilised to increase crop resilience. For instance, scientists have employed genetic engineering to create crops that are more tolerant of drought, high temperatures, and salinity as well as pests and diseases. Other crop management options, such as optimising irrigation systems, utilising cover crops to enhance soil health, and applying crop rotation strategies, can be employed in combination with genetic engineering to increase crop resilience. Future generations can benefit from improved crop resilience and a stable and secure food supply through comprehending plant-environment interactions.

Third: Sustainability: The sustainability of crop management strategies is significantly impacted by interactions between plants and their surroundings. Sustainable crop management entails growing crops in a way that meets the demands of both the present and future generations while protecting natural resources and promoting the long-term health of the environment. Various plant-environment interactions may affect sustainability. For instance, a significant element influencing agricultural growth and productivity is the availability of water. Crop management techniques that emphasized water conservation can increase sustainability in locations with limited water supplies. This can entail growing crops that are more suited to arid environments or switching to drip irrigation from overhead irrigation. Similar to how plant-environment interactions are influenced by other factors, soil health has an impact on sustainability. Crop yields can be lowered by soil deterioration brought on by erosive processes, nutrient depletion, and chemical pollution, which can also endanger agriculture's long-term viability. Crop rotation, cover crops, and decreased tillage are examples of sustainable crop management techniques that promote soil health. These techniques can increase the soil's ability to support healthy plant growth and increase the long-term viability of agriculture. By eliminating the need for artificial fertilisers and pesticides, which can have detrimental effects on the environment, genetic engineering can also help with sustainable crop management. Pesticide use, which can be detrimental to the environment and human health, can be decreased, for instance, by using crops that have been genetically modified to be resistant to pests and diseases. In addition, crops that are designed to utilise nutrients more effectively can lessen the need for synthetic fertilisers, which can hasten the deterioration of the soil and pollute the water. The development of sustainable crop management techniques that promote the long-term health of the environment and satisfy the demands of the present and future generations depends on an understanding of plant-environment interactions. By increasing crop production efficiency and lowering agriculture's environmental effects, genetic engineering technologies can support sustainable crop management.

Cost savings: The cost of crop management measures can also be significantly impacted by interactions between plants and their surroundings. Farmers may choose the crops to plant, the best time to plant them, and the best management techniques by understanding how environmental conditions affect crop development and output. For instance, crops that are well-suited to the local environment are more likely to grow and yield high quantities, lowering the need for expensive inputs like fertilisers and pesticides. Similarly to this, knowing how temperature and water availability affect crop development can help farmers manage temperature and optimise irrigation, saving money on water and energy. In addition, crop management costs may be reduced by using genetic engineering technology. The use of expensive pesticides and other chemical treatments can be decreased by using crops that have been genetically modified to be resistant to diseases and pests. The demand for synthetic fertilisers, which can be expensive, can be reduced by crops that are designed to use nutrients more effectively. For the creation of crop management strategies that are both affordable and sustainable, understanding plant-environment interactions is crucial. By increasing crop production efficiency and lowering the demand for costly inputs, genetic engineering technologies can assist in further lower the cost of crop management.

2.4 Metabolomic of Plant Physiology and Development: Insights on Interaction with the Environment

Metabolic profiling was first described by Baylor College of Pharmacy researchers in the early 1970s, which is where the name “metabolomics” originates (Rodrigues et al. 2021). A huge number of molecules with unknown structures are targeted by metabolomics (Calabrese et al. 2022). When a large number of unidentified natural compounds with various properties must be treated at once, analytical chemistry is severely challenged (Castelli et al. 2022). Another concept in 1999 was brought forth by Nicholson and his colleagues: “metabonomics,” defined as “the quantitative measurement of the dynamic multiparametric metabolic response of living systems to pathophysiological stimuli or genetic modification” (Xiao et al. 2020). Consequently, in 2001, “metabolomics” was a term defining the “comprehensive and quantitative analysis of all metabolites in a biological system” (Chen et al. 2019). A biological sample’s metabolome, which can be disclosed to assess genetic makeup and reactions to environmental stresses, in essence, the whole organism’s pool of metabolites, a tissue, and a cell at a given time. Identifying and measuring tiny molecular contents as well as comprehending the involvement of chemical reactivity in controlling cellular processes in many biological species are all part of the “OMICs” research fields. For the exploration of phenotyping, environment-gene interactions, drug detection and, biomarker identification, Razzaq and his colleagues’ investigations in metabolomics are essential (Razzaq et al. 2019).

The group with a proud variety of metabolites among many biological systems plants, with thousands of chemicals previously recognized and many more still undiscovered (Wang et al. 2019). It’s critical to enhance and develop existing analytical methods and procedures as well as to take platforms for metabolomics advantage to uncover various plant’s untapped metabolomes, explain intricate biological pathways, and revealed uncovered regulatory networks that control plant development and growth (Foito and Stewart 2018).

The study of metabolic changes in plants that take place in response to abiotic stressors is now made possible via metabolome analysis. A significant number of metabolites whose accumulation is impacted by exposure to stressful events have already been identified using this method. Nevertheless, despite the numerous advancements made in this field, much work is still needed to uncover novel metabolites and pathways that haven’t yet been connected to stress tolerance and response as well as to understand the intricate interaction and coordination between many metabolic processes (Bueno and Lopes 2020). Research on the levels of the genome, transcriptome, proteome, and metabolome is carried out to elucidate the mechanisms of plant reactions throughout their interactions with the environment (Chele et al. 2021).

It is important to keep in mind that metabolites play dual functions in stress tolerance and signalling molecules to best comprehend the function of stress-related metabolites in the response to abiotic stress (Mierziak et al. 2021). The majority of studies view the creation, accumulation, or depletion of metabolites as the plant cell’s last, downstream reaction to external stimuli (Lyu et al. 2021). However, it is important to determine if the reported metabolic network alterations are the result of changes in the expression of a gene or if the changes in transcriptome are in response to a particular metabolic disruption. Numerous other small molecules may be essential in signaling pathways besides hormones and other known mediators like glucose and sucrose; given the current state of knowledge, it is likely that only some of the metabolites with mediator roles in the control of transcription in response to stressors have been discovered till now.

To achieve this, it is crucial to take into account the dynamic temporal process of the reaction by integrating the "omics" data collected at various stages throughout the stressful exposure process. Researchers will probably be able to reassemble the entire chain by integrating the -omics techniques, of cellular activities resulting in rapid reactions and adaptation to the diverse abiotic stress factors, which have significantly improved our knowledge of how plants respond to stress circumstances globally. Therefor some important abiotic stress parameters should be discussed such as;

2.4.1 Pollution

Several stresses, such as xenobiotics or an increase in the natural concentration of substances like Sulphur, Phosphorus, and Nitrogen, can have an impact on organisms. By providing biological and phenotypic data in a high bandwidth approach, metabolomics has aided in a simple interpretation of how these disturbances affect creatures like humans, plants, and animals (Matich et al. 2019). The synthesis of secondary and primary metabolites, such as proteins, organic acids, polysaccharides, amino acids, and phenolic compounds, which are critical for Heavy Metals (HM) stress response, is also altered by relationships between plants and their microbiota. Guanine, adenine, lysine, adenosine, alanine, glycine, leucine, jasmonate, and arginine levels significantly increased in the numerous plant's roots in response to metal stress, while methionine and glutamic acid levels concurrently decreased (Pidatala et al. 2018).

Comprehensive, targeted metagenomics and metabolomics were employed to analyse the main various metabolome result patterns and the accompanying composition of the microbial flora in the root system of *Phragmites australis* under various Acid Mine Drainage (AMD) pollution. Overall, AMD pollution had a considerable impact on the root's major metabolomic profile, with the rhizosphere influenced by the effects more than the endosphere. Choline, histamine, niacinamide, guanosine, thymidine, methionine, and ophthalmic acid are more prevalent than usual, suggesting their relevance in the *P. australis* root-sediment interface under AMD pollution. In the rhizosphere, increasing dimethylglycine, carnitine, methionine, inosine, and Adenosine monophosphate (AMP), and their association with HM content (Cu, Cr, Fe, and Zn), Total Dissolved Solids (TDS) and pH under high and mid -AMD sites gives hints of how they might contribute to *P. australis* root fidelity, and growth related to HM stress detoxification and response. Based on root metabolomics and rhizosphere microecology investigations, new approaches to promoting *P. australis* growth and root reliability under AMD stress were also suggested. *P. australis* changes its root metabolite exudation profile under AMD stress, which is important for attracting beneficial rhizosphere microorganisms (e.g., *Mesorhizobium, Delftia*, *Rhizobium*, *Bacillus*, and *Bradyrhizobium*) for inducing of plant growth under HM and pH stress, but also influencing some microbial taxa (e.g., *Methylocystis, Bacillus*, *Arthrobacter*, *Massilia*, and *Delftia*) key to processes of HM detoxification (Kalu et al. 2021).

Phytoremediation plays a significant role in the detoxification of pollutants which is a successful procedure that exploited biochemical and molecular mechanisms of the interaction between plants and microorganisms (Rane et al. 2022). With the use of this technique, polluted wastewater can be treated biochemically and affordably (Chandanshive et al. 2020). The secretion of plants' secondary metabolites affected their rhizospheric microbiota by enhancing their growth within the rhizosphere (Jacoby and Kopriva 2018). Many secondary metabolites, such as plant's volatile compounds are compiled underground to attract.

There are reports of certain secondary metabolites, particularly volatile chemical compounds in plants, accumulating underground to draw in beneficial bacteria (Abbas et al. 2022). In the rhizosphere, plant roots exude a variety of secondary compounds that draw advantageous microorganisms and create a special ecosystem. For instance, in the plant-Arbuscular mycorrhizal association, the flavonoids produced by plant roots are crucial for enhancing spore formation, hyphal development, and root initiation (Tian et al. 2021a). Flavonoids are considered a chemoattractant to stimulate the growth of host-specific rhizobia (Shah and Smith 2020).

One of the prime candidates for Pb phytoremediation is Vetiver grass due to its high biomass and its hyper-accumulated Pb ability (Otunola et al. 2022). Vetiver showed a dramatic rise in the levels of the essential metabolites that responded to Pb, such as coenzymes, organic acids and amino acids (Pidatala et al. 2018).

2.4.2 Agricultural Processes

Uncontrollable and unplanned agricultural processes can cause more environmental problems. Pesticides are sprayed on the ground; however, not all of them reach their intended targets, and a sizeable portion of them remain as residues in the soil and are taken by plants. The use of pesticides is essential for increasing agricultural productivity (Schleiffer and Speiser 2022). Yet, their excessive use could have negative effects on human health, the safety of food, and crop yield (Zhang and Yang 2021).

The processes governing the specificity of pesticides and their interaction with transporters are summarized below (Parween et al. 2016).

I Pesticide reaction mediated by plant enzymes

1. Cytochrome P450 metabolism of pesticides
2. Hydrolase metabolism of pesticides

  3. Laccase metabolism of pesticides

II Pesticides being metabolized by enzymes in plants

  1. Conjugation by S–thiols
  2. Glycosyltransferases catalyze Pesticide metabolism
  3. Condensation in the metabolism of pesticides
  4. Acetylation in the metabolism of pesticide
  5. Methylation in the metabolism of pesticide

III Pesticides metabolism by ATP–binding cassette (ABC) transporters

Additional regulatory on the metabolism of pesticides such as Safeners, Brassinosteroids, DNA methylation and histone modification, Jasmonic acid, and Salicylic acid.

By definition, herbicides harm plants through abiotic stress. Herbicides are the main weed-control strategy used in modern agricultural production globally, helping to preserve crop yield and financial gain (Heap 2014). Herbicides can cause some phytotoxicity to crop plants and decrease Leaf Area Index (LAI), Shoot Dry Weight (SDW), and plant height, and modify plant metabolism by releasing ROS, even though these processes of innate selectivity aid in crop output. The majority of the changes brought on by herbicide treatment in plants are connected to ROS production and the resulting oxidative stress (Kaur 2019).

When compared to plants that were cultivated in the field under less-than-ideal conditions, proteome profiling can help in the identification of unexpected alterations that would otherwise go undetected. Benevenuto and his colleagues suggest that genetic alteration is the second primary source of quantitative variation in protein relative abundance and levels of phytohormones/related compounds, after environmental influences like the use of herbicides. They compare the proteome profile of herbicide-tolerant maize to its nearly isogenic non-Genetically Modified (GM) variation under herbicide stresses, taking into account phytohormone levels and associated chemicals. Many variations in compound levels (jasmonic acid, methyl ester of jasmonic acid and cinnamic acid) and relative protein abundance (11 proteins) under the same environmental settings between the GM plant and its non-GM near-isogenic variation, indicating that genetic alteration itself may also play a significant role in the emergence of pleiotropic effects. The findings of this study do not support the major equivalency between the tested GM maize (NK603) and its non-GM near-isogenic variety, taking into consideration the effects of variations in protein profiles and metabolite levels, including hormones and associated chemicals (Benevenuto et al. 2017).

Deforestation is the main cause of biodiversity loss, soil erosion, and climate change (Souza et al. 2023). The main factor contributing to worldwide deforestation, which reduces the amount of water transpired by plant leaves, is land use change brought on by agriculture (Freitas et al. 2021). It is assumed that ongoing deforestation will cause a further spread of understorey plants, and a decrease in species number, tree density and habitat complexity. A decline in microhabitats and aboveground biomass can lead to a decrease in faunal species and biomass which in turn would influence nutrient cycling and impair the nursery function of the area. Also, important ecosystem services, particularly coastal protection against storms and prevention of coastal erosion are most likely affected (Nordhaus et al. 2019). After the major genomic breakthroughs in forest tree research during the last decade, analyses of gene expression (transcriptomics), proteins (proteomics), and metabolites (metabolomics) have contributed to shedding new light on biological processes responsible for forest tree environmental responses and adaptation. Metabolomics studies represent the ultimate response of biological systems to genetic or environmental changes (Rodrigues et al. 2021).

2.4.3 Oxidative Stress

Reactive oxygen species (ROS) are produced naturally as a byproduct of normal oxygen metabolism (Chen and Raji 2020). The apoplast, mitochondria, chloroplasts, and peroxisomes are the main locations in the cell where ROS are produced. These Radicals may cause DNA damage, protein oxidation, and lipid peroxidation in cells, which could ultimately cause plant cell death. Under normal conditions, the generation and elimination of ROS are steadily balanced, but various biotic and abiotic stress factors, such as exposure to heavy metals, bright or dim light, pathogens, insects, and extreme temperatures, impair this equilibrium, leading to a high generation of ROS that should be mitigated by the antioxidant machinery in cells (Janků et al. 2019). Two groups constitute the antioxidant system of defence:

(i) Enzymatic antioxidants such as glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), as well as superoxide dismutase (SOD), catalase, ascorbate peroxidase (APX), general peroxidases (PRX), including guaiacol peroxidase (GPX);
(ii) Non-enzymatic antioxidants, including carotenoids, plastoquinone/ubiquinone, reduced glutathione (GSH), ascorbic acid (AA), and flavonoids. Together, these two sets of metabolites and enzymes control plant signalling, immunological response, and growth and development, with the primary goal of scavenging ROS (Garcia-Caparros et al. 2021).

The foremost consequences of ROS at a cellular and biochemical level are:

(a) Nucleic acids' conformation is disturbed by a variety of processes, such as the oxidation of deoxyribose, strand breakage, removal or modification of nucleotides, alteration of bases, and cross-linking of proteins with DNA (He et al. 2018).
(b) Peroxidation of the Lipid resulting in the breakage of longer chains, an increase in fluidity, and an increase in membrane permeability (Ozgur et al. 2018).
(c) Oxidation of the Proteins causes many changes, including peptide chain breakage, protein crosslinking, and change in electric charge (Domínguez et al. 2021).

When ROS damage is severe, the next possible outcome is programmed cell death (Mittler 2017). Because they are scavenged by a variety of antioxidative processes, ROS molecules are unable to harm cells under normal circumstances. Although ROS were previously thought of as unwanted by-products that caused the oxidation of various molecules and structures, this idea has partially evolved into the idea of ROS signalling (Waszczak et al. 2018), maintaining low ROS concentrations despite higher ROS generation. As a result, it appears that an increase in ROS concentration in various subcellular compartments is relatively temporary and simply reflects the effectiveness of scavenging mechanisms, rather than directly causing programmed cell death (PCD) (Conway and McCabe 2018).

However, in stressful circumstances such as the presence of heavy metals, high light intensity, dramatic temperature changes, UV-B radiation, air pollution, scarce water supplies, salt, and herbicides, the equilibrium between ROS scavenging and frequent generation may be interrupted (Cortese-Krott et al. 2017) and causes their scavenging through enzymatic and nonenzymatic compound-based plant antioxidative machinery (Sewelam et al. 2016).

Plants are the group with the most diversity of metabolites among the many biological systems, with thousands of chemicals previously recognized and many more still undiscovered. It's critical to develop and enhance existing analytical techniques and protocols as well as to take advantage of metabolomic platforms to uncover more of the plant's untapped metabolome, explain intricate biological pathways, and uncover hidden regulatory networks that control plant growth and development (Castro-Moretti et al. 2020). The study of metabolic changes in plants that take place in response to abiotic stressors is now made possible via metabolome analysis. A significant number of metabolites whose accumulation is impacted by exposure to stressful events have already been identified using this method. Nevertheless, despite the numerous advancements made in this field, much work is still needed to uncover novel metabolites and pathways that haven't yet been connected to stress response and tolerance as well as to understand the intricate coordination and interaction among the various metabolic pathways (Lephatsi et al. 2021). Research on the levels of the genome, transcriptome, proteome, and metabolome is carried out to elucidate the mechanisms of plant reactions throughout their interactions with the environment.

It is important to keep in mind that metabolites play dual functions in stress tolerance and signalling molecules to better comprehend the function of stress-associated metabolites in abiotic stress response (Heinemann and Hildebrandt 2021). The majority of studies view the creation, accumulation, or depletion of metabolites as the plant cell's last, downstream reaction to external stimuli (Lyu et al. 2021). However, it is important to determine whether the reported changes in metabolic networks are the result of changes in gene expression or if the transcriptome changes are in response to a particular metabolic disruption. Numerous other small molecules may be essential in signalling pathways in addition to hormones or other canonical mediators like sucrose and glucose; it appears likely that only a portion of the metabolites with a mediator function in the regulation of transcription in response to stresses have been identified till now.

To do this, it is crucial to take into account the temporal dynamics of the reaction by integrating the "omics" data collected at various stages throughout the stressful exposure process. Researchers will probably be able to reconstruct the entire chain of cellular events leading to quick responses and adaptation to the various abiotic stress stimuli thanks to the integration of the -omics approaches, which have significantly improved our understanding of global plant systems in response to stress conditions. Therefore some important abiotic stress parameters should be discussed such as temperature, drought, salinity, and oxidative stress.

2.4.4 Temperature

Environmental stress such as high temperature has a significant impact on plant growth, reproduction, and development. Thus, plants have developed complex mechanisms to recognize and adapt to stress. These include modifications to cellular signalling pathways, variations in the expression of genes, and the synthesis of heat shock proteins (Hasanuzzaman et al. 2013; Hatfield and Prueger 2015).

The effects of heat stress on plants can be studied using omics approaches which provide a comprehensive understanding of the metabolic and gene expression changes that occur in response to stress. According to Masouleh and Sassine (Masouleh and Sassine 2020), plants overproduce flavanoids, phenylpropanoids, and phenolic metabolites in response to heat stress. In another study, the regulation of heat stress factor B1 (HsfB1) was shown to play a role in enhancing plant thermotolerance in *Solanum lycopersicum* L. (tomato) leaves. Overexpression of HsfB1 has been associated with increased accumulation of phenylpropanoid and flavonoid metabolites, such as caffeoyl quinic acid isomers (Paupière et al. 2020). HsfB1 suppression, on the other hand, has been linked to higher levels of the polyamine putrescine, sucrose and glucose. This suggests that heat tolerance in tomato leaves is not dependent on the accumulation of a specific group of metabolites, but rather is a result of complex metabolic adjustments involving multiple pathways. Prolonged warming of *Arabidopsis thaliana* leaves, for example, has been shown to enhance glycolysis but inhibit the tricarboxylic acid (TCA) cycle, whereas heat shocks have been shown to negatively affect pyruvate conversion to acetyl coenzyme-A and the TCA cycle (Wang et al. 2020a). Furthermore, high-temperature stress has been shown to alter the levels of several metabolites in wheat (*Triticum aestivum* L.) including an increase in pipecolate and L-tryptophan and a decrease in anthranilate and drummondol after 10 days of anthesis. In addition, the biosynthesis of secondary metabolites and the aminoacyl-tRNA pathway were reported to be the most affected metabolic pathways in response to high-temperature stress (Thomason et al. 2018). Another study discovered a two-stage response to 3 days of heat stress in *Pinus radiata*, with significant changes in the metabolite profile of leaves, with the major metabolic pathways involved in the heat stress response being cytokinins (CKs), fatty acid metabolism, and flavonoid and terpenoid biosynthesis.

Another important abiotic stressor that affects plant growth and development is cold stress, which has been extensively studied in a variety of plant species, including tomato, wheat, maize, silver grass, and *A. thaliana* (Paupière et al. 2020, 2017; Qi et al. 2017; Sun et al. 2016; Le Gall et al. 2017). Among these, *A. thaliana* is one of the most widely studied species. Many metabolites in *Arabidopsis* are increased by cold stress, including proline, sugars, and intermediates of the tricarboxylic acid (TCA) cycle (Cook et al. 2004). According to a study by Korn et al. (Korn et al. 2010) and Wienkoop et al. (Wienkoop et al. 2008), raffinose has been identified as a potential biomarker of cold tolerance in *Arabidopsis*, though the specific response may differ between ecotypes. According to the findings, some metabolite changes in response to heat stress are similar to those in response to cold stress, such as increases in amino acids derived from pyruvate and the TCA cycle.

Overall, the effect of heat stress on plant metabolomics is complex and varies depending on the species, the severity and duration of the stress, and other environmental factors. Understanding these changes in metabolite levels, however, can aid in the development of strategies to improve plant tolerance to heat stress and mitigate the negative effects of climate change specifically on crop production.

2.4.5 Drought

Drought stress can negatively impact plant growth and metabolism by interfering with plant respiration, photosynthesis, and stomatal movement. As a result, plants have developed several drought-resistance strategies. Morphological and structural changes, the activation of drought-resistant genes, hormone synthesis, and increased osmotic regularity are all common responses. However, the specific reaction of a plant to drought stress can vary depending on the species, the intensity and duration of the stress, and the environmental circumstances. These mechanisms are intricate and interconnected. When there is a lack of water, plants undergo physical responses to reduce water loss and increase water uptake, which has an impact on metabolism. Cells may accumulate osmoregulatory such as sugars, ethanol, polyamines, and amino acids, including proline, to maintain cell turgor and prevent dehydration. These compounds aid in the maintenance of water balance within the cell by increasing solute concentration and decreasing water loss (Ghatak et al. 2018; Chaves et al. 2003).

When compared to other plant organs, leaves are more susceptible to drought stress. This is because leaves are the primary sites of photosynthesis and transpiration, both of which require a constant supply of water. Several metabolomic studies in leaf tissues about drought stress have been conducted, and proline accumulation in dehydrated leaves was frequently discovered (Witt et al. 2012; Urano et al. 2009; Skirycz et al. 2010). Proline accumulation is thought to be a protective mechanism that allows plants to tolerate and survive stress. It has been observed in a wide range of plant species, including crops like wheat, rice, and maize, as well as trees like poplar and eucalyptus (Urano et al. 2009; Krasensky and Jonak 2012; Lugan et al. 2010; Hochberg et al. 2013). The majority of plant metabolomics studies were conducted on aerial parts, primarily leaves. Dehydration has been extensively studied at the metabolomic level in *A. thaliana.* The aerial part of this species accumulates amino acids and polyamines in response to dehydration, and it has been suggested that abscisic acid (ABA) plays an important role in this process. ABA is a hormone that regulates many physiological processes in plants, including stress responses to dehydration. However, unlike amino acids and polyamines, ABA is not known to regulate raffinose accumulation. It is thought to be produced independently of this hormone, possibly by activating specific enzymes (Urano et al. 2009). The other studies found ringed amino acids such as proline, tryptophan, phenylalanine, and histidine were found to accumulate most in corn leaves under drought stress. These amino acids are known to play a role in the osmotic adjustment and stabilization of proteins and membranes under stress conditions (Witt et al. 2012; Kang et al. 2019).

Drought-tolerant (DT) and drought-susceptible (DS) cultivars are important because of their ability to adapt to and perform under varying water availability conditions. Their responses to drought stress have been compared using metabolic tools. In particular, it has been discovered that, following drought stress treatment, the DT variety of Chinese wheat or *Triticum aestivum* genotypes accumulates higher levels of thymine, the amino acids L-cysteinyl glycine and fructoselysine, and several phenolic compounds in their leaves compared to the DS variety. On the other hand, elevated proline levels were only seen in the DS variety, which is in line with earlier research that revealed proline to be a typical osmoprotectant that builds up in response to drought stress (Guo et al. 2020). In addition, drought promotes secondary metabolite production in the field, such as complex phenols, terpenes, and alkaloids. These metabolites are increased by osmotic stress, including osmoprotective substances like mannitol (Wu et al. 2017). According to published studies, drought-affected *Hypericum polyanthemum* (de Matos Nunes et al. 2014), *Oryza sativa* (Quan et al. 2016), *Salvia officinalis* (Bettaieb et al. 2011), and *Hordeum vulgare* (Piasecka et al. 2017) and resulted in higher levels of secondary metabolite production. By comparing the metabolic profiles of DT and DS plants, researchers can identify specific metabolites that are associated with drought tolerance and use this information to better understand the underlying mechanisms of the drought stress response. This can help to identify key metabolic pathways involved, as well as potential biomarkers that can be used to screen for drought-tolerant plant varieties, especially in breeding programs.

Plant biomass decreased as a result of the drought. Heat stress can also occur as a result of drought stress because the plant receives less cooling as transpiration decreases. Many physiological, biochemical, and metabolic changes that occurred in response to stress, on the other hand, can be reversed after recovery. Researchers were able to assess plant recovery from water stress by using metabolomics and proteomics. For instance, metabolomics has revealed that numerous compounds in plant leaves undergo concentration changes in reaction to drought stress during the flowering stage, but these changes can be undone by rehydrating the plant. Several primary organic acids, including isocitric, citric, and glyceric acid, increased sixty hours after rewatering, while others, including glucose, raffinose, glycine, N-carboxyglycine, and proline, decreased. This is according to a study from metabolomic analysis research (Correia et al. 2018; Michaletti et al. 2018). Additionally, proline dropped more in cultivars resistant to drought. This implies that after stress and refreshment, the behaviour of several metabolites can be seen in early grain-filling flag leaves. Moreover, plants that experience a complex metabolic reaction in response to drought and cold stresses, can also aid the plant in adjusting to the stress. Overall, different "omic" studies and genetic engineering approaches represent a promising avenue for developing drought-tolerant crops that can aid in mitigating the effects of drought on agricultural productivity.

2.4.6 Salinity

Salinity is a significant abiotic stressor for plants. High soil salinity can limit the ability of plants to absorb water and nutrients by disrupting the uptake and transport of nutrients, which can have negative effects on plant metabolism and growth (Hauser and Horie 2010). Salinity stress can also disrupt the delicate balance of ions in the plant, leading to further metabolic changes and stress responses. Metabolome comparisons of different plant species in response to salt stress have been carried out to understand how different plants cope with salt stress and to identify potential salt tolerance mechanisms. These include a study using targeted metabolomics to examine the phytohormone response to salt stress in *Arabidopsis* seedlings (Šimura et al. 2018), and maize (Richter et al. 2015). Moreover, an investigation of the response of salt-resistant transgenic tobacco plants to salt stress was also reported (Kissoudis et al. 2015). The study found that transgenic plants had higher levels of several metabolites known to play important roles in plant stress tolerance, such as proline, glutathione, and trehalose. The study also discovered that the pentose phosphate metabolic pathway (PPP) was activated, which could have contributed to the decrease in fructose levels. Fructose is a sugar that is known to be sensitive to oxidative stress and may be degraded under stressful conditions. The activation of the PPP may have diverted the flow of glucose-6-phosphate, a precursor to fructose, to the synthesis of nucleotides and the production of NADPH, which could have helped the plant cope with salt stress and maintain redox homeostasis.

A metabolome comparison study of one-month-old *Cucumis sativus* and *Solanum lycopersicum* plantlets subjected to salt stress was conducted. They discovered that the metabolomes of these two plants responded differently to salt stress. In particular, saponins, proline, and total antioxidant capacity were significantly lower in *S. lycopersicum* than in *C. sativus* (Abdel-Farid et al. 2020). In another study, the metabolomes of two closely related species, *Thellungiella halophila* (a halophyte) and *A. thaliana* (a non-halophyte) were analysed. In response to salt stress, both plants increased proline and sugar levels. *T. halophila* on the other hand, had higher concentrations of proline and sugars than *A. thaliana*, indicating that the halophyte is primed for salt tolerance (Gong et al. 2005). In a separate study, *Salicornia brachiata*, *S. maritima*, and *S. portulacastrum* accumulate various compounds in response to salinity. Proline concentrations increased in *S. portulacastrum* and *S. maritima*, while glycine, betaine, and polyols increased in *S. maritima* and *S. brachiata*. These compounds function as osmoprotectants, assisting plants in maintaining water balance and preventing salt stress damage. Interestingly, the three species showed differences in secondary metabolite accumulation in response to salt stress. In the presence of NaCl, *S. brachiata* accumulated more flavonoids and other phenolic compounds, whereas *S. portulacastrum* accumulated less of these compounds and more carotenoids.

Borrelli et al. (Borrelli et al. 2018) investigated the metabolomic changes in five genotypes of Durum wheat (*Triticum durum*) when exposed to different NaCl concentrations. At the highest salt concentration (200 mM), all genotypes showed an increase in proline concentration in shoots and a decrease in organic acids, including TCA-cycle intermediates, resembling flood-induced oxygen depletion. Furthermore, metabolites such as gamma-aminobutyric acid, threonine, leucine, glutamic acid, glycine, mannose, and fructose accumulated differently based on genotype. Therefore, the accumulation of these metabolites in some genotypes and not in others could indicate a potential difference in their ability to manage salt stress.

Metabolomics has made significant contributions to the identification and characterization of salt-tolerant (ST) plant varieties. However, it is important to note that ST biomarkers differ between cultivars, and each cultivar responds differently due to the distinct genetic makeup and physiological characteristics of salt stress. In the aerial parts of wild legume (*Lotus japonicus*) seedlings exposed to salinity, Sánchez et al. (Sanchez et al. 2008) discovered a decrease in asparagine and glutamine (primary products of nitrogen assimilation), and an increase in glucuronic and gulonic acids, as well as ononitol, threonine, and serine. The increase in both sugar acids could be a result of the plant's effort to detoxify reactive oxygen species (ROS), which are produced as a result of salt stress. In a later experiment by Sánchez-López et al. (2011), ononitol, threonine, and serine, along with other analytes, were found to increase in both salt-tolerant (ST) and salt-sensitive (SS) *Lotus* species under salt stress. Nonetheless, organic acid levels, including threonic acid and TCA-cycle intermediates such as malic acid, succinic acid, and citric acid, decreased in all genotypes. This decrease in organic acid levels could be due to the plant reducing its metabolic activity under low salt stress to conserve energy and resources. Despite the generalities, the SS genotypes showed a few significant changes, including an increase in gulonic acid and a decrease in aspartic acid, while the tolerant genotypes showed an increase in asparagine. In a study on barley, the salt-tolerant cultivar had higher levels of hexose phosphates and TCA-cycle intermediates than the salt-sensitive cultivar (Widodo et al. 2009). These metabolites are important in energy metabolism and stress response, and their accumulation in the salt-tolerant cultivar may contribute to its ability to cope with salt stress. In a separate study on barley (Wu et al. 2013), the ST genotype was found to accumulate more proline and carbohydrates, such as fructose and glucose, in its roots as compared to the SS genotype. These two molecules are known to play a role in osmotic adjustment and the maintenance of cellular integrity under salt stress, which may contribute to the higher salt tolerance of the ST genotype. A study on salt-stressed ST rice varieties discovered that serotonin and gentisic acid levels in the leaves increased significantly (Gupta and De 2017).

While, in other research on rice cells cultured in a 10 mM NaCl solution, it was found that exposure to salt stress resulted in changes in the metabolomic profile of the cells. The most notable changes observed were a rapid increase in glucose and a decrease in 2-amino butyric acid. Ornithine had the highest growth rate at the beginning of the study period, while proline had the highest growth rate at the end. When exposed to 100 mM NaCl, the levels of several metabolites increased significantly, including proline, cysteine, threonine, methionine, isoleucine, mannose, gentibiose, and fructose 6-P (Liu et al. 2013). As salt stress increased in in vitro *Spinacia oleracea* sprouts, the sodium ion content increased, but the potassium and calcium ion contents did not significantly decrease. In cultures with a higher salt concentration, however, the concentration of Na^+ and K^+ ions in tissues increased (Muchate et al. 2019). The increased levels of soluble sugars and antioxidant enzyme activity in these in vitro cultures also increased osmotic adjustment. The study found that 20-hydroxyecdysone was the metabolite that accumulated significantly more when the salt concentration was high. In conclusion, the complex regulatory networks involved in the stress response in plants can be better understood by integrating metabolomics data with other “omic” data. This may enable the discovery of crucial metabolites, pathways, and potential biomarkers for stress tolerance. In the end, this knowledge can be used to create innovative approaches to plant breeding and improvement, aiding in the effort to address the issue of global food security in facing environmental stresses like climate change.

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Chapter 3
How Environment-Plant Interactions Regulate Vascular Architecture and Ecological Adaptation

Roni Aloni

Abstract The chapter clarifies how environments alter the architecture, adaptation, and evolution of plant vascular tissues, and how they are regulated and controlled by hormonal signals. Plants are sessile organisms that cannot change their location; therefore, they must adapt to changes in their environments. The environment promotes morphological, physiological, and anatomical modifications in plants, which adapt them to changes in their environment. Understanding the mechanisms that regulate plant adaptation can help predict the expected effects of global warming on agricultural crops.

Keywords Auxin · Cambium sensitivity · Cytokinin · Earlywood vessel differentiation · Environmental adaptation · Latewood fibers · Pattern formation · Plant evolution · Ring-porous wood · Vascular architecture

3.1 Introduction

The water transporting tissue, the xylem of higher plants, is characterized by vessels and fibers. A vessel is a long tube build of vessel elements with endings walls in the lower and upper ends. Along a vessel, transport of water between vessel elements occurs through perforations (openings), while fibers are long cells that can develop thick lignified cell walls that support the plant body (Evert 2006). Vascular tissues along the plant axis are characterized by a general architectural pattern; vessels are narrow and in high density at the upper parts of stems and they gradually become wider, and their numbers decrease towards the roots (Zimmermann 1983). This vascular architecture is induced and controlled by the polar movement of the auxin hormone originating in young leaves (Aloni and Zimmermann 1983).

The impact of environments on vascular tissues is caused by their influence on plant development. Under optimal conditions, plants reach maximum dimensions,

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_3

with typical wide vessels at the base of their stem. On the other hand, growth-limiting factors that restrict development result in small plants with narrow vessels. The decrease in plant growth under stress conditions, do not allow the regular development of wide vessels. Therefore, plants that grow in limiting environments are usually small and their vessel system is characterized by many narrow vessels in high density (Aloni 1987), which are considered safe systems that allow plants to survive even under serious conditions (Tyree and Zimmermann 2002) when many of the vessels might become nonfunctional. The remaining water-conducting vessels will continue to support these small plants.

A unique adaptation pattern has occurred in temperate deciduous ring-porous trees that have undergone an extreme adaptation during their long evolution, resulting in the development of huge earlywood vessels in the beginning of the growth season. These very wide earlywood vessels, which are induced by extremely low auxin streams (Aloni 1991, 2022), often function during only one growth season, and then they are plugged by tyloses or gum (De Micco et al. 2016). The hormonal mechanisms that control the development of these architectural patterns will be explained below.

Cereals grown under extreme conditions may separate the vessel system of the shoot from the vessels of the root. This safe separation pattern protects the vessels of the root from possible damage originating in the shoots (Luxová 1986; Aloni and Griffith 1991) and are promoted by extreme environments.

3.2 The Hormonal Signals

The major signaling molecules that regulate plant development and vascular differentiation are the plant hormones, also called phytohormones (Went and Thimann 1937). The hormones can be produced in any living plant cell at extremely low concentrations. They may act locally or at a distance from the producing cells.

The four primary phytohormonal signals that control plant development and vascular differentiation are: auxin, cytokinin, gibberellin and ethylene (Fig. 3.1). These primary hormones are moving signals that are transported in specific pathways through the primary (originate from procambium) and secondary (originate from cambium) vascular tissues (Aloni 2010, 2015, 2021). *Auxin* is the young leaf signal (Jacobs 1952; Sachs 1981; Aloni et al. 2003), *gibberellin* is the mature leaf signal (Dayan et al. 2012), *cytokinin* is the root cup signal (Aloni et al. 2004, 2005), and *ethylene* is produced in differentiating xylem cells, and its production is enhanced under stress (Taiz et al. 2022). The continuous flow of these hormonal signals enables the plant to continuously respond to changing environmental cues.

Understanding the role of each hormonal signal is the key to understand how these moving signals design plant development, structure and vascular tissue architecture under different environmental conditions.

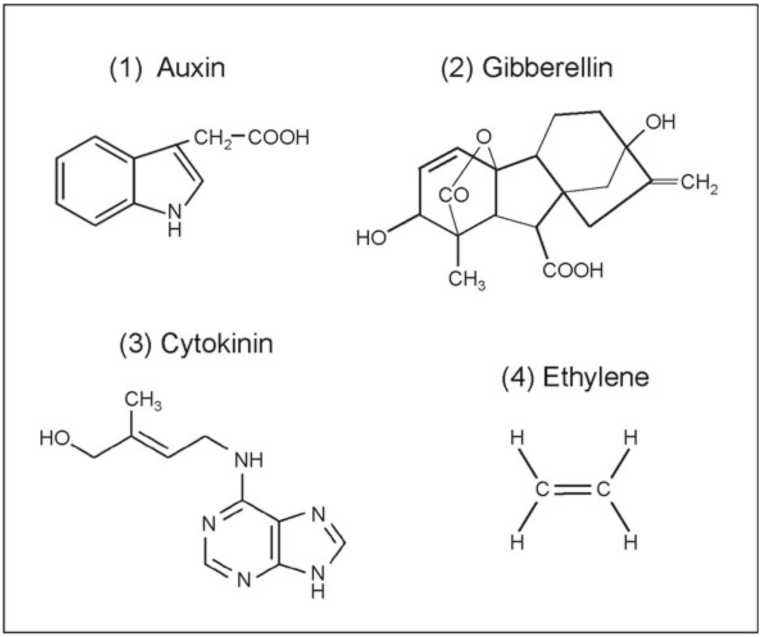

Fig. 3.1 Molecular structure of the four primary hormonal signals that control vascular differentiation in plants: auxin, gibberellin, cytokinin and ethylene

3.2.1 Auxin (IAA)

Developing buds and young growing leaves synthesize the auxin hormone, namely, indole-3-acetic acid (IAA), which is primarily produced at the leaf periphery (Aloni 2001; Aloni et al. 2003; Baylis et al. 2013; Yagi et al. 2021), moves polarly downward to the root tips and induces vessels along the auxin pathways (Jacobs 1952; Sachs 1981; Aloni 2010, 2021). Auxin is a limiting factor for vessel differentiation, in its absence there is no vessel development. The auxin, which moves polarly from the young leaves to the roots, induces vessels along the procambium, parenchyma cells and cambium. Auxin stimulates cambial reactivation in spring and induces earlywood vessel formation along the cambium (Aloni 1991, 2022). The polar movement of IAA is continuous, ensuring the formation of continuous vessels, which transport water from root to leaves. Wounding that interrupt the auxin flow, results in bypasses of new auxin streams that induce vessel regeneration around the injury (Jacobs 1952; Sachs 1981; Berleth et al. 2000; Scarpella and Helariutta 2010; Aloni 2021).

3.2.2 Cytokinins (CKs)

Root tips, specifically the root caps, are sources of cytokinins that promote cell division in the cambium and vessel differentiation (Aloni et al. 2005, 2006; Matsumoto-Kitano et al. 2008; Nieminen et al. 2008). Cytokinins from the root tips increase the sensitivity of the cambium to the auxin signal that originates in young leaves and buds (Baum et al. 1991; Aloni 1993, 1995; Aloni et al. 2003). Cytokinin prevents the rapid occurring IAA conjugation (Coenen and Lomax 1997), therefore, elevated CK concentration enables the transport of extremely low-IAA concentrations via the cambium, which may explain the increased sensitivity of the cambium to very low concentrations of the auxin hormone. Experimental evidence from transformed plants (Zhang et al. 1995; Eklöf et al. 1997) supports the idea that reduced auxin concentrations can elevate cytokinin concentration, which would enhance tissue sensitivity to the auxin signal (Trewavas 1983; Aloni 1991; Bradford and Trewavas 1994; Barbez et al. 2012). The experiments demonstrate that auxin or cytokinin modify the content of the other hormone by affecting its rate of synthesis. Reduced IAA concentration increases free CK level (Palni et al. 1988; Zhang et al. 1995; Eklöf et al. 1997). Elevated CK enhances cambium sensitivity to extremely low-concentration-IAA streams originating in swelling buds and creates the special physiological conditions that enable slow vessel widening until secondary wall deposition, resulting in the very wide earlywood vessels of ring-porous trees (Aloni 1991, 2001, 2021, 2022).

3.2.3 Gibberellins (GAs)

Mature leaves are major sources of gibberellin (Hess and Sachs 1972; Aloni 1979; Dayan et al. 2012). The GA is the specific hormonal signal that induces fiber differentiation (Aloni 1979; Dayan et al. 2012). The transport of GA along the plant axis is not polar; therefore, GA induces fibers both above and below the producing leaves (Dayan et al. 2012; Aloni 2021). GA, which promotes cambial activity, reduces vessel width, resulting in narrow vessels in the latewood (Aloni 2021, 2022). Ring-porous trees develop auxin-producing young leaves in the beginning of the growth season; but during most of the season they have mainly mature leaves (Aloni et al. 1997), therefore at the end of the growth season, the latewood of ring-porous trees is characterized by numerous hard lignified latewood fibers and narrow vessels, both are regulated by the GA originating in their mature leaves (Aloni 2022).

3.2.4 Ethylene (C_2H_4)

The gas ethylene is a plant hormone that is synthesized locally in various plant tissues in response to stress. Wounding, flooding, wind, bending, high auxin levels, elevated cytokinin concentrations and methyl jasmonate promote ethylene synthesis in plants. Elevated C_2H_4 concentrations inhibit stem elongation and may promote leaf and fruit abscission. Ethylene stimulates defense responses to injury or disease and reduces vessel width (Aloni et al. 1998; Hudgins and Franceschi 2004; Taiz et al. 2022).

Ethylene stimulates tracheary element (TE) differentiation in *Zinnia elegans* cell culture (Pesquet and Tuominen 2011). The C_2H_4 peaks at the time of TE maturation correlating with the activity of the ethylene biosynthetic 1-aminocyclopropane-1-carboxylic acid (ACC) oxidase, and the maturing *Zinnia* TEs accumulate ethylene (Pesquet and Tuominen 2011). Blocking ethylene signaling by using silver thiosulphate (STS) appears to block TE maturation (Bollhöner et al. 2012).

In wood, the ethylene produced in the differentiating tracheary elements diffuses in the centrifugal direction and this radial ethylene flow through the cambium initials induces the vascular ray (by promoting cell divisions in the cambial fusiform initials) and the enlargement of existing rays (Lev-Yadun and Aloni 1995; Aloni et al. 2000; Aloni 2013a).

Ethylene serves as a sensor of the plants environment that informs the plant about a flooding event. When the continuous regular centrifugal transport of ethylene outward to the plant environment is blocked by flooding water, the ethylene accumulates in the cortex, or the bark. This accumulation boosts local C_2H_4 concentrations, which may induce aerenchyma (a spongy tissue with large air spaces between the cells allowing gases circulation inside the plant) (Li et al. 2006), which enables aeration of flooded stems and roots. High ethylene concentrations also promote lateral and adventitious root formation (Aloni et al. 2006, 2013b) by local interruptions of the polar auxin flow, causing local sites of high-IAA concentrations above the interruption site, which induce lateral and adventitious root tips (Aloni 2021).

3.3 The Importance of Vessel Width for Water Conductance

The hydraulic performance of trees is crucially affected by vessel diameter (Tyree and Zimmermann 2002; Lucas et al. 2013; Hacke et al. 2017; Williams et al. 2019; Aloni 2021), which also affects wood adaptation (Aloni 1987, 2015) and xylem pathology (Aloni and Ullrich 2008; Ullrich et al. 2019). Therefore, it is important to understand and clarify the mechanisms that control the diameter of these vascular conduits in plants. Vessel diameter has a very important functional significance in water conduction. In ideal capillaries, conductivity is proportional to the fourth power of the radius, or diameter (Zimmermann 1983), which means that at a given pressure gradient the relative volumes of water flowing through capillaries, or vessels, of diameters: 1, 2, 3, 4, and 5, are: 1, 16, 81, 256, and 625, respectively. A cross section of a ring-porous wood demonstrates that most of the water would have flown through the very wide earlywood vessels, whereas the narrow latewood vessels would be inefficient in water conductance (Fig. 3.2B). Yet, the narrow latewood vessels are important for plant survival as they continue to function when the wide earlywood vessels stop functioning, following cavitation and embolism.

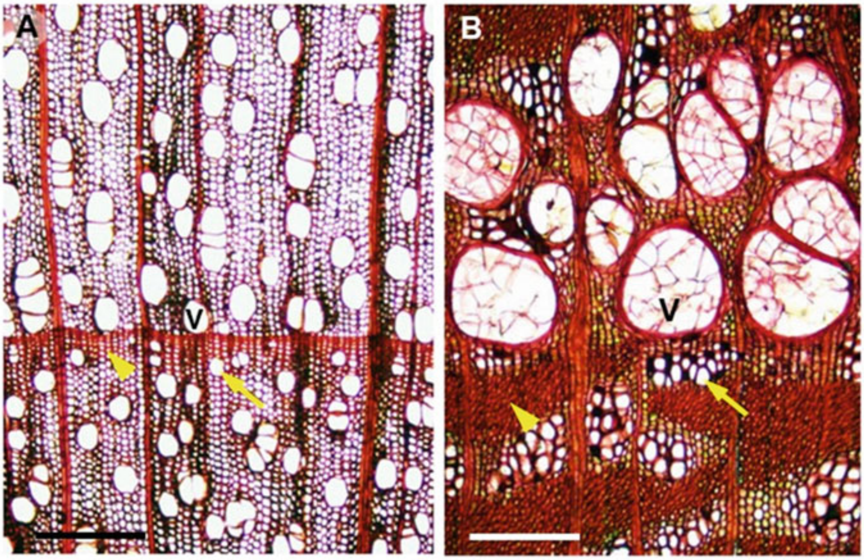

Fig. 3.2 Transverse sections showing the borderline and transition from the latewood (*down*) to earlywood (*up*), in the diffuse-porous wood of *Acer rubrum* (**A**), in comparison with the ring-porous wood of *Robinia pseudoacacia* (**B**), analyzed during winter dormancy, stained with safranin and fast green. In both photomicrographs, earlywood vessels are marked by V, latewood vessels are marked with an arrow, and latewood fibers with an arrowhead. Both micrographs are at the same orientation and magnification (scale bars = 500 μm). A, the diffuse-porous wood shows functional open vessels with relatively similar width forming a continuous pattern, which was induced by the continuous production of auxin-producing young leaves along the growth season. The vessels of the new year are wider than those of the previous season due to the increased distance of the new year's leaves from the transverse-section site. The earlywood fibers have thin secondary walls, while the latewood fibers (arrowhead) have somewhat thicker secondary cell walls associated with narrow vessels (arrow) due to leaf maturation, which promoted gibberellin production toward the end of the growth season. B, the very wide and vulnerable earlywood vessels (V) in the ring-porous wood are already plugged by tyloses at the end of the growth season. These wide vessels were induced by extremely low-auxin-concentration streams originating in dormant looking buds, in a slow widening process along a few weeks, which started before bud break. Whereas, the latewood of the previous year contains the narrow functioning latewood vessels (arrow) that would transport water for more than one growth season. The ring-porous latewood is also characterized by numerous latewood fibers with very thick lignified secondary cell walls. Both, the safe narrow latewood vessels and thick-wall fibers were induced by the gibberellin-producing mature leaves

3.4 Basic Patterns in Vascular Tissues

A well-documented phenomenon is the downward gradual and continuous increase in vessel size from leaves to roots. This widening in vessel diameter was found along leaves from the tip to the base of the leaf (Colbert and Evert 1982; Lechthaler et al. 2019). A continuous gradual increase in vessel diameter and vessel length was found from twigs to branches, downward along the stem and into the roots of *Acer rubrum* trees (Zimmermann and Potter 1982). This basic pattern was found in dicotyledons as well as monocotyledons (Tomlinson and Zimmermann 1967; Carlquist 1976; Zimmermann 1983). The vessels are narrow at the leaves, and their diameter increases gradually downward and continuously along the stem (Carlquist 1975; Zimmermann and Potter 1982; Aloni and Zimmermann 1983; Sorce et al. 2013; Lazzarin et al. 2016; Williams et al. 2019) and the root (Riedl 1937; Fahn 1964), with a decrease in vessel density from leaves to roots, which was reported for many species (Fegel 1941; Carlquist 1976; Aloni and Zimmermann 1983; Leitch 2001; Sorce et al. 2013; Zhao 2015).

Vessel diameter determine the hydraulic performance of plants. Conduit width gradually increases, while vessel density decreases downward, from the young leaves toward the roots. The *auxin gradient hypothesis* (originally named the *six-point hypothesis*; Aloni and Zimmermann 1983) proposes that the auxin hormone flowing polarly from young leaves to root tips acts as a morphogenetic signal which forms a long-distance decreasing IAA concentration gradient that controls conduit width and density along the plant axis. Along the gradient, the distance from the auxin-producing-young leaves to the differentiating cells results in decreasing amount of auxin with increasing distance from the leaves. Thus, the amount of auxin flowing through the differentiating cells decreases downwards. Consequently, the duration of the differentiation process increases along the decreasing auxin gradient from leaves to roots. The final size of a conduit is determined by the rate of cell differentiation. Since cell expansion ceases after the secondary wall is deposited, high-auxin concentrations near the young leaves induce rapid differentiation, allowing only limited time for cell widening, finally resulting in narrow vessels. Conversely, slow differentiation further down permits more cell expansion before secondary wall deposition and therefore results in wide vessels at the base of the stem. Vessel density is controlled by and positively correlates with the auxin concentration; consequently, vessel density decreases from leaves to roots. The *auxin gradient hypothesis* was confirmed experimentally (Aloni and Zimmermann 1983; Aloni 2021).

3.5 The Primary Mechanism of Vascular Adaptation in Plants

Vascular plants grow in different environments, ranging from deserts to rain forests and from arctic regions to the tropics. Comparative anatomical studies (e.g., Baas and Carlquist 1985; De Micco et al. 2008; Wheeler and Baas 2019) reveal similarities in structure of the vascular system in plants grown in extreme habitats *versus* ones grown in favorable environments. Desert (Carlquist and Hoekman 1985; Fahn et al. 1986), arctic, and alpine shrubs (Carlquist 1975) are characterized by very narrow vessels in high density. Such vascular systems are considered adaptive safety mechanisms against drought and freezing (Baas et al. 2004; Lucas et al. 2013). Conversely, forest trees and lianas, which characterize the tropics and rain forests, have very wide vessels arranged in low density at the base of their stems (Carlquist 1975; Zimmermann 1983; Ewers 1985; Tyree and Sperry 1989), which affords maximal efficiency of water conduction (Ellmore and Ewers 1985; Tyree and Ewers 1991; Tyree and Zimmermann 2002; Olson et al. 2021) and is considered to be an adaptation to mesic conditions. In order to explain the adaptation of plants' vascular systems to the environment, Aloni (1987) proposed the *vascular adaptation hypothesis* suggesting that the environment controls the plant's vascular system through its control of plant's development, height, and shape. Limiting conditions suppress plant growth and shorten the active growth period, which restrict plant development resulting in small plants. Conversely, favorable conditions allow growth activity throughout the year, enabling more growth and consequently well-developed plants with maximal height. The height of the plant and the degree of its branching determine gradients of auxin along the plant's axis. In small shrubs, which are typical to extreme stressful environmental conditions, the distances from the young leaves to the roots are very short and no substantial decreasing gradient of auxin can be formed. Therefore, the concentrations of auxin along these small plants are relatively high and result in rapid differentiation of numerous very narrow vessels in the greatest densities (as predicted by the *auxin gradient hypothesis*, Aloni and Zimmermann 1983). Conversely, in large trees and in long lianas, the very great distances from the young auxin-producing leaves to the roots enable a substantial decrease in auxin concentrations in their lower parts, leads to slow conduit differentiation that allows more cell expansion before secondary wall deposition, resulting in very wide vessels in low density at their base. The *vascular adaptation hypothesis* (Aloni 1987) was confirmed experimentally (Aloni 1988, 2021) and by analyzing the correlation between plant size and vessel diameter on a large scale of collected species from a wide range of growth conditions (Olson and Rosell 2013). Finally, the hypothesis explains why a tree that grows in very limited conditions will produce numerous narrow vessels in high density, in comparison with a well-grown tree of the same species that develops under favorable conditions and will produce wide vessels in low density at its base.

3.6 The Extreme Adaptation of Ring-Porous Trees

An extreme adaptation of plants to their environments occurred in the temperate deciduous ring-porous trees. Ring-porous trees have developed from diffuse-porous trees under selective pressures in limiting environments especially during the past 50 million years, when the global climates have been undergoing active changes (Evert and Eichhorn 2013; Wheeler and Baas 1991, 2019). The *limited-growth hypothesis* (Aloni 1991) suggests that during the evolution of temperate deciduous hardwood trees, limiting environments limited vegetative growth, reduced leaf production which decreased auxin synthesis; these changes, which promoted cytokinin production caused an increase in the sensitivity of the cambium to extremely low-concentrations streams of auxin originating in dormant looking buds, before bud break. These internal physiological conditions enable slow and continuous expansion of earlywood-vessel widening in the beginning of the growth season, resulting in very wide earlywood vessels (Fig. 3.2B).

An interesting example that such changes could occur, are the diffuse-porous trees (*Populus euphratica*) and ring-porous trees (*Quercus ithaburensis*) that can change their porosity under opposite environmental conditions. They produce a ring-porous pattern under stress conditions, while a diffuse-porous pattern under favorable environments (Liphschitz 1995).

In deciduous ring-porous tree the sensitive cambium undergoes extremely fast reactivation before bud break, which occurs almost simultaneously in the branches and along the trunk. This is why the bark of deciduous ring-porous trees may be peeled a few days before any bud swelling can be observed in spring. Conversely, deciduous diffuse-porous trees require several weeks for a ‘wave’ of cambial reactivation to extend from the twigs of a large tree downward to the base of its trunk (Priestley and Scott 1936).

The first wide earlywood vessels of ring-porous trees are initiated six to two weeks before the onset of leaf expansion, allowing the earlywood vessels to expand along a few weeks before bud opening and, therefore, become very wide. Conversely, in diffuse-porous species, the first earlywood vessels are initiated two to seven weeks after the onset of leaf expansion, and due to their rapid differentiation, they remain relatively narrow (Suzuki et al. 1996; Takahashi et al. 2013; Kudo et al. 2015, 2018; Pérez-de-Lis et al. 2016, 2018; Lavrič et al. 2017; Puchałka et al. 2017; Gričar et al. 2020).

Diffuse-porous species start the growth season a few weeks earlier than ring-porous trees and have a longer growth season which is characterized by continuous production of young leaves during a few months. Conversely, ring-porous trees have been adapted to a shorter growth season in limiting environments, to leaf out later than diffuse-porous trees, produce young leaves for only a short period of a few weeks and later they have mainly mature leaves (Lechowicz 1984; Aloni et al. 1997).

Experimentally, an extremely low-auxin concentration (0.003% NAA in lanolin) applied to disbudded shoots of the ring-porous tree *Melia azedarach*, induced slow differentiation resulting in wide earlywood vessels in the deciduous ring-porous trees, whereas a high-auxin concentration (1% NAA in lanolin) induced rapid differentiation resulting in narrow earlywood vessels like in a diffuse-porous wood (Aloni 1991).

Development of new young-IAA-producing leaves along the growth season of diffuse-porous trees stimulates continuous production of new vessels along the entire growth season with relatively thin-wall fibers. Whereas in ring-porous trees, the dominating mature leaves, which produce gibberellin, induce the development of numerous well-developed hard lignified fibers during most of the growth season with only a few narrow vessels, building a strong trunk wood, resistant to extreme stormy conditions (Aloni 2022).

The wide earlywood vessels are very efficient in water transport, but therefore vulnerable and tend to become occluded by tyloses (Fig. 3.2B) or gum towards the end of their relatively short season (De Micco et al. 2016). Conversely, diffuse-porous trees produce narrow earlywood vessels that operate in water transport along a few years.

3.7 The Unique Hydraulic Architecture of Cereals

Cereals adapted to the stress of drought or extremely cold weather produce a hydraulic "safety zone" in their root-shoot junctions, which protect the vessels of their roots from embolism originating in the shoot (Luxová 1986; Aloni and Griffith 1991). A study of root-shoot junctions in six cereal species (Aloni and Griffith 1991) revealed that there are two types of hydraulic architectures in cereal roots: (i) a completely unsafe system typical to mesic conditions, where the vessels of the roots are continuous with the vessels in the shoots (Fig. 3.3A, B), *versus* (ii) a very safe root vessels adapted to stress, as in winter rye, in which the vessels of the roots are separated from those of the shoots by non-perforated tracheary elements (Fig. 3.3C). The xylem anatomy of the seminal roots is generally correlated with the species root morphology. Rye, wheat, and barley, which develop four to six seminal roots, show a high degree of vascular segmentation resulting in the formation of safe root vessels, while maize, sorghum and oats, which typically develop a primary seminal root, contain unsafe root vessels that are continuous through the mesocotyl and through the first node (Aloni and Griffith 1991). These finding show that Zimmermann's (1983) *segmentation concept*, which was developed following studies on woody perennial trees, can be broadened to include herbaceous plants, demonstrating the formation of vessel endings and tracheary elements with no perforations (Fig. 3.3C) in junction between the shoot and the seminal roots of spring barley (Luxová 1986; Aloni and Griffith 1991), winter rye, and wheat (Aloni and Griffith 1991) that are adapted to stress. This primary xylem structure in cereals adapted to stress indicates that a "safety zone" can be developed at their root/shoot junctions, through which gaseous emboli and fungal spores cannot pass. These findings show that Zimmermann's (1983) concept of hydraulic segmentation of lateral organs from the main stem as well as the "safety

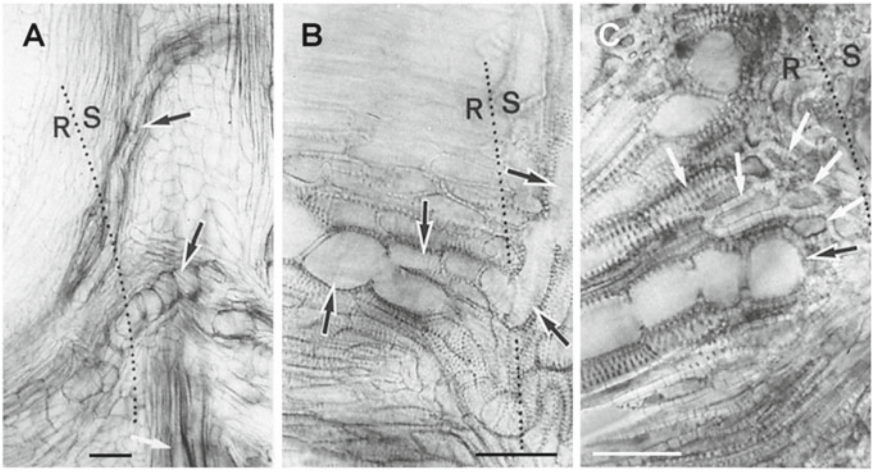

Fig. 3.3 Photomicrographs of the root-shoot junction, showing longitudinal thick sections of the root-shoot junction. The tissues are all unstained and cleared in lactic acid. All photographs are longitudinal views of the junction with the border between the root (R) and shoot (S) tissues delineated by a dotted line. **A** Adventitious root junction in corngrass, which is a corngrass mutation of maize (*Zea Mays*, Cg mutant) showing the entry of two metaxylem vessels from the root (black arrows) into the shoot. The lower part of a longitudinal vessel of the shoot is marked by a white arrow. **B** Close-up view of a continuous metaxylem vessel (arrows) in the junction between an adventitious root and the shoot in corngrass. **C** Root-shoot junction of a seminal root in winter rye (*Secale cereal* cv. Musketeer) showing the upper portion of the central metaxylem vessel, which ends at an imperforate wall (black arrow), and the small tracheary cells with no perforations, with simple pitting (white arrows), which connect the vessel of the root to vessels in the shoot. Bars = 50 μm (**C**), 100 μm (**A**, **B**). (From Aloni and Griffith 1991)

zone" of leaf/stem junction in palms (Zimmermann and Tomlinson 1965; Zimmermann and Sperry 1983; Zimmermann 1983; Sperry 1985) can also be applied to the hydraulic architecture and "safety zone" occurring between the root/stem junctions in cereals adapted to stress.

3.8 Conclusions

Although large trees can create local microenvironments beneath them, where smaller plants can grow without stress in varying levels of shade and humidity, plants are generally unprotected in their habitats and exposed to the abiotic environment. Plants grow well in favorable conditions, where there is no need for adaptation, while limiting environments promote plant adaptations for their survival.

The primary influence of the environment on plants is by controlling plant development and shape, which regulate internal gradients of the auxin signal throughout the plant, from the young-producing leaves to the roots. A restrictive environment results in short plants in which the signal levels remain high and no significant auxin gradient is created, therefore resulting in rapid vessel differentiation that remain narrow in high density and are therefore considered safe. Conversely, comfortable environments allow optimal development of large trees and long vines, promoting significant gradients of decreasing auxin concentrations along their axis, resulting in a slow and continuous process of vessel expansion in the lower parts of the stem, until the secondary wall is deposited, therefore resulting in wide well-transporting vessels in low density. This basic and universal mechanism enables the vascular adaptation of plants to their environment.

The early-evolutionary different type of unique adaptation of plants to their environment occurred in temperate deciduous ring-porous trees during the last 50 million years. The evolution of these special trees has occurred in different plant families under various stress conditions by increasing cambial sensitivity to extremely low-auxin streams, enabling them to slowly form the very wide earlywood vessels in the beginning of the growth season, as was explained above. These are very efficient but not safe earlywood vessels that usually operate during one season and then they are plugged. Nevertheless, the universal basic pattern of increasing vessel width and decreasing vessel density from leaves to roots occur normally also in ring-porous trees.

The evolution of cereals to stress occurred much later than that of the ring-porous trees. Under stress conditions some cereals can separate the primary vessels of their roots from the shoot, thus preventing air entrance to the primary root vessels when the shoot vessels are damaged.

It is possible that new adaptation mechanisms will be discovered, keeping us interested in studying plants under stress conditions.

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Chapter 4

Modern Approaches in Studying the Role of Plant-Microbial Interactions: A Way Towards the Development of Sustainable Agriculture

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Abstract In natural environments, plants are exposed to complex microbiota. Plants interact with the environment through various parts such as root, shoot, stem, or leaves with microbes present in the surrounding environment. These interactions could be beneficial, neutral and harmful in terms of plant growth, nutrition as well as adaptation to stress conditions. Therefore, it is important to utilize beneficial interactions for the development of sustainable agriculture. Healthy plant-microbes relationship can be

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_4

utilized to enhance soil fertility and plant productivity. Studying the plant-microbes interactions is a critical step to develop sustainable agriculture practices. In earlier days, studying these interactions was a cumbersome job, but with the advances in the science field, several techniques such as NGS sequencing, transcriptomics, metagenomics, proteomics, and metabolomics are developed to study these interactions. Keeping in mind, the importance of plant–microbe interactions for the development of sustainable agriculture, the present chapter broadly described various interactions between the two, tools to describe the interactions, and new challenges to study these interactions along with future perspectives.

Keywords Mutualism · Plant–microbe interactions · Sustainable agriculture · Transcriptomics

4.1 Introduction

Soil is very essential for the sustenance of biodiversity above and below ground. Just one teaspoon of soil holds more number of microorganisms than there are people on the planet (De Deyn and Kooistra 2021). In living soils, microbiota plays important roles in the activation of nutrient elements for plants such as N-fixation, P and Fe activation as well as interactions and communication between plants and microorganisms, for balancing the ecological equilibrium in soil. Microorganisms are responsible for around 90% of soil functions, including the organic matter decomposition, nitrogen fixation, increase in bioavailability of nutrients to plants and soil biota, storage of carbon in soil humus and release of CO_2 and CH_4 to surrounding soil and air (actively or passively) (Nannipieri et al. 2003).

Microorganisms need carbon and nutrients in organic matter for their growth as they dissolve organic materials. They discharge extra nutrients into the soil so that plants can utilize them. By fixing atmospheric nitrogen, diazotrophic bacteria and cyanobacteria such as *Azotobacter*, *Bacillus*, *Beijerinckia*, *Clostridium*, *Klebsiella*, *Nostoc*, *Anabaena*, *Anabaenopsis*, etc. contribute to improving the overall nitrogen status of soil (Bothe et al. 2010). Moreover, bacteria and fungi that solubilize phosphate improve the soil's availability of phosphorus to plants. Rhizosphere refers to the soil zone that extends up to 1 cm from the root surface, depending on the type of plants, soil moisture, and soil texture (Carminati et al. 2016). The rhizosphere

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is the metabolically active region around plant roots that is home to various microbial communities that are influenced by the root exudates produced by the plants. Exudates from plant roots continuously excrete ions, free oxygen, water, enzymes, mucilage, and a variety of primary and secondary compounds that include carbon (Uren 2000). These metabolites form an exclusive nutrient-rich zone around the plant root that becomes a key determinant for the unique composition of different microbial communities in the rhizosphere. This process is known as "Rhizo-deposition" which is the key process to recycling carbon from living plants into the soil subsystem of the larger ecosystem (Yadav et al. 2008). Rhizo-deposition raises the energy status of the nearby soil. This is correlated with the R/S ratio, that is, the microbial biomass in the rhizosphere (R) to bulk soil (S). Usually, this proportion is greater than one. Microorganisms strengthen the soil structure, defending it from erosive pressures. Microorganisms interact with the environment in different ways, some of them fix atmospheric nitrogen, increase the availability of phosphorus in the rhizosphere, pesticides oxidization, control plant pathogenic microbes population, soil structure improvement, managing the biological fertility of the soil, thereby contributing to plants' growth and development (Benedetto et al. 2017; Saeed et al. 2021).

Through intricate feedback processes, interactions between exudates, soil microbiota, and plant physiology have the potential to dynamically influence rhizospheric ecosystems and change plant phenotypes. Plants may be better able to endure environmental disturbances including unusual temperature change, drought, and salinity connected to climate thanks to the rhizosphere microbiota's ability to produce phytohormones, promote growth, and guard against infections (Lu et al. 2018). *Emticicia, Methylobacterium*, and *Filimonas* were among the rare (relative abundance 1%) rhizosphere microbes and rare bacteria can actively influence plant development and disease resistance as well as soil biochemical activities (Mendes et al. 2013). Approximately 10% up to 44% of the carbon fixed by plants during process of the photosynthesis is excreted in the rhizosphere by the plant roots (Prescott et al. 2022). Some primary metabolites secreted by the plants include organic acids, sugars, amino acids, lipids, proteins, enzymes, coumarins, flavonoids, aliphatics and aromatics compounds.

Important nutrient elements are immobilized and mineralized by soil microorganisms, which modulate the recycling of nutrients by acting as a source and sink in ecosystems (Jacoby et al. 2017). Decay and the cycling of water and nutrients to crops and plants are essential activities that depend on microorganisms. As they contribute to the breakdown of organic matter, microbes release vital nutrients and carbon dioxide into the soil, fix nitrogen, and assist in the mineralization process, which helps turn nutrients into forms that plants can use (Fig. 4.1).

The majority of this soil deterioration is caused by intensive farming, which is dependent on chemical inputs, and more intense farming won't help this situation at all. For plants and other organisms, healthy soils react as umbrellas, absorbing up and maintaining water while modulating the pace at which excess water drains through and away. Microorganism-rich soils aid in the breakdown of dangerous substances, lowering contamination levels and thereby lowering pollution (Verma 2021).

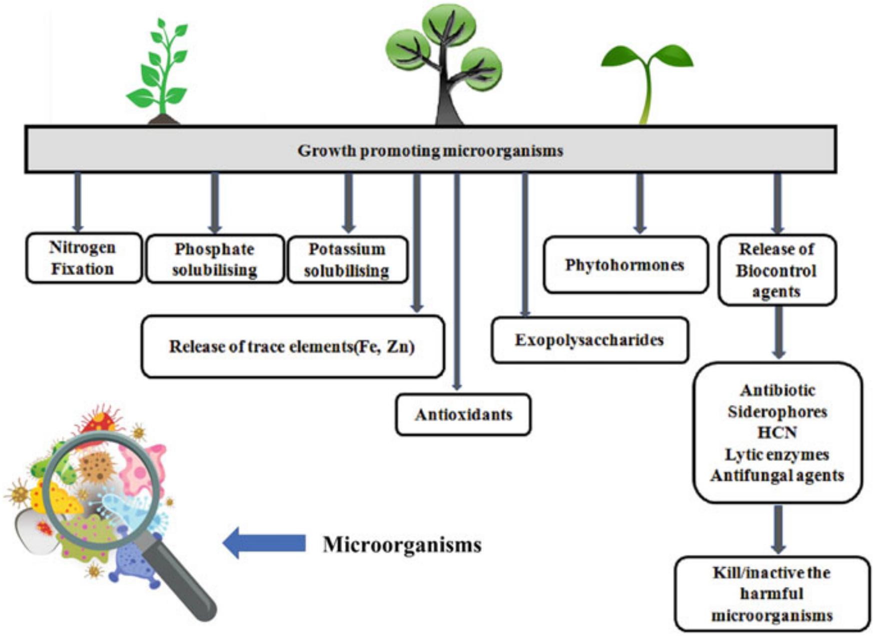

Fig. 4.1 Interaction among the soil, plants and microorganism. Plant and microorganism obtain their nutrients from soil and changes the soil properties

Interactions between plant–microbial are crucial for plant growth, development, fitness and productivity. Based on the definite habitat, plants' microbial communities are classified as the rhizo-, phyllo-, and endospheric regions (Gupta et al. 2021). Similarly, symbiotic and antagonistic interactions between plants and microbes exist, and understanding these interactions is crucial for advancing agricultural practice and crop yield (Agrahari et al. 2020).

4.2 Types of Plant-Microbial Interactions

Plant-microbial interactions are crucial in shaping different ecosystems' dynamics and functioning. These interactions involve many microorganisms, including microorganisms, fungi, archaea, and viruses. The symbiotic relationships between flora and microbes are numerous, starting from mutualistic to pathogenic associations (Lyu et al. 2021). Understanding the different types of plant-microbial interactions is important to study the complexities of atmosphere tactics and promote sustainable agriculture (Busby et al. 2017). In this section, four primary kinds of plant-microbial interactions: mutualism, commensalism, parasitism, and pathogenesis are discussed (Table 4.1).

Table 4.1 Types of plant-microbial interactions 2012 (Adapted from Mus et al. 2016; Skiada et al. 2020; Shtark et al.)

S. No	Interaction type	Example
1	Mutualism	(a) Rhizobium-legume symbiosis (b) Mycorrhizal associations (c) Endophytic partnerships
2	Commensalism	(a) Rhizobium-legume symbiosis (b) Mycorrhizal associations (c) Endophytic partnerships
3	Parasitism	(a) Rusts (b) Smuts (c) Powdery mildews
4	Pathogenesis	(a) Bacterial leaf blight in rice (b) Fusarium wilt in tomatoes (c) Tobacco mosaic virus in tobacco

4.2.1 Mutualism

Mutualistic plant-microbial interactions are characterized by mutual interactions among every companion. These interactions can be categorized into different types, together with rhizobium-legume symbiosis, mycorrhizal establishments, and endophytic partnerships. Rhizobium-legume symbiosis includes nitrogen-fixing microorganisms (rhizobia) that live in root nodules of leguminous plants (Hamza and Alebejo 2017). The rhizobia convert atmospheric nitrogen right into a form that vegetation can employ, while flora offers the microorganism with carbohydrates (Datta et al. 2015). Mycorrhizal entities involve the collectively beneficial relationship between flora and high-quality fungi. The fungi affect nutrient uptake by using extending their hyphae into the soil, at the identical time as vegetation offers carbon belongings to the fungi (Mohammadi et al. 2011). Endophytic partnerships involve microbes that inhabit the internal tissues of flowers without inflicting harm. These endophytes can confer numerous interactions with the host, which encompass greater high-quality nutrient acquisition, pressure tolerance, and protection in competition with pathogens (Toby Kiers et al. 2010).

The mutualistic interactions between plants and microorganisms are ruled via a complex interaction of genetic, biochemical, and physiological methods (Zeilinger et al. 2016). Plant reputation and signaling mechanisms permit plant life to understand and respond to the presence of useful microorganisms. In flip, microorganisms release unique signals and metabolites that have an impact on plant increase, improvement, and strain responses (Ortíz-Castro et al. 2009). These interactions are tightly regulated and frequently exhibit specificity, in which positive plant species associate with precise microbial companions. Understanding the mechanisms underlying mutualistic plant-microbial interactions is of great importance in agriculture, horticulture, and ecosystem functioning (Herrera Paredes and Lebeis 2016). Harnessing these associations can lead to the development of sustainable agricultural practices, biofertilizers, and biocontrol strategies (Fig. 4.2).

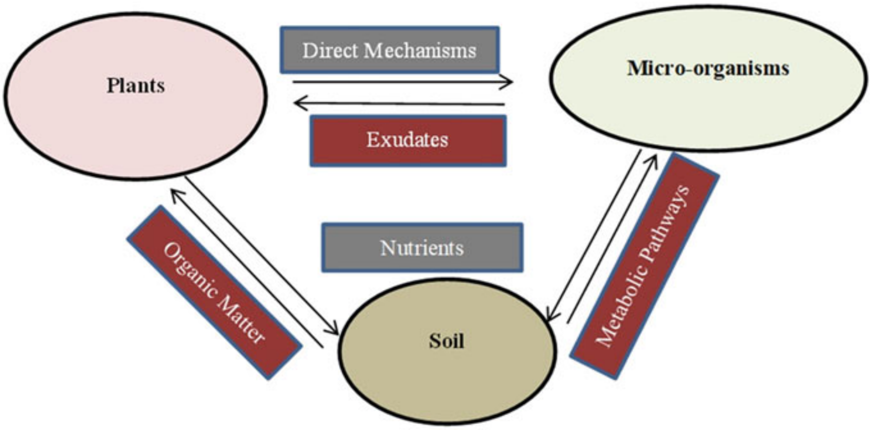

Fig. 4.2 Major challenges to studying the soil microbe interaction and its relation to plants

4.2.2 *Commensalism*

Commensal plant-microbial interactions arise whilst one partner advantages, while the opposite stays are unaffected. In those interactions, microbes can colonize the plant's surfaces or occupy ecological niches without causing any harm or offering big blessings. For example, epiphytic bacteria that live on the leaf surfaces of plant life might also make use of vitamins from the surroundings without inflicting any unfavorable results on the host (Compant et al. 2021). Some bacteria can also shape biofilms on plant surfaces, which may have implications for nutrient cycling and resistance to environmental stresses.

The mechanisms underlying commensal plant-microbial interactions are not fully understood (Igiehon and Babalola 2018). Those associations are likely an outcome of the microorganism's capacity to colonize plant surfaces or utilize plant-derived resources (Berlec 2012). The plant's surface structures, chemical composition, and exudates may additionally offer positive surroundings or nutrient sources for the commensal microorganisms. However, the lack of a reciprocal advantage to the plants suggests that the interactions may not involve precise signaling or physiological mechanisms that decorate plant boom, improvement, or strain tolerance.

4.2.3 *Parasitism*

Parasitic plant-microbial interactions involve microbes that derive nutrition from the host plant (Igiehon and Babalola 2018). These interactions can result in damage or sickness signs in the plant. Examples of parasitic interactions consist of pathogens that purpose sicknesses like rusts, smuts, and powdery mildews. Pathogens may also infect diverse plant components, consisting of leaves, stems, roots, or ends leading to reduced plant increase, yield losses, or even plant demise (Jerushalmi et al. 2020). The mechanisms hired via pathogens to invade and colonize host vegetation can range widely, inclusive of the secretion of pollutants, manipulation of plant protection responses, and nutrient acquisition from the host.

Understanding the dynamics of parasitic plant-microbial interactions is crucial for the development of effective management strategies to mitigate the damage caused by plant pathogens. Integrated pest management approaches, including the use of resistant plant varieties, cultural practices, biological control agents, and chemical treatments, are employed to minimize the impact of parasitic microorganisms on crop production and plant health (Stoddard et al. 2010).

4.2.4 Pathogenesis

Pathogenesis refers to the capacity of microbes to cause diseases in plants. These interactions are usually damaging to the host plant and can lead to severe economic losses in agricultural systems. Bacterial, fungal, viral, and nematode pathogens are examples of microorganisms that can reason plant sicknesses (Baker et al. 1997). They can disrupt ordinary plant physiology, induce necrosis, modify metabolic pathways, and impair nutrient uptake. Plant pathogens frequently appoint sophisticated strategies to evade or suppress plant defense mechanisms, permitting hit contamination and colonization.

Some pathogens are capable of colonizing plant tissues and disrupting normal cellular processes. They often secrete virulence factors, including enzymes, toxins, and effectors, that contribute to the pathogenicity of the bacteria (Flores-Díaz et al. 2016). These factors enable the bacteria to penetrate the plant's surface, interfere with signaling pathways, suppress immune responses, and manipulate host metabolism, leading to disease symptoms such as leaf spots, blights, wilts, and cankers.

Fungal pathogens are a diverse group of microorganisms that cause significant damage to plants. They have various modes of infection, including direct penetration of the plant's surface, production of specialized infection structures, or colonization of natural openings. Fungal pathogens can induce symptoms such as leaf lesions, fruit rot, stem cankers, and root rots, reducing plant vigor and yield (Koike et al. 2003). Fungi can also produce toxins or allergenic compounds that further affect plant health and can impact human and animal health as well (Fig. 4.3).

The diverse plant-microbial interactions demonstrate the intricate relationships between plants and microorganisms in terrestrial ecosystems. From mutualistic associations that enhance nutrient acquisition and stress tolerance to parasitic and pathogenic interactions that can devastate plant health, understanding these interactions is crucial for sustainable agriculture, ecosystem functioning, and disease management (Abo Nouh 2019).

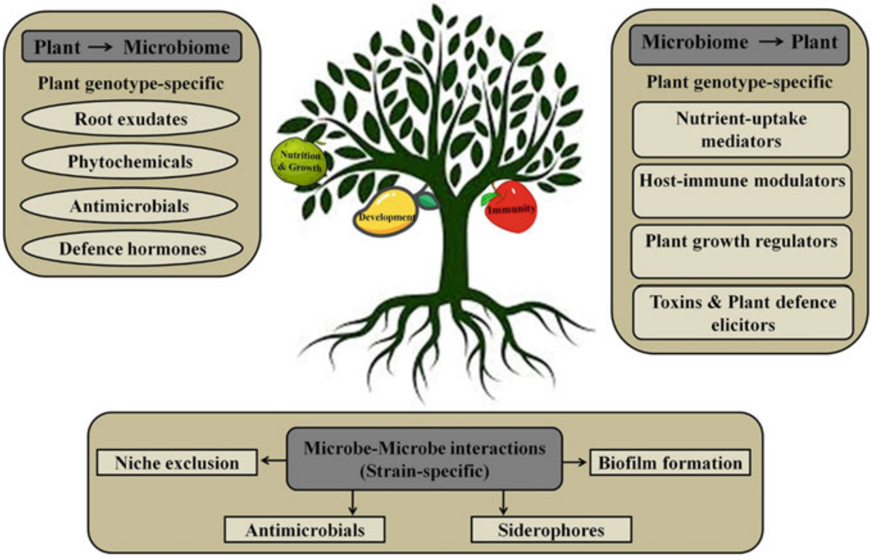

Fig. 4.3 Various ways through which plant growth is promoted/enhanced by effective microorganisms

4.3 Methods Used to Study Plant–Microbe Interactions

Several techniques have been developed to study the importance of plant–microbe interactions in sustainable agricultural practices. These techniques mainly include conventional, biochemical, and modern molecular methods (Joshi et al. 2023).

4.3.1 Conventional Methods

Conventional methods mainly aim to identify the microorganisms present in the soil. These methods involve the isolation of microbes from soil and their growth on different agar media such as synthetic, selective and special media to differentiate the organisms based on the pattern of colony formation followed by biochemical characterization of colonies. Conventional methods utilized microscopy to identify microorganisms based on their physical parameters such as shape and length of bacteria. Microscopy involves bright-field, dark-field and phase-contrast microscopy to visualize colored unstained and live samples respectively (Liu et al. 2014). However, these methods were only limited to the identification of microbes that can be grown on available culture media.

4.3.2 Biochemical Methods

Biochemical methods have importance in plant pathology for the detection of infectious agents, which are necessary to recognize for the prevention of infectious diseases and the development of sustainable agriculture. These methods used to study the relationship between plants and microbes are mainly based on interactions of proteins, i.e. antigen and antibody. These interactions either be direct or indirect. The assays which measure the direct interactions between antigen and antibody include immunoprecipitation, immunoagglutination and immunodiffusion.

Immunoprecipitation could be useful in the detection of specific proteins in a sample. In this assay, antibodies specific to the protein will be incubated with agar gel and a sample having a specific protein will be added to the gel through wells. The interaction between two proteins leads to a precipitation reaction. This assay indicates the presence of enzymes in soil and antigen present on the bacterial surface and their interaction with proteins of plants can be detected (Corthell 2014).

Immunodiffusion also involves the agar media where antigen and antibody are poured into different wells, which react to form a precipitation band (Licata et al. 2015). This assay can recognize pathogens' presence in soil samples (Joshi et al. 2023).

In an agglutination reaction, the antibodies are coated on a surface of carrier particles which, when incubated with a sample, indicate the presence of antigen in the form of an agglutination reaction.

Biochemical methods where antibody and antigen do not interact directly are known as labeled immunoassays. These assays involve Enzyme-linked Immunosorbent Antigen (ELISA), Radioimmunoassay (RIA) and immunofluorescence (Dass and Mallick 2019). ELISA is a powerful technique for quantifying participating molecules such as mycotoxins, viral proteins, or antigen (Zhang and Vrient 2020). In this assay, antigen containing sample was added to the microtiter plate followed by an enzyme-bound antibody. The antibody-antigen reaction can be detected by adding a substrate of the enzyme, changes color in the presence of antigen and can be quantified using a UV-visible spectrophotometer. It is a popular technique due to its sensitivity, specific reaction and less time required for the reaction. ELISA has several applications in studying plant-soil microbe interactions. It is employed in the detection of several plant pathogens such as *Phytophthora cinnamon*, the causative agent of turf disease, *Rhizoctonia solani* causing brown rot of plant stems (Dass and Mallick 2019).

Radioimmunoassay (RIA), as the name implies needs the radiolabeling of molecules for detection. Several radiolabels such as ^{125}I, ^{131}I and ^{3}H are used for the detection of plant pathogens such as *Botrytis cinera* causing bunch rot in grapevines (Dass and Mallick 2019).

On the other hand, immunofluorescence uses fluorophores to label antigen–antibody complexes and detected them under a fluorescence microscope (Joshi and Yu 2017).

4.3.3 Molecular Methods

Molecular methods provided the knowledge of mechanisms of plant–microbe interactions. These methods involve techniques from PCR to high-throughput sequencing.

4.3.3.1 Polymerase Chain Reaction (PCR)

PCR is the amplification of DNA from different organisms and can be quantified (Singh et al. 2014). PCR can be used to identify several bacteria as well as quantify different genes expressed in bacteria (Joshi et al., 2023).

4.3.3.2 16S rRNA Gene Sequencing

This is based on the 16S ribosomal RNA (rRNA), which is present only in bacteria and remains conserved. 16S rRNA sequencing is a major step in the identification of microorganisms on the molecular level and is of utmost importance in phylogenetic analysis and taxonomic classification of bacteria. This technique is already used to identify microorganisms in the rhizosphere (Jacoby and Kopriva 2019). Identifying rhizospheric bacteria helps to understand the stability and adaptability of bacteria around plants. Also, provide insights into plant–microbe interactions, which could help increase the productivity of plants.

Over the past decades, advanced integrated novel molecular approaches, such as transcriptomics, metagenomics, proteomics, genome editing metabolomics, phenomics, ionomics and bioinformatics, explored host-specific plant–microbe interactions in a broader way (Talukdar and Sinjushin 2015; Wu et al. 2017; Muthamilarasan et al. 2019; Shelake et al. 2019). These approaches contribute to understanding the relationship between the microbial community and environmental functions.

4.3.3.3 Next-Generation Sequencing (NGS)

Next-generation sequencing (NGS) technologies have enabled high-throughput, rapid data generation at low cost for genomes, epigenomes, transcriptomes and proteomes. NGS can help study plant microbiome and their connection to the environment (Kumar and Sharma 2020). Several microbes, such as *Gammaproteobacteria* and *Betaproteobacteria* were recognized in soil by NGS and have a role in controlling the infection caused by *Rhizoctonia solani* (Kumari et al. 2017). Also, NGS can help study the plant's microbiome composition. The synthetic Microbial Communities (SynCom) technique consists of co-cultures of several taxa under certain conditions to imitate the composition (Shayanthan et al. 2022). This technique helps to understand the interactions among members of the microbial community (de Souza et al.

2020) and reported enhanced plant growth in a greenhouse (Armanhi et al. 2021; Choi et al. 2021; Lee et al. 2021) as well as greenhouse conditions (Wang et al. 2021).

4.3.3.4 CRISPR/Cas9

In the era of recombinant technology, several genome-editing techniques have evolved to edit organisms' genomes to study the function of the same. CRISPR/Cas9 is one of the advanced gene editing tools in which CRISPR-associated 9 (Cas 9) nuclease found in bacteria is used by the immune system to defend the viral invasion. This nuclease has been used for genome editing at specific sites (Shelake et al. 2019). This technique has been proven to be a significant game-changer in agriculture. Presently, CRISPR-based methods are employed in studying plant-host interactions. It also has been used to improve plant resistance against biotic stresses such as fungi, bacterial and viral diseases, or abiotic stresses like cold, drought and salt and to improve the crops' nutritional value (El-Mounadi et al. 2020). In addition, CRISPR/Cas9 proved to be very useful in controlling plant diseases. Prabhukarthikeyan et al. 2020 created a mutation in the coding area in the *OSSWEET13* gene which enhanced the resistance against xoo infection in plants caused by *Xanthomonas oryzae* pv. Oryzae. CRISPR/Cas 9 can also be employed to study plant microbiome interactions and how these interactions affect the production of secondary metabolites (El-Mounadi et al. 2020).

4.3.3.5 Other Molecular Methods

Other molecular approaches such as metagenomics, transcriptomics, proteomics, metabolomics, phenomics and ionomics also contribute to understanding the function of various microbial species around the plants and the impacts of their interactions on the environment.

Metagenomics analyzes the genome of multiple microbial species and reveals the nature of the relationships between plants and bacteria and fungi microbes (Martí 2019). This method demonstrated the diversity of endophytic bacteria and fungi in maize plants (Fadiji and Babalola 2020). Apart from DNA, RNA including messenger RNA (mRNA), ribosomal RNA (rRNA), micro RNA (miRNA) and long-noncoding RNA (lncRNA), as part of the transcriptome allows to quantify the gene expressions of various genes which affected and biotic stresses. Transcriptomics is used to detect stress levels or infections in plants via gene expression analysis (Garg et al. 2016; Tavassoly et al. 2018).

On the other hand, proteomics studies the proteins of the cell or organism known as proteome (Holger Husi 2014). Proteomics is a vital approach in studying plant-pathogen interactions. Proteome study of tomato- *Cladosporium flavum* revealed the virulence gene product (avr a) expressed by *rst* gene in fungi (Gonzalez-Fernandez and Jorrin-Wovo 2012).

Another emerging approach in studying plant–microbe interactions is known as metabolomics. This branch of omics studies the metabolites present in a cell (Burgess et al. 2014). These metabolites constitute carbohydrates, lipids, or other secondary metabolites. This mass spectrometric approach has grown extensively in the last decade in the field of studying bacteria and fungi interactions with plants. This technique provided both quantitative as well qualitative data to study the symbiosis between plants and microbes as well as helped to describe the tolerance mechanisms in plants against abiotic stresses (Gupta et al. 2022). Metabolomics also revealed the chemicals involved in the signaling process during quorum sensing (Bharagava et al. 2019). For example, citric acid containing exudates from cucumber was found to attract *Bacillus amyloliquefaciens* SQR9 and form biofilm around roots were recognized using metabolomics (Zhang et al. 2014). Metabolomics is also employed to study the exudates secreted by grassroots during development and their effect on the rhizosphere (van Dam and Bouwmeester 2016).

4.4 Engineering of Soil Microbes and Their Applications in Sustainable Agriculture

In the present time of high demand for food for the growing global population, extensive use of pesticides, and changing climate conditions need a balance between food production and a sustainable environment. The tiny members of the rhizosphere are an important part of the agricultural ecosystem, therefore, they can be utilized to establish eco-friendly ways to enhance crop productivity to meet the world's population. Soil microbes have been already employed in the field of sustainable agriculture.

With climate change, frequent and unfavorable environmental conditions affect plants' growth as well as productivity. In addition to environmental conditions, man-made chemicals and pesticides to enhance crop productivity also have been major contributors to the disturbance of plants' health. These chemicals not only affect plants but also soil fertility, and water resources, cause environmental pollution, and agriculture sustainability and also enter into the food chains (Fu et al. 2022). Moreover, pesticides kill the microbes of soil known to benefit the plants and secretion of exudates and thus the nutrient availability to plants (Meena et al. 2020). To regain soil rhizosphere, phytomicrobiome engineering is a fascinating area of synthetic biology (Quiza et al. 2015). The aim of engineering these microbes is to enhance the resistance in plants against biotic and abiotic stresses, increase plant growth and productivity and benefit the environment from this synergistic relationships between plants and microbes (Dessaux et al. 2016). These microbes can be engineered through traditional techniques such as the modification of supplements in soil. Though, these modifications can equally support the growth of pathogens which can further interfere between the plant and beneficial microbes' interactions. Therefore, high-throughput molecular techniques such as omics techniques, and genome editing technologies including CRISPR/Cas9 which are able to focus on specific sites and are more efficient are needed. Many soil microbes were engineered in recent years to improve, aiming to replace the lethal chemical substances used in agricultural practices and to enhance agronomic production in a sustainable way (Table 4.2). The engineering of microbes has several applications such as enhanced plant growth, nutritional quality, protection against various diseases, reactive oxygen species and also the tolerance against abiotic stresses including salt, and heat stress (Ke et al. 2021).

4.5 Current Challenges in Studying the Interactions of Soil Microbes with Plants

The interactions between soil microorganisms and plants are critical aspects in many ecological processes and agricultural output. Understanding the complex dynamics and mechanisms that underpin this connection is critical for long-term agriculture and environmental management. However, investigating the complex interactions between soil microbes and plants have several difficulties. This section will explore the present issues in studying the interactions of soil microbes with plants, stressing the limitations and potential solutions to these hurdles.

Soil microbe interactions must be studied in order to improve agricultural practices and ecosystem functioning. Several obstacles, however, limit substantial study in this sector. These hurdles include microbial variety, geographical and temporal heterogeneity, the complexity of plant–microbe signaling, and the integration of omics technology.

4.5.1 High Microbial Diversity

The high microbial diversity in soil ecosystems presents a significant challenge when studying the interactions between soil microbes and plants. This diversity encompasses a wide range of microorganisms with diverse functional roles, making it difficult to unravel the complexities of plant–microbe interactions (Delgado-Baquerizo et al. 2016). The high microbial diversity poses limitations on our ability to comprehensively study the complex dynamics and mechanisms underlying the relationship between soil microbes and plants. Traditional culture-based techniques are limited in capturing the true extent of microbial diversity in soil (Katz et al. 2016). Many soil microorganisms are unculturable under laboratory conditions, leading to a biased understanding of microbial composition and function. This cultivability gap hampers the exploration of the diverse microbial taxa involved in plant–microbe interactions.

Table 4.2 List of engineered microbes for sustainable agriculture practices

Plant/Plant species	Beneficial microbes	Functions	References
Lens culinaris	*Chryseobacterium* sp. PSR10	Solubilization of Phosphate in soil	Singh et al. (2018)
Glycine max	*B. firmus SW5*	Produce anti-oxidative enzymes to enhance tolerance to salinity	El-Esawi et al. (2018)
Poncirus trifoliata	*F. mosseae*	Drought stress and Hyphal water absorption rate	Zhang et al. (2018)
Sarracenia species	Endophytic diazotrophic bacteria	Nitrogen fixation	Sexton et al. (2020)
Avicennia marina	*Halomonas* species	Protect against heavy metal stress	Mukherjee et al. (2019)
Zea mays	Endophytic bacteria e.g. *Bacillus* and *Brevibacillus*	Accelerate plant growth	ALKahtani et al. (2020)
Piper nigrum	*Bacillus subtilis*, *Bacillus siamensis*, *Brevibacillus gelatini*, *Pseudomonas geniculata*, *Pseudomonas beteli*, *Burkholderia ubonensis*, and *Burkholderia territorii*	Protect plants against soil-borne fungus, *Fusarium solani*	Lau et al. (2020)
Phaseolus vulgaris	*Aneurinibacillus aneurinilyticus* and *Paenibacillus* species	Enhance the activity of 1-Aminocyclopropane-1-carboxylic acid (ACC) deaminase to protect the plants from salinity stress	Gupta and Pandey (2020)
Solanum lycopersicum	*A. pullulans* 490 *C. rosea* 016	Produces biosurfactants and biocontrol activity	Köhl et al. (2020)
Oryzae sativa	*Bacillus pumilus* strain JPVS11	Protect from salt tolerance	Kumar et al. (2020)
Saccharum officinarum	*B. xiamenensis*	Phytoremediation	Zainab et al. (2021)
Oryza sativa	*Aspergillus niger*	Promoted germination rate, enhanced growth As well as biomass	Stanley-Raja et al. (2021)
Gossypium hirsutum	*Brucella* sp. PS4	Helpful in degradation of pesticides	Ahmad et al. (2022)
Solanum lycopersicum	*E. cloacae* PM23	Reduction of reactive oxygen species and Sodium ion homeostasis	Ali et al. (2022)
Solanum lycopersicum	*B. safensis* (SCAL1)	Produce exopolysaccharides and enhance ACC deaminase to relieve heat stress	Mukthar et al. (2022)

High microbial diversity often leads to functional redundancy, where multiple microbial species perform similar ecological functions (Louca et al. 2018). This redundancy complicates the identification of specific contributions from individual microbial taxa to plant–microbe interactions (Singh et al. 2015). Moreover, the interactions between different microorganisms can be complex and context-dependent, further challenging the interpretation of their roles in plant health and productivity.

4.5.2 Geographical and Temporal Heterogeneity

Geographical and temporal heterogeneity are significant challenges encountered while studying the interactions of soil microbes with plants. Soil microbial communities exhibit spatial and temporal variations influenced several factors such as land management practices, soil type, climate, and plant species (Lauber et al. 2013). Understanding the implications of this heterogeneity is crucial for unraveling the complex dynamics of plant–microbe interactions. Geographical variations at different scales, as well as temporal fluctuations, significantly influence the composition, diversity, and functioning of soil microbial communities, thereby affecting the dynamics of plant–microbe interactions. Geographical heterogeneity for soil microbe interaction arises from variations in soil properties, climate, land management practices, and biotic factors across different geographic locations (Burns et al. 2015).

Soil microbial communities also exhibit temporal heterogeneity. Microbial populations can vary over time due to seasonal changes, crop rotation, successional stages, and land management practices (Tardy et al. 2015). There may be dynamic shifts in response to environmental conditions and plant–microbe interactions, making it challenging to capture the transient nature of interactions and their effect on plant health and productivity. Sampling strategies also show variability across different locations and time points. Representative sampling is crucial to obtain reliable data that accurately reflect the microbial community composition and their interactions with plants. However, selecting representative sites and time points can be challenging variability in soil microbial communities (O’Brien et al. 2016). In addition to this, variations in sampling techniques and protocols can affect the comparability of results in plant–microbe interactions and association studies.

Considering multiple locations in experimental designs allows researchers to capture the diversity and dynamics of soil microbial communities (Franzosa et al. 2015). However, conducting long-term experiments to capture temporal changes in microbial communities requires considerable time, resources, and logistical planning. Furthermore, controlling environmental variables while accounting for natural variations can be challenging, particularly in field-based studies.

4.5.3 The Complexity of Plant–Microbe Signaling

A complex network of signals and responses poses a significant challenge in analyzing the plant–microbe relationship (Sukumar et al. 2013). It involves a diverse form of chemical and molecular signals that regulate processes such as nutrient uptake, defense activation, and growth promotion. Understanding the complexity of plant–microbe signaling is an important step to decipher the mechanisms underlying these interactions (Giron et al. 2013). Signaling molecules include phytohormones, volatile organic compounds, secondary metabolites, and small peptides. The production and perception of these molecules can vary depending on the specific microbe and plant species involved, making it challenging to predict the specific signals involved in plant–microbe interactions. Plant–microbe signaling is also influenced by factors such as plant developmental stage, environmental conditions, and the presence of other microorganisms (Cheng et al. 2019). Different microbes can induce diverse responses in plants, depending on the specific physiological and genetic context of the plant (Rosier et al. 2018). In addition to this, there is significant crosstalk between different signaling pathways in plants. Crosstalk can occur between different hormone signaling pathways or between defense signaling and growth-promoting pathways.

Genetic and epigenetic factors additionally contribute to the complexity of plant–microbe signaling. Plant genes involved in signaling pathways can show off allelic variations and polymorphisms that have an impact on the outcomes of plant–microbe interactions (Howles et al. 2005). Epigenetic modifications, along with DNA methylation and histone modifications, can also affect gene expressions and finally can impact the reaction of flowers to microbial signals. Understanding the genetic and epigenetic regulation of plant–microbe signaling is critical for interpreting the underlying mechanisms.

4.5.4 Integration of Omics Technologies

Omics technology, together with genomics, transcriptomics, proteomics, and metabolomics, have revolutionized the study of plant–microbe interactions in soil ecosystems (Gamalero et al. 2022). However, integrating the sizable number of facts generated through these omics processes presents a tremendous task. Omics technology generates considerable amounts of facts, necessitating green facts management and evaluation pipelines. The excessive-throughput nature of those technologies affects huge datasets that require suitable management and retrieval strategies. Integrating multi-omics information from distinct molecular tiers (genomics, transcriptomics, proteomics, metabolomics) is critical for obtaining a complete knowledge of plant–microbe interactions. However, integrating records from diverse omics platforms is tough due to variations in experimental techniques, information formats, and analytical tools (Diwan et al. 2022). Harmonizing information throughout specific omics disciplines and growing standardized protocols for statistics integration is crucial for generating significant insights into the complicated interplay among soil microbes and flora.

4.6 Conclusion

Interactions between plants and microbes has several interfaces. There are processes like nitrogen fixation, tolerance to stress, or resistance to pathogens that directly or indirectly involve microorganisms. These interactions have a significant impacts on the growth of plants. Therefore, it is of utmost importance to study these interactions for the sake of the development of sustainable agricultural practices. In the present chapter, various interactions between plants and microorganisms have been described. Also, this chapter described several techniques which have been developed to study these interactions. Along with these techniques, their advantages in understanding the growth of plants and the contribution of the environment in this process were explained as well. Later, the role of microbial engineering in pant-microbe interactions and their contribution to sustainable agriculture was also defined. Lastly, present challenges to studying the plant–microbe interactions were described in detail.

4.7 Future Prospects

Interactions between different microorganisms are usually complex and context-dependent, which further challenge the analysis of their roles in plant health and productivity. Considering multiple locations in experimental designs have to consider to find out the dynamics of soil microbial communities. Understanding the genetic and epigenetic regulations of plant–microbe signaling is critical for interpreting the underlying mechanisms. As several omics techniques have been developed to study plant-microbial interactions. However, the role of these techniques in plant–microbe interactions is underutilization and yet to be explored in a wider way. The combination of different techniques might help to study plant–microbe interactions and answer several questions on the way road to sustainable agriculture. Due to recent advances, now it is possible to engineer the microbes to obtain specific applications. But along with their applications, it is essential to consider the concerns such as biosafety, and contamination of the environment associated with the use of engineered microbes. Deatil risk assessment studies are required in order to ensure safe applications of the engineered organisms in the environment.

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Chapter 5
Emerging Roles of Nanomaterials in Plant-Salinity Interaction

Soheila Abdoli and Kazem Ghassemi-Golezani

Abstract Agricultural production faces many environmental challenges such as soil salinity, that reduces plant growth and productivity. Recently, nanomaterials have been gaining an increased interest in agricultural systems, particularly for promoting salt tolerance and crop performance. Nanoparticles are known as particles which have a size of less than 100 nm in diameter, which easily penetrate into the plant cells. These particles may exhibit both negative and positive effects on the plants under different environments, depending on types, physio-chemical properties and concentration. Low concentrations of nanoparticles have often dual functions: (a) moderate adverse effects of salt stress, (b) provide more efficient nutrient forms for plants. Nanomaterials could be applied as nano-priming and coating of seeds, foliar spray, and soil treatments. Changes in various physiological and biochemical pathways of plants under salinity by these materials have been well documented. These changes can reduce the harmful impacts of salinity on plants, leading to better performance and sustainable production of various crops. Thus, this chapter reviews the most recent and promising developments on plant-salinity interactions in response to nanomaterial treatments.

Keywords Nanomaterials · Nano-priming · Nanotoxicity · Plant growth · Salinity

5.1 Introduction

Developing, synthesizing, characterizing and application of materials after modification of their size and shape in nanoscale is termed as nanotechnology. Different types of nanotechnology-based products (nanoparticles and their derived nanomaterials) have been increasingly used for development of numerous sectors and novel technologies such as electronics, optics, food packing, textiles, medicine and pharmaceuticals, biosensors, agriculture and compounds for environmental remediation (Kottegoda et al. 2017; Khan et al. 2019; Giorgetti 2019; Mansoor et al. 2022) This is most likely

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_5

due to the specific and worthy physicochemical properties of nanoparticles (NPs) in comparison with bulk materials. Based on their morphology, size, properties and the constituents, nanomaterials are of different types. In general, nanomaterials are classified into carbon-based, metal-based, semiconductor, and nanocomposites (Kolahalam et al. 2019). The metal- and carbon-based materials are most common and have been well investigated. These materials have some inimitable physicochemical characteristics such as very small size, and high surface area, reactivity, conductivity, and optical sensitivity, which are likely attributed to the unique adverse biological effects in ecosystems (Nel et al. 2006).

The nanoparticles can be synthesized by three different biological, physical and chemical methods. The biological method that is known as green synthesis, is a single step, energy-saving, eco-friendly and economically viable method, in which microorganisms (bacteria, fungi, alga) and various parts of plants can be used for the production of nanomaterials. The physical methods are classified to “top-down” and “bottom-up” groups. In “top-down” method, the mechanical milling technique leads to the pulverization of big materials into smaller particles. However, in the “bottom-up” method, the smaller ions are chemically combined to form larger materials. The laser evaporation, RF plasma and thermal decomposition or thermolysis are physical methods of NPs synthesis. The synthesis of nanoparticles by chemical method occurs by a variety of “bottom-up” techniques. The pure and controlled particle size can be obtained in this method. The most common techniques used in this approach are co-precipitation, sol–gel, hydrothermal, and microwave assisted synthesis (Kolahalam et al. 2019).

The appropriate rate of nanomaterials application in different sectors particularly in agriculture are innumerable, but the high rate of these materials may have toxic effects. Therefore, this chapter focuses on the agricultural application and toxicity of NPs, considering recent works on different plant species and highlights the ameliorative effects of different nanomaterials in plant-salinity interactions.

5.2 Nano-based Technology in Agriculture

Nano-based technologies dealt with materials ranging between 1 and 100 nm in diameter, called nanomaterials (Remédios et al. 2012). Nanotechnology is an emerging technique and shares a wide range of applications in various fields of modern life (Giraldo et al. 2019; Zhao et al. 2022). Recently, the nano-based technology has gained more attention in protecting plants under biotic and abiotic stresses and sustainable production. The major topics for nanomaterial application in agriculture can be considered as plant growth regulators to improve stress tolerance in plants (Ghassemi-Golezani and Abdoli 2021). It has been well documented that application of nanomaterials in appropriate concentration can promote plant performance to counter a range of environmental threats. Carbon-, metal- and metal oxide-based nanoparticles can enhance germination, seedling growth, photosynthesis, nutrient availability, biochemical compounds and plant growth (Abdoli et al. 2020; Mahmoud and Abdelhameed 2021; Alam et al. 2022) due to unique optoelectronic, physiochemical and catalytic properties. For instance, the reactive oxygen species scavenger potential of CeO_2 nanoparticles is the result of their greater number of surface oxygen vacancies. It was found that multi-walled carbon nanotubes can regulate expression of genes involved in antioxidant activities of rapeseed plant under salt stress. The beneficial effects of these NPs on mitigating salt toxicity were also related to alteration in transcription of Na^+/H^+ exchanger (*NHX1*) and K^+ transporter (*KT1*) (Zhao et al. 2019).

Nanoparticles can be also applied as superior nanocarriers for delivery of special genetic materials such as RNA and plasmid DNA, as well as proteins to an extensive range of plant species (Demirer et al. 2019; Watanabe et al. 2021). Kwak et al. (2019) reported that chitosan-complexed single wall carbon nanotubes successfully transferred DNA to the chloroplasts of several plant species. This capacity is more likely related to very small size, high surface area, and several binding sites of NPs. These nano carbons require neither *Agrobacterium* infection, that is limited to a small number of genetically modified plant species, nor gene gun bombardment, which damages plants and has low efficiency. The nanomaterials might be applied as nano-sensors to detect the characteristics of water and soil, residues of pesticides, and plant pathogens (Beegum and Das 2022). It has been reported that smart nanosensor can be used to translate plant signaling molecules associated with health status into digital information, which is monitored by standoff electronic devices (Giraldo et al. 2019). High surface of hydroxyapatite nanoparticle causes slow and controlled release of urea as fertilizer, suggesting the feasibility of this nanomaterial application in crop production (Kottegoda et al. 2017). Numerous studies have revealed that some nutrients at nano-scale can be applied as nano-fertilizer to improve the efficiency of nutrients in lower rates, that lowers environmental hazards and increases plant production (Soliman et al. 2015). The nanomaterials also used as pathogen diagnostics and toxic agrochemicals tracing. According to Zhao et al. (2022), Zn-based nanoparticles have potent antipathogen activity. The colloidal solution of Zn, Ag, Fe, Mn, and Cu nanoparticles amplified antioxidant properties of wheat plants under *Pseudocercosporella herpotrichoides* infection (Panyuta et al. 2016). Soil amendment by NPs can potently remediate heavy metals and toxics in soil through immobilizing pollutant, accelerating degradation, and regulating rhizosphere microbial community to improve crop immune responses (Ma et al. 2022). Remediation of heavy metals from soil by green synthesized iron oxide nanoparticles has been confirmed by Andrade-Zavaleta et al. (2022). Therefore, nanomaterials can play a pivotal role in sustainable agriculture for improving crop growth and productivity.

5.3 Uptake and Translocation of Nanoparticles

Nanoparticles are emerging as delivery vehicles for plants in genetic transformation (Demirer et al. 2019), bio-stimulants (Abdoli et al. 2020), and fertilizers (Soliman et al. 2015). Understanding the nanoparticles entrance and translocation in plant tissues facilitates the application of nanotechnology to enhance efficiency of nanomaterials in agriculture. However, the mechanisms of NPs entrance through barriers are not yet thoroughly understood. The first hindrance that nanoparticles must overcome to influx the cell is the cell wall. Depending on the reactivity, penetration and movement of NPs within the plant may differ (Li et al. 2016). It may be restricted by the pore size, that is defined as the space between the cell wall components and the wall matrix. It is almost unveiled that the changes in the chemical composition of the cell wall is involved in the NPs passage. The chemical properties of the cell wall can affect the size of pores in the walls and apoplastic exchange of macromolecules (Kurczynska et al. 2021). Another possible mechanism for the NPs passage through the cell wall is the laceration induced by NPs accumulation on the wall surface. In a study, the mechanism of Ag NPs passage through the cell wall of *Lactuca sativa* was investigated in detail. Initially, the Ag NPs contacts the outer cell wall, presenting two states of oxidation (Ag^+ and Ag^0). Afterwards, the Ag^+ interacts with oxygen, resulting in a rupture of hydrogen bonds on cellulose microfibrils. This breakdown of hydrogen bonds creates spaces enough to Ag NPs free passage via the cell wall (de Paiva Pinheiro et al. 2021).

After passing the cell wall obstacle, the nanomaterials must cross through the cell membrane to enter the cytoplasm. The selective absorptivity of plasmalemma and plasma membrane of plant cells allows diffusion of small nonpolar ions through the membrane (Ghorbanpour and Wani 2019). After entrance to the plant cells, NPs move through either apoplastic or symplastic pathway, and by xylem and phloem vessels to the different plant organs such as flowers, fruits and seeds. In apoplastic pathway of root uptake, the NPs cross the cell wall through pores or damaged parts and then distribute in the intercellular spaces, that eventually enter into the vascular system. There are evidences supporting apoplastic entry of nanoparticles in *Arabidopsis thaliana* (Avellan et al. 2017) and *Cucumis sativus* (Ma et al. 2011). However, in symplastic pathway, the NPs penetrate into cell membrane and cytoplasm by different internalization process, departing from one cell to another via plasmodesmata to enter vascular system. In both routs, the NPs can enter in vascular system, where casparian strips are not well developed (Khan et al. 2022a). In a study on *Citrus maxima* seedlings, the γ-Fe_2O_3 and α-Fe_2O_3 NPs applied in rhizosphere internalized into the cells by endocytosis and diapirism process, respectively (Li et al. 2018). The uptake of nanoparticles in both apoplastic and symplastic pathways could be limited by the porosity of cell wall, and diameter and width of plasmodesmata (Wu and Li 2022). The efficiency of absorption and transport of NPs vary in different plant species, depending on physiochemical and electrochemical properties of NPs, phyllosphere and rhizosphere (Giorgetti 2019; Khan et al. 2022a). It was reported that the iron NPs were transported through the vascular system from the root to the shoot of maize plant (Pariona et al. 2017). Similarly, Li et al. (2020) stated that carbon-based nanomaterials transported from roots to aerial part of plants through vascular system. Previous literatures demonstrated that negatively charged Ce NPs were efficiently translocated from root to the shoot in tomato, lettuce, corn and rice plants. This translocation was the highest for dicotyledons compared to monocotyledons due to the larger airspace volume in dicotyledons leaves (Spielman-Sun et al. 2019).

Negatively charged CeO_2 NPs have been found to accumulate more than neutral/positive CeO_2 NPs in leaf cells of *Arabidopsis thaliana* (Wu et al. 2017). However, there are some evidences that demonstrates the translocation of NPs from the aerial part of plants to the roots, indicating reverse movement from phloem to xylem (Gao et al. 2023). The efficient translocation of Au NPs from leaf to the root has been confirmed by Ha et al. (2021), proving that Au NPs could be also transported by phloem.

5.4 Nanotoxicity

Production, application, and disposal of NPs result in their massive release into the environment. The NPs of both natural and chemical origin can be found in different environments, which may accumulate over time especially in soil, sludge, and water (Remédios et al. 2012). Nanotoxicity is one of the major topics of interest in nanoscience, which adversely affects plants and ecosystem balance. Increasing concerns regarding toxicity of nanoparticles, may limit application of nanotechnologies in agricultural sector. It should be noticed that our knowledge about long-term unfavorable effects of nanoparticles on soils, plants and humans is limited. The nanotoxicity in water, soil and plant greatly depends on the composition, size and concentration of the nanoparticles. In the soil, the NPs undergo a series of bio/geo-transformations, which determine the availability and toxicity of NPs to plants (Ali et al. 2021). The type of nano-materials and plant species, the size and concentration, morphology and zeta potential of NPs are some important factors that influence the NPs phytotoxicity (Ahmad et al. 2022). After releasing into the environment, the NPs can change their chemical properties. Therefore, the bioavailability of NPs for living organisms may be strongly influenced by abiotic factors. The environmental risk associated with nanotechnology was well discussed under different conditions. Application of improper concentration of NPs causes oxidative stress in plant cells via ROS generation (Ma et al. 2017). Balážová et al. (2020) stated that application of ZnO nanoparticles at 400 mg/L in tobacco plants increases accumulation of reactive oxygen and nitrogen species, and damages plasma membrane, mitochondria and endoplasmic reticulum, which may lead to cell death. High concentration of ZnO NPs inhibited normal growth in *Fagopyrum esculentum* plants (Lee et al. 2013). Shaw and Hossain (2013) discovered the inhibitory effect of CuO-NPs on seed germination of rice, which is related to oxidative damages. Similarly, wheat plants suffered various negative effects such as increased enzymes associated with oxidative stress and lipid peroxidation when exposed to concentrations higher than 200 mg/L, SiO_2 NPs (Karimi and Mohsenzadeh 2016). Abdelsalam et al. (2018) reported that exposure of wheat plants to Ag NPs caused chromosomal aberrations such as incorrect orientation at metaphase, scattering, chromosomal gaps and multipolar anaphase.

5.5 Application of Nanomaterials to Improve Salt Tolerance of Plants

Soil salinity is one of pivotal environmental issues that threats crop productivity worldwide. salinity can negatively affect different morphological, physiological, biochemical, and molecular processes in plants, causing influx of hazard Na^+ ions, oxidative stress, membrane damages, metabolic disruption, and reducing plant growth and yield (Ghassemi-Golezani and Abdoli 2022a). Increasing osmotic potential as a result of salinity limits water absorption during seed imbibition, leading to a low germination rate. Hormonal stimulation and hydrolytic enzymes activities related to seed germination could be strongly affected by salt stress, altering seed metabolism (Lee and Luan 2012). Salinity triggers generation of excessive ROS and accumulation of toxic ions in plant cells, thereby limiting seedling growth, damaging photosynthetic apparatus, and depleting cellular energy (Ghassemi-Golezani and Abdoli 2021; Abdoli and Ghassemi-Golezani 2021). The K^+ uptake is strongly inhibited by excess Na^+, that interferes with several K^+-dependent activities and disrupts metabolic processes (Munns and Tester 2008). Activation of the different antioxidant compounds, signaling molecules and phytohormones have been considered as the main mechanism for ionic and oxidative homeostasis and Na^+ exclusion from cytosol (Mangal et al. 2023).

Nanotechnology is considered as an effective approache to improve stress tolerance of plants, alleviating the injurious impact of salinity via enhancing availability of K^+, reducing Na^+ uptake, stimulating antioxidants and regulating redox and ionic balances, accumulating bioactive compounds and osmo-regulators and improving photosynthesis (Ghassemi-Golezani and Abdoli 2021; Ghassemi-Golezani et al. 2021). The beneficial effects of NPs for promoting salt tolerance have been previously reported in various plant species such as canola (Rossi et al. 2016), ajowan (Abdoli et al. 2020), jalapeño pepper (Ye et al. 2020), rice (Prerna et al. 2021), wheat (Farooq et al. 2022), tomato (Guerriero et al. 2023) and maize (Alhammad et al. 2023). Although several reports confirmed the ameliorative effects of NPs on plants under salt stress, the crosstalk of nanoparticles and intracellular mechanisms underlying the enhanced tolerance of plants to salt stress are not completely understood. Nevertheless, the NPs can be applied in low doses through various routes including seed priming, foliar spray and soil treatments to improve physiological and metabolic performance of plants (Fig. 5.1).

5.5.1 Seed Nano-priming and Coating

Seed germination and seedling establishment are the most sensitive stages to salt toxicity in different plant species. It lowers germination rate and uniformity, leading to poor plant performance and productivity (Ghassemi-Golezani and Abdoli 2022b; Alhammad et al. 2023). Seed nano-priming and/or coating are newly emerged and

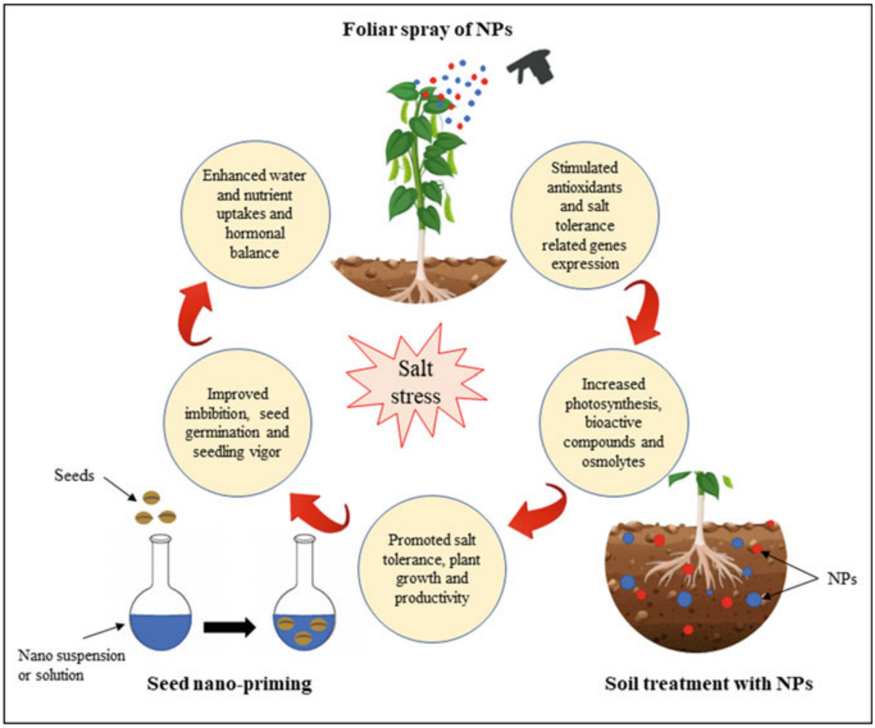

Fig. 5.1 The general aspects of improving plant performance under salinity by various forms of nano-applications

low-cost approaches to promote stress tolerance in plants, which induce specific physiological and biochemical changes in seeds and plants. In nano-priming, seeds are imbibed in nano-suspensions or nano-formulations for a certain period of time (Baz et al. 2020; Khan et al. 2021). Even though nanoparticles may be taken up, their majority remain on the seed surface (Duran et al. 2017). A permanent and strong binding proportion between seeds and nanoparticles has been recently proved in nano-primed seeds. Internal metabolic functions may be responsible for improved germination properties in nano-primed seeds. Internal hormonal (GA and ABA) balance in nano-primed seeds can regulate absorption and translocation of nanoparticles inside the seeds (Chandrasekaran et al. 2020). The ROS signaling is very pivotal to break seed dormancy and stimulate seed germination through regulation of GA biosynthesis and storage mobilization, which can be triggered by agglomeration and accession of nanoparticles to the seed coat (Khan et al. 2022a). The ameliorative effects and tolerance mechanism induced by nano-priming on different salt stressed plants have been well documented (An et al. 2020; Khan et al. 2021; Cembrowska-Lech and Rybak 2023).

The effects of priming with different nanoparticles and related mechanisms on salt tolerance of different plant species were presented in Table 5.1. Different physiological, metabolic and molecular pathways in seeds as well as plants may be positively influenced by seed nano treatments, causing better plant growth and performance under stressful conditions. Nano priming effectively improved seed germination, seedling emergence rates, starch metabolism and soluble sugars in several plant species (Khan et al. 2021; El-Badri et al. 2021a, b). In salt-stressed wheat seedlings, chitosan and green tea nanocomposites were found to be able to promote protein accumulation and improve photosynthetic pigments and plant defense system (Farooq et al. 2022). The accelerated water uptake by seeds primed with CeO_2 NPs upregulated *AMY1* and *AMY2* genes encoding α-amylase (Khan et al. 2021). Maintaining ionic and redux homeostasis in plant cells is important for salt tolerance, which may be achieved by nanoparticles (Zhou et al. 2021; Ghassemi-Golezani and Abdoli 2021). Seed nano-priming with CeO_2 NPs improved salt tolerance of rapeseed by improving K^+ and lowering Na^+ contents of the leaves (Sheikhalipour et al. 2021). Similar results were reported in putrescine-functionalized carbon quantum dot (Put-CQD) nano-priming, which enhanced K^+ and diminished Na^+ uptake, thereby promoting plant salt tolerance by regulation of ions homeostasis (Gohari et al. 2021b). Recent studies have shown that some nanoparticles such as nanoceria have large number of surface oxygen vacancies, acting directly as a potent catalytic scavenger of ROS under salinity (Zhou et al. 2021). In addition to direct scavenging of ROS, nanoparticles can enhance antioxidant enzymes activities to scavenge ROS. According to An et al. (2020), seed priming with CeO_2 NPs upregulated peroxidase related genes including *GhD09G1420, GhA03G2152, GhD08G2330, GhA03G1517, Gh09G1415, GhD11G2183*, and *GhA10G2288* in salt stressed cotton plants. Moreover, seed nano-priming have been reported to induce salt tolerance by hormonal regulation of cells. El-Badri et al. (2021b) found that improved salt tolerance of rapeseed plants by nano-priming with zinc oxide and selenium nanoparticles (ZnO NPs and Se NPs) is related to the stimulated GA biosynthesis genes.

The efficiency of nano-priming may be controlled by seed coat properties related to uptake and translocation of NPs. It has been proved that seeds of different plant species have different parenchyma cell layers and free air-spaces, which are important factors in seed imbibition. The seeds with less parenchyma cell layer and high free air-spaces require a lower dosage of NPs to achieve a better seed germination. However, seeds with a greater number of parenchyma cell layers need a higher rate and magnitude of zeta potential NPs (Khan et al. 2023).

5.5.2 Foliar Application of Nanoparticles

Foliar application of NPs as nano-fertilizers, and nano-stimulants, is an interesting technique to improve crop growth and productivity under a wide range of environmental conditions (Abdoli et al. 2020). Compared to soil application, foliar spraying of NPs has been reported to be more effective in penetrating into plant cells and

Table 5.1 The effects of seed nano-priming on performance of various plant species

Plant species	Nanomaterials	Size and zeta potential	Dose	Time of seed treatment	Effects	References
Triticum aestivum L	Ag NPs	15–29 nm, zeta potential not reported	2, 5 and 10 mM	24 h	Elevated soluble sugars and proline contents, and the activity of POD, but lowered CAT activity	Mohamed et al. (2017)
Triticum aestivum L	PHF NPs	Characterization data not reported	10, 40, 80, and 120 nM	10 h	Promoted root and shoot growth, antioxidant activities of CAT, POD, and APX, free amino acids, ascorbic acid, chlorophyll and soluble sugars, and lowered MDA and H_2O_2 levels in plant tissues	Shafiq et al. (2019)
Gossypium hirsutum L	CeO_2 NPs	2.1 ± 1.4 nm, −51.7 ± 11.5 mV	500 mg/L	24 h	Increased seedling growth and root vitality, expression of genes associated with ROS and ionic homeostasis, decreased in ROS generation	An et al. (2020)
Pennisetum glaucum L	Ag NPs	50–100 nm, zeta potential not reported	10, 20 and 30 mM	20 h	Improved plant growth related attributes, relative water and proline contents, antioxidants and phenolics	Khan et al. (2020)
Capsicum annuum L	Mn_2O_3 NPs	50 nm, −8.2 ± 0.7 mV	0.1, 0.5 and 1 mg/L	4–6 h	Promoted root growth, potassium contents, modified protein and lignin, regulated manganese SOD expression, helped plants to acclimate salt stress	Ye et al. (2020)

(continued)

Table 5.1 (continued)

Plant species	Nanomaterials	Size and zeta potential	Dose	Time of seed treatment	Effects	References
Zea mays L	TiO_2 NPs	10–25 nm, zeta potential not reported	60 ppm	24 h	Enhanced germination percentage and energy, seedling vigor index and growth, reduced electrolyte leakage, lipid peroxidation and Na^+ uptake	Shah et al. (2021)
Oryza sativa L	Fe_2O_3 NPs	15–22 nm, zeta potential not reported	25 mg/L	12 h	Improved seed germination and seedling growth, and diminished ROS production	Prerna et al. (2021)
Brassica napus L	ZnO NPs	20 nm, zeta potential not reported	25, 50 and 100 mg/L	8 h	Increased germination parameters, accumulated high levels of osmolytes, modified gene expression patterns, protected photosynthetic pigments and maintained redox hemostasis through instigating antioxidants	El-Badri et al. (2021a)
Brassica napus L	Se NPs and ZnO NPs	10–55 nm, −32.4 ± 2 mV for Se NPs, 20 nm for ZnO NPs	150 µmol/L Se NPs, and 100 mg/L ZnO NPs	8 h	Decreased abscisic acid, but increased gibberellic acid level through regulating expression of abscisic acid and gibberellic acid related genes, and promoted seed germination and early seedling growth	El-Badri et al. (2021b)
Triticum aestivum L	ZnO NPs	Characterization data not reported	50, 100 and 500 mg/L	24 h	Induced various changes in electrophoretic profiles of shoot proteins, and mitigated adverse effects of salinity on growth, photosynthetic pigments, photosynthetic efficiency, and leaf ultrastructure	Abou-Zeid et al. (2021)

(continued)

Table 5.1 (continued)

Plant species	Nanomaterials	Size and zeta potential	Dose	Time of seed treatment	Effects	References
Brassica napus L	CeO_2 NPs	8.5 ± 0.2 nm, −43.3 ± 6.3 mV	0.1 mM	1, 3, and 8 h	Enhanced germination rate and α-amylase activity, enabled higher K^+ retention and lower Na^+ accumulation in plant tissues, and reduced H_2O_2 and $O_2^{\bullet-}$ generations and MDA content	Khan et al. (2021)
Triticum aestivum L	CS-GTE NC	Characterization data not reported	0.02, 0.04 and 0.06%	8 h	Augmented protein content, photosynthetic pigments and antioxidants capacity, and improved membrane stability	Farooq et al. (2022)
Solanum lycopersicum L	MWCNTs	30–50 nm, zeta potential not reported	50, 250 and 500 mg/L	24 h	Increased chlorophylls, ascorbic acid, glutathione, proteins, phenols contents, lipid peroxidation, and fruit bioactive compounds	González-García et al. (2022)
Brassica napus L	CeO_2 NPs	9.2 ± 0.4 nm, −38.7 ± 2.4 mV	0.1 mM	8 h	Enhanced endogenous salicylic acid and ROS scavenging	Khan et al. (2022b)
Hordeum vulgare L	PVP-coated Ag NPs	Characterization data not reported	1, 20 and 40 mg/L	2 h	Elevated expression of *HvSOD, HvCAT, HvGR* or *HvGPX*, enzymatic antioxidants activities	Cembrowska-Lech and Rybak (2023)
Zea mays L	ZnO NPs	Characterization data not reported	50 and 100 mg/L	24 h	Increased germination percentage and energy, imbibition rate and K^+ content, decreased Na^+ accumulation	Alhammad et al. (2023)

CS-GTE NC: Chitosan and green tea nanocomposite, PHF NPs: Polyhydroxy fullerenes nanoparticles, PVP-coated Ag NPs: Polyvinylpyrrolidone-coated Ag nanoparticles improving salt tolerance (Chen et al. 2022). Foliage absorption of NPs occurs mainly through stomata and pores (Avellan et al. 2019). Some factors such as size, charge and surface tension of NPs, size of stomata and pores of cuticle, wax deposits on leaf surface, leaf adhesion ability of NPs, and phloem sieve plate properties may limit foliage uptake of NPs and thus affect the efficiency of foliar spray (Avellan et al. 2019; Wu and Li 2022). After penetration into the leaf via stomata or cuticula, the nanoparticles reach phloem by two apoplastic and/or symplastic pathways, directing to different parts of the plant. Some modification techniques such as coating or encapsulation may affect the adhesion, lipophilicity, or hydrophilicity of NPs, helping NP penetration to the leaves (Avellan et al. 2019).

Previous studies have revealed that foliar spray of NPs can enhance defense and resistance against salt stress, resulting in better physiological performance and high yield of plants (Table 5.2). For example, it has been reported that foliar application of zinc oxide nanoparticles can increase salt tolerance of canola (Hezaveh et al. 2019), safflower (Yasmin et al. 2021), wheat (Lalarukh et al. 2022) and faba bean (Mogazy and Hanafy 2022), showing an increase in photosynthesis and growth, compared with untreated plants. Decrement of Na^+ uptake, improving nutrients hemostasis, photosynthetic pigments, antioxidant capacity, plant growth and productivity by foliar application of NPs have been well documented (Abdoli et al. 2020; Ullah et al. 2022). Gohari et al. (2021a) reported that CeO_2 NPs spray increased antioxidant capacity of grapevine under salt stress. Improvement of salt tolerance in cucumber plants treated with poly (acrylic) acid coated nanoceria (CeO_2 NPs) was associated with better stimulation of antioxidant system (Chen et al. 2022). Foliar applied engineered urea functionalized hydroxyapatite nanoparticles in sunflower alleviated salt toxicity through elevating chlorophyll and osmolyte contents, improving antioxidant potential and ROS detoxification (Ullah et al. 2022). Green nano-silica (GNS) ameliorated negative impacts of salinity on banana via increasing essential nutrients absorptions, antioxidants and osmoregulation compounds (Ding et al. 2022). Foliar spray of 1 mg per plant Mn_3O_4 NPs was found to successfully mitigate oxidative damages of salinity in cucumber through upregulating shikimate and phenylpropanoid products including catechin, resveratrol, quinic acid, chlorogenic acid, dihydroxycinnamic acid, benzenetriol, hydroxybenzoic acid and trihydroxybenzene (Lu et al. 2020). Nano-chitosan-encapsulated nano-silicon donor exhibited a great potential in equilibrating cellular redox homeostasis of wheat seedlings by balancing H_2O_2 content in the leaves and roots, thereby protecting lipid membrane, proteins and photosynthetic apparatus under salt stress (Hajihashemi and Kazemi 2022). According to Shafiq et al. (2019), fullerol (40 and 80 nmM) spray on salt stressed wheat plants resulted in improved photosynthetic activity, osmolytes accumulation and K^+ and Ca^{2+} contents, which contributed to enhancement of yield related parameters. Relevant transcriptomic findings revealed that the antioxidative defense related genes recovered to the normal level after CeO_2 NPs application, indicating that CeO_2 NPs demoted ROS generation via their intrinsic antioxidative enzyme properties (Liu et al. 2022). Guerriero et al. (2023) found that the expression of some stress-responsive genes reduced and several proteins related to cyto-protection against oxidative stress were enhanced in foliar sprayed of tomato plants by nano-porous quercetin-loaded

Table 5.2 Responses of various plant species to foliar application of nanomaterials under salinity

Plant species	Nanomaterials	Size and zeta potential	Dose	Effects	References
Moringa peregrina L	ZnO and Fe_3O_4 NPs	10–15 nm for ZnO NPs, 10–12 nm for Fe_3O_4 NPs	30, 60 and 90 mg/L	Augmented growth parameters, N, P, K^+, Mg^{2+}, Mn^{2+}, Fe, Zn contents, chlorophyll, carotenoids, proline, carbohydrates, and antioxidant potential, limited Na^+ and Cl^- uptake	Soliman et al. (2015)
Triticum aestivum L	Zn and Fe oxides NPs	Characterization data not reported	1.5 g/L	Enhanced CAT, POD and PPO activities, chlorophyll content, proline and soluble sugars and plant productivity	Babaei et al. (2017)
Solanum lycopersicum L	Cu NPs	Characterization data not reported	250 mg/L	Increased Na^+/K^+ ratio, phenols, vitamin C, glutathione contents, activities of PAL, APX, SOD, CAT and glutathione peroxidase	Pérez-Labrada et al. (2019)
Brassica napus L	ZnO NPs	10–30 nm, zeta potential not reported	20 and 80 mg/L	Induced expression of the *ARP* gene and Hill reaction, and deduced the expression of *MYC*, *MPK4*, and *SKRD2* genes and ion leakage at 20 mg/L ZnO NPs	Hezaveh et al. (2019)
Dracocephalum moldavica L	Fe_2O_3 NPs	20–40 nm, zeta potential not reported	30, 60, and 90 ppm	Improved leaf area, anthocyanin, total phenolic and flavonoid contents, and antioxidant defense including activity of guaiacol peroxidase, ascorbate peroxidase, catalase and glutathione reductase	Moradbeygi et al. (2020)

(continued)

Table 5.2 (continued)

Plant species	Nanomaterials	Size and zeta potential	Dose	Effects	References
Cucumis sativus L	Mn_3O_4 nanozymes	Characterization data not reported	1 and 5 mg $plant^{-1}$	Up-regulated shikimate and phenylpropanoid pathways and boosted endogenous antioxidant defenses	Lu et al. (2020)
Trachyspermum ammi L	Fe_2O_3 NPs	20–40 nm, zeta potential not reported	3 mM	Increased H^+-ATPase and H^+-PPase activities, endogenous SA, DPPH activity, and seed essential oil, lowered the Na^+ uptake and translocation to the shoot	Ghassemi-Golezani and Abdoli (2021)
Pennisetum glaucum L	Modified graphene NPs	Characterization data not reported	20 mg/L	Augmented protein content, chlorophylls a and b and carotenoids, and eventually plant growth and yield	Mahmoud and Abdelhameed (2021)
Phaseolus vulgaris L	Se NPs	Characterization data not reported	0.5, 1.0 and 1.5 mM	Improved photosynthesis, osmo-protectants, nutrient and Se contents, K^+/Na^+ ratio, enzyme activities, and cell integrity, plant growth and yield, and reduced oxidative stress	Rady et al. (2021)
Triticum aestivum L	TiO_2 NPs	30–95 nm, zeta potential not reported	20, 40, 60 and 80 mg/L	Enhanced osmotic and water potential, enzymatic and non-enzymatic antioxidants, soluble sugars and proteins, proline and amino acid content, and diminished malondialdehyde content at 20 and 40 mg/L	Mustafa et al. (2022)

(continued)

Table 5.2 (continued)

Plant species	Nanomaterials	Size and zeta potential	Dose	Effects	References
Triticum aestivum L	NC, NS, and NC-NS	Characterization data not reported	0.05% and 0.1% w/v	Elevated enzymatic and non-enzymatic antioxidants, and osmo-protectants	Hajihashemi and Kazemi (2022)
Solanum lycopersicum L	Si NPs	Characterization data not reported	100 mg/L	Increased nutrient content, carbohydrate metabolism, stomatal conductance, and SOD and CAT activities and plant growth	Alam et al. (2022)
Triticum aestivum L	ZnO NPs	Characterization data not reported	20, 50 and 80 mg/L	Enhanced leaf pigments, total soluble sugars and proline, nutrients uptake, antioxidant potential and finally plant length and weight	Lalarukh et al. (2022)
Zea may L	CeO_2 NPs	10 nm, 14.5 ± 1.1 mV	10, 20, and 50 mg/L	Recovered antioxidative related genes, down-regulated of genes related to lignin synthesis in the phenylpropanoid biosynthesis pathway, and inhibited ROS generation through their intrinsic antioxidative properties	Liu et al. (2022)
Cucumis sativus L	CeO_2 NPs	7.8 ± 1.6 nm, −31.0 ± 2.8 mV	0.1 mM	Eliminated ROS through enhancing the SOD, POD and CAT activities, and GSH and ASA contents in plant tissues	Chen et al. (2022)
Cymbopogon flexuosus L	Si NPs	7 nm, zeta potential not reported	150 mg/L	Minimized oxidative stress, and promoted photosynthetic performance and enzymatic antioxidant system, stomatal conductance, and plant growth	Mukarram et al. (2023)
Vitis vinifera L	CS-SA NCs	70–100 nm, zeta potential not reported	0.1 and 0.5 mM	Increased proline, hydrogen peroxide, malondialdehyde, total soluble protein, soluble carbohydrate, antioxidant potential and photochemical efficiency of photosystem II	Aazami et al. (2023)

CS-SA NCs: Chitosan based salicylic acid nanocomposite; NC: Nano-chitosan; NS: Nano-silicon; NC-NS: Nano-chitosan-encapsulated nano-silicon donor silicon-stabilized hybrid lipid nanoparticles under salinity. Mitigation of salt stress in *Melissa officinalis* plants by Se NPs is most likely attributed to the reduction of lipid peroxidation and oxidative stress through enhanced activity of antioxidant enzymes and transcript levels of phenylalanine ammonia lyase and rosmarinic acid synthase genes (Ghasemian et al. 2021). Similarly, foliar spray with CeO_2 NPs alleviated detrimental effects of salinity on *Dracocephalum moldavica* via improving agronomic traits, photosynthetic pigments and antioxidative capacity, leading to better performance of plants (Mohammadi et al. 2021).

5.5.3 Nano-treatment of Soil and Substrate

Nanomaterials may be directly applied to soil in the form of nano-fertilizers as well as nano-stimulants to mitigate negative impacts of salinity on plants and also to overcome nutrients deficiency induced by high Na^+ levels in saline soils. It can be also supplied as nutrient solution in hydroponic and other substrates. Root epidermis and exudates, casparian strip, transpiration rate and aggregation ability of nanoparticles can influence effective absorption of NPs in rhizosphere application (Wu and Li 2022). Regardless of substrates, nanoparticles can considerably improve growth and performance of plants under salinity (Table 5.3). Hojjat and Kamyab (2017) found that Ag NPs can ameliorate the negative effects of salinity on germination of fenugreek seeds through stimulating defense mechanisms. Addition of 90 μg/mL MWCNTs suspensions into Petri dishes during germination of salt stressed grape seeds promoted germination ability and defense system, and decreased MDA production and membrane damage of cells (Li et al. 2022). Application of graphene nanoparticles to substrate (5 g kg^{-1}) significantly enhanced antioxidant capacity and growth of alfalfa plants under salt and alkali stresses (Chen and Wang 2021). Individual and/or combined application of zinc, boron, silicon and zeolite nanoparticles to the soil noticeably improved water and nutrients status, proline and chlorophyll contents, photosynthesis rate, stomatal conductance, antioxidant enzymes activities, plant growth parameters and tuber yield of potatoes. Soil amendment with these nanoparticles also increased gibberellic acid and decreased abscisic acid contents (Mahmoud et al. 2019). Salt exposed (100 mM NaCl) rice plants hydroponically supplied with biocompatible poly (acrylic acid) coated cerium oxide nanoparticles showed a higher plant growth, chlorophyll content and grain yield. This treatment also stimulated the transcription of *nia2* (a gene encoding nitrate reductase) and regulated the dephosphorylation of its protein, leading to an enhancement in nitric oxide production and plant salt tolerance (Zhou et al. 2021). Treatments of sandy substrate with nitric oxide-releasing chitosan nanoparticles were resulted in a higher leaf S-nitrosothiols and chlorophyll contents, photosynthetic efficiency and growth of salt stressed maize plants, compared to untreated plants (Oliveira et al. 2016). According to Rossi et al. (2016), CeO_2-NPs application led to positive changes in physiological performance and growth of canola plants under salinity. Adding solution of three nanoparticles (Se NPs, Cu NPs and SiO_2 NPs) to the substrate caused

Table 5.3 The beneficial effects of soil and substrate treatment with nanomaterials on salt stressed plants

Plant species	Nanomaterials	Size and zeta potential	Dose	Effects	References
Brassica napus L	CeO_2 NPs	55.6 nm, −51.8 mV	200 and 1000 mg kg^{-1}	Enhanced chlorophyll a, net photosynthesis rate, proline contents and root and leaf weights	Rossi et al. (2016)
Zea may L	Snitroso-MSA-CS NPs	38.81 ± 18.10 nm, +17.7 ± 0.1 mV	50 or 100 mM	Improved chlorophyll content, maximum efficiency of PSII and plant growth	Oliveira et al. (2016)
Trigonella foenum-graecum L	Ag NPs	Characteristics were not reported	10, 20, 30 and 40 μg/mL	Increased germination percentage and speed index, seedling length and fresh and dry weights	Hojjat and Kamyab (2017)
Brassica napus L	CeO_2 NPs	52.6 nm, −51.8 mV	500 mg kg^{-1}	Augmented plant photosynthesis, shortened the apoplastic barriers in roots, altered Na^+ fluxes and transport to the shoot	Rossi et al. (2017)
Silybum marianum L	Graphene oxide	Characteristics were not reported	0.01, 0.05, 0.1%	Elevated chlorophyll content, maximum quantum yield of PSII, membrane stability index, osmolytes and plant growth	Safikhan et al. (2018)
Cucumis sativus L	Si NPs	10 nm, zeta potential not reported	100, 200, 300 and 400 mg kg^{-1}	Enhanced silicon, K^+ contents and K^+/Na^+ ratio in root, stem and leaf, regulated osmotic balance and stomatal opening, and diminished Na^+ uptake	Alsaeedi et al. (2019)
Phaseolus vulgaris L	TiO_2 NPs	Characteristics were not reported	100 mg kg^{-1}	Increased AMF colonization, molecular intensity ratio and relative density of paired inocula AMF Nest or chitin synthases gene and salt tolerance of plants	El-Gazzar et al. (2020)
Medicago sativa L	Graphene	20–70 nm, zeta potential not reported	5, 10 and 20 g kg^{-1}	Augmented weight and length of plants, chlorophyll content and antioxidant enzymes activities at 5 g kg^{-1}	Chen and Wang (2021)

(continued)

Table 5.3 (continued)

Plant species	Nanomaterials	Size and zeta potential	Dose	Effects	References
Carthamus tinctorius L	Biochar-based nanocomposites of Mg and Mn	Characteristics were not reported	25 g kg^{-1}	Enhanced soil pH and cation exchange capacity, nutrient bioavailability, chlorophyll content and water use efficiency, and reduced soil SAR, ESP and osmolyte accumulation	Farhangi-Abriz and Ghassemi-Golezani (2021)
Zea may L	Cu NPs	22.4–44.2 nm, zeta potential not reported	25, 50 and 100 mg kg^{-1}	Demoted cellular levels of reactive oxygen species and lipid peroxidation through stimulation of antioxidant enzymes, thereby improved root and shoot lengths and weights	Noman et al. (2021)
Anethum graveolens L	Biochar-based nanocomposites of Fe and Zn	Characteristics were not reported	30 g kg^{-1}	Increased soil pH and cation exchange capacity, improved absorption of K, Ca, Mg, Fe, and Zn, and reduced exchangeable sodium percentage of soil and sodium and chloride absorption rates by plants, and activities of root tonoplast H^+-pumps	Rahimzadeh and Ghassemi-Golezani (2022)
Solanum tuberosum L	K and Si NPs	Characteristics were not reported	20 and 55 ppm	Elevated leaf relative water content, stomatal conductance, chlorophyll content, photosynthesis rate, proline, and GA_3, plant growth and tuber yield, and diminished CAT, POD, and PPO activities and ABA	Mahmoud et al. (2022)
Trilicum aestivum L	ZnO NPs	53.79 nm, zeta potential not reported	0.06 and 0.12 g pot^{-1}	Improved chlorophylls a and b contents, plant height, shoot and spike lengths, root weight and grain yield at 0.12 g pot^{-1}	Adil et al. (2022)
Vicia faba L	CaP-NPs	6.41–11.3 nm, zeta potential not reported	16 mg/L	Enhanced proline and soluble sugars, antioxidant enzymes, and total phenolics, photosynthetic pigments, plant growth parameters, and reduced oxidative stress indicators	Nasrallah et al. (2022)

AMF: Arbuscular mycorrhizal fungi, CaP-NPs: Calcium phosphate nanoparticles, ESP: Exchangeable sodium percentage, SAR: Sodium adsorption ratio, Snitroso-MSA-CS NPs: Nitric oxide-releasing chitosan nanoparticles a remarkable increase in bioactive compounds in salt stressed bell pepper. Antioxidant potential of bell pepper were amplified by nanoparticles through increasing glutathione peroxidase, ascorbate peroxidase, catalase and phenylalanine ammonia lyase activities, and phenols, flavonoids, and glutathione contents, leading to better tolerance of salinity by plants (González-García et al. 2021).

The nanoparticles may be combined with different carbon materials before application. Some recent reports stated that enriching biochar with nutrients (biochar-based nanocomposites) can improve soil and biochar characteristics, maintain water content of plants tissues at an optimum level, increase the nutrients absorption rate, growth and salt tolerance of plants. Soil amendment with biochar-based magnesium and manganese nanocomposites increased pH and cation exchange capacity of soil and water and essential nutrients uptakes by plants. High sodium sorption capacity of biochar-based nanocomposites resulted in decreasing sodium uptake and damages caused by salt stress on plant performance (Farhangi-Abriz and Ghassemi-Golezani 2021). Application of biochar-based nanocomposites of iron and zinc led to a higher production of monoterpenes and considerable DPPH-inhibitory effect of dill essential oil under salt stress (Ghassemi-Golezani and Rahimzadeh 2022). It was also found that simultaneous application of biochar with nano-potassium and nano-silicon augmented beneficial effects of biochar on salt stressed potato plants. Supplying nanoparticles with irrigation water to the soil improved nutrient and hormonal statuses, antioxidant potential, photosynthesis and osmo-protectants, leading to higher tuber yield and quality (Mahmoud et al. 2022).

5.6 Conclusions and Future Prospects

Plant production is suffering pivotal losses due to some environmental challenges such as salinity, leading to oxidative damage and ultimately yield losses. Nanomaterials at appropriate doses have positive roles in agriculture, particularly in defending against salt toxicity and improving plant productivity. The NPs with special physicochemical characteristics can effectively regulate morphological, physiological, biochemical and molecular processes in stressed plants and subsequently amplify plant immunity and growth. Therefore, it is highly likely that nano-enabled strategies such as seed nano-priming and coating, foliar spray and soil and substrate treatment will become a critical and sustainable tool to improve plant performance under salt stress. Future investigation on plant mechanistic responses to application of novel NPs by appropriate methods in various environmental conditions is highly encouraged.

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Chapter 6
Exploring the Critical Function and Molecular Mechanism of WRKY Transcription Factor Family in Regulating Plant Response Under Abiotic Stress Conditions

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Abstract Environmental stresses adversely affect plant growth and development. However, the signaling pathways and metabolic response mechanisms may differ, and most types of abiotic stresses affect the cellular redox homeostasis ultimately affecting the yield performance of the plant. In response, plants evolve several regulatory proteins that act as central regulators of abiotic stress responses involved in temperature, salinity, and oxidative stresses. Plants rapidly respond through complex genetic and biochemical networks primarily by transducing signals to stress-related transcription factors (TFs) such as MYB, bZIP, AP2/EREBP, NAC, and WRKY of which WRKY is the most extensively studied TF family in different plant stress responses. The WRKY gene family encodes a large group of transcription factors (TFs) that play essential roles in diverse stress responses and developmental processes. Here, we summarize the regulatory mechanisms of WRKY transcription factors and their responses to different abiotic stress conditions. We also discuss the future perspectives of WRKY transcription factor research.

Keywords Environmental stresses · Developmental processes · Signaling pathways · Transcription factors

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_6

6.1 Introduction

Being sessile in nature plants continuously encounter different abiotic stress factors such as drought, salinity, solar UV-B, nutrient deficiency, freezing, scorching, and waterlogging (Chen et al. 2012). These factors can affect growth at different developmental stages of plants and often they are associated with one another, potentially restricting plant growth, and development or even affecting species distribution in a particular area (Chen et al. 2012). To counteract these adverse effects, plants have evolved several intricate mechanisms at multiple cellular levels which may increase the tolerance against these adverse conditions. Moreover, recognition of stress signals and regulation of stress-related genes to activate adaptive responses are the crucial steps leading to plant stress tolerance (Chinnusamy et al. 2004). The temporal and spatial regulation of the stress-related genes occurs mainly at the transcriptional level.

Several transcription factors (TFs) such as MYB, NAC, bZIP, AP2, and WRKY play important roles in the regulation of plant response via regulating stress-responsive gene expression. It has been observed that the MYB family transcription factors are involved in secondary metabolite biosynthesis, cell cycle regulation, and abiotic stress response in plants (Chen et al. 2014). In *Arabidopsis thaliana,* AtMYB11, AtMYB12, and AtMYB111 are independently activating the flavonol synthase (FLS), flavanone-3-hydroxylase (F3H), chalcone isomerase (CHI), and chalcone synthase (CHS) which may increase plant tolerance via production of different types of flavonols (Pandeyet al. 2012; Misraet al. 2010). Furthermore, in *Malusdomestica,* MdMYB31, MdMYBA, and MdMYB1 can regulate anthocyanin biosynthesis (Cao et al. 2020). It was observed that overexpression of stress-responsive NAC (SNAC) showed improved drought tolerance in rice (Nakashima et al. 2012). In transgenic rice, overexpression of *OsNAC2/6*, and *OsNAC10* genes showed improved drought and salt tolerance (Nakashima et al. 2009; Jeong et al. 2010). Apart from these, the bZIP transcription factors have diverse functions such as GmbZIP1 being involved in the enhancement of salt tolerance in transgenic soybean plants (Gao et al. 2011). From various studies, it has been observed that under cold stress conditions GmbZIP44, GmbZIP62, and GmbZIP78 enhance the synthesis of proline to increase the osmotic tolerance via activating the expression of downstream genesincluding *ERF5*, *KIN1,* and *COR78* (Liao et al. 2008). Another transcription factor family, AP2/ERF transcription factors play an important role in maintaining plant growth and development and also regulate abiotic stress responses (Xu et al. 2011). Interestingly, the WRKY transcription factor family is an important transcriptional regulator of biotic and abiotic stress-responsive genes, and they are evolutionarily well-conserved from algae to flowering plants (Bakshi and Oelmuller 2014). The plant-specific WRKY TFs are one of the largest TF families and they are involved in diverse plant processes, including growth, development, and stress signaling through auto and cross-regulation with other stress-responsive genes and transcription factors (Bakshi and Oelmuller 2014). Previous studies have suggested that the WRKY TFs participated in various biotic-stress responses via the regulation of various developmental and physiological processes (Chen et al. 2012). Recently some researchers are focused on identifying the function of WRKY TFs in abiotic stress responses. In this chapter, we have summarized the structural characteristics and classification of WRKY TFs and then we have described the molecular function of WRKY TFs in abiotic stresses.

6.2 Transcription Factors Involved in Abiotic Stress Response

Under abiotic stress conditions, plants activate various signaling pathways that lead to changes in the expression of stress-responsive genes. Transcription factors are key players in these signaling pathways, as they can activate or repress the expression of genes involved in multiple stress responses (Fig. 6.1) (Shinozaki and Yamaguchi-Shinozaki 2007).Transcription factors can interact with other signaling components such as protein kinases and phosphatases to modulate the activity of downstream targets, and they can also form complexes with other transcription factors to coordinate the expression of multiple stress-responsive genes (Fig. 6.1) (Nakashima et al. 2014). Transcription factors can regulate the expression of genes involved in the biosynthesis of osmoprotectants such as proline and glycine betaine, which help plants to maintain cellular water balance under drought and salinity stress. Furthermore, other transcription factors can regulate the expression of genes involved in the synthesis of stress-related hormones such as abscisic acid (ABA), which plays a crucial role in the regulation of stomatal closure and the induction of stress-responsive genes (De Zelicourt et al. 2016). Several transcription factor families play important roles in the response of plants to abiotic stresses (Golldacket al. 2011).

6.3 MYB Transcription Factors

MYB proteins contain one or more MYB domains, which consist of about 50 amino acids arranged in three alpha helices. The MYB domain contains a DNA-binding motif that recognizes specific sequences in the promoter region of target genes and activates their expression (Dubos et al. 2010). The MYB family of transcription factors is characterized by the presence of one or more MYB DNA-binding domains, which typically consist of three imperfectly conserved helix-turn-helix motifs. The DNA-binding domains of MYB transcription factors are involved in recognizing and binding to specific DNA sequences, often with high affinity and specificity. There are three main types of MYB DNA-binding domains based on their structure: R1, R2, and R3 (Cao et al. 2020). Different MYB transcription factors can contain one or more of these DNA-binding domains in various combinations, which can affect their specificity and affinity for different DNA sequences. In plants, R2R3-MYB transcription factors play a crucial role in regulating responses to various abiotic

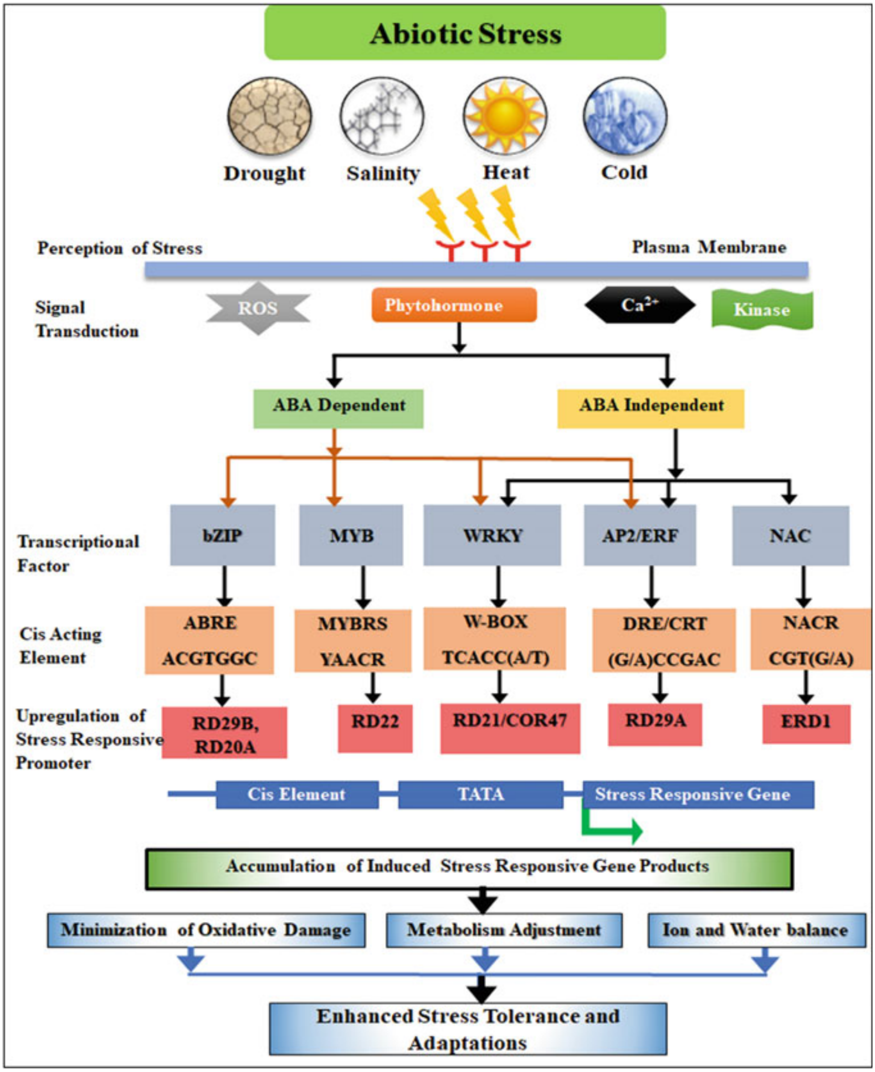

Fig. 6.1 Schematic representation showing the complexity of abiotic stress signaling pathways in plants: from signal perception to stress response. Transcription factors play a central role in the regulation of abiotic stress response in plants

stresses, such as drought, salinity, and extreme temperatures (Stracke et al. 2001). These transcription factors bind to specific DNA sequences in the promoter regions of stress-responsive genes, activating or repressing their expression. Additionally, some MYB transcription factors contain other functional domains outside of the DNA-binding domains, which can affect their overall activity and function. For example, in *Arabidopsis thaliana*, the R2R3-MYB transcription factor MYB44 is involved in regulating the response to drought stress. MYB44 promotes the expression of genes involved in water uptake and retention, such as aquaporins and dehydrins, while repressing genes involved in growth and development, such as cell cycle regulators (Rusconi et al. 2013). Similarly, the R2R3-MYB transcription factor MYB96 is involved in the response to salt stress. MYB96 activates the expression of genes involved in ion homeostasis and detoxification, such as sodium/proton antiporters and glutathione S-transferases (Cheng et al. 2013).

6.4 The bZIP Family of Transcription Factors

The bZIP transcription factors are a family of transcription factors that play important roles in regulating the expression of stress-responsive genes involved in tolerance to various abiotic stresses, including drought, salinity, and cold stress (Wang et al. 2018). These TFs have a conserved basic region that binds to DNA and a leucine zipper motif that facilitates protein dimerization. The leucine zipper motif consists of a repeated sequence of leucine residues that form a coiled-coil structure, allowing bZIP TFs to dimerize and bind to specific DNA sequences as a heterodimer (Wang et al. 2022).

6.5 AP2/ERF Transcription Factors

AP2/ERF transcription factors are another transcription factor family that plays important roles in the response of plants to abiotic stress (Nakano et al. 2006). AP2/ERF proteins include DREB that bind DRE/CRT cis-acting elements in the promoter regions of target genes and regulate the expression of stress-responsive genes involved in tolerance to various abiotic stresses, including drought, salt, and cold stress (Lata and Prasad 2011). There are two subgroups of AP2/ERF transcription factors such as DREB1 And DREB2 that are involved in cold and heat shock response, respectively. Moreover, the AP2/ERF transcription factors are involved in various signaling pathways that are activated by stress, including those that involve ABA, ethylene, and jasmonic acid. They regulate the expression of genes involved in stress tolerance, such as those involved in osmotic adjustment, ion transport, and detoxification of reactive oxygen species (Mizoi et al. 2012; Licausi et al. 2013).

6.6 NAC (NAM, ATAF1/2, and CUC2) Transcription Factors

These TFs have a highly conserved N-terminal DNA-binding domain (NAC domain) that binds to DNA and a variable C-terminal transcriptional activation domain. The NAC domain consists of five alpha helices that form a structure resembling a winged-helix-like DNA-binding domain. The NAC domain can recognize a range of DNA sequences, and NAC TFs often function as dimers (Puranik et al. 2012). In *Arabidopsis thaliana*, the NAC transcription factor AtNAC019 is involved in regulating the expression of genes involved in drought stress tolerance by modulating the levels of ABA and regulating the expression of genes involved in osmotic adjustment (Nakashima et al. 2009).

6.7 WRKY Transcription Factors

WRKY transcription factors are a family of transcription factors that are involved in the regulation of various biological processes in plants, including the response to biotic and abiotic stresses (Chen et al. 2019). The WRKY family is named after the conserved WRKY domain, which is a DNA-binding domain that recognizes a specific motif in the promoter regions of target genes. Under abiotic stress conditions such as drought and salinity, WRKY transcription factors can activate or repress the expression of genes involved in the stress tolerance and signal transduction pathways (Rushton et al. 2010). WRKY transcription factors can also interact with other transcription factors and signaling molecules to coordinate the expression of stress-responsive genes (Eulgem et al. 2000).

6.8 Structural Organization of WRKY Transcription Factors

WRKY is one of the important and major transcription factor families in plants. Recently, several members of the WRKY TFs family have been identified in various plant species and they are well distributed throughout the plant kingdom, including 104 in *Populus* (He et al. 2012), 102 in *Oryza sativa*, 83 in *Pinus monticola*, 81 in *Solanum lycopersicum*, 74 in *Arabidopsis thaliana*, 55 in *Cucumis sativus*, 37 in *Physcomitrella patens* (Li et al. 2020a, b), 197 in *Glycine max* (Chen et al. 2012).WRKY TFs have highly conserved approximately 60 amino acids long four stranded β-sheet with the zinc coordinating Cys/His residues forming a zinc-binding pocket. The plant-specific WRKY DNA binding domain (DBD) is present at the N-terminal and zinc finger motifs at the C-terminal (Phukan et al. 2016; Li et al. 2020a, b). The N-terminal DNA binding domain of WRKY TFs contains highly conserved seven peptide WRKYGQK motif, which forms the core region of the DBD (Schmutz et al. 2010). From previous studies, it has been observed that part of a four-stranded β-sheet enters the major groove of DNA that was called a β-wedge. This sheet is almost perpendicular to the DNA helical axis. As initially predicted, amino acids in the conserved WRKYGQK conserved motif interact with the W-Box DNA sequences mainly through extensive apolar contacts with thymine methyl groups (Yamasaki et al. 2012). However, these conserved regions have some variations such as WRKYGQK, WRKYGKK, WSKYGQK, WRKYGMK, WKRYGQK, WVKYGQK, WKKYGQK (Huang et al. 2012; Li et al. 2020a, b). The C-terminal Zinc finger motifs are two types such as C_2-H_2 (C-$X_{4\text{-}5}$-C-$X_{22\text{-}23}$-H–X-H) and C_2-HC (C-X_7-C-X_{23}-H–X-C) (Fig. 6.2) (Jiang et al. 2017). It was observed that both the N-terminal DBD sequence and the C-terminal Zn-finger motif are essential for WRKY TFs binding to W-box (C/T)TGAC(T/G) in the promoter of the target gene (Yamasaki et al. 2005).

Based on the number of WRKY domains and types of Zinc finger motifs, WRKY TFs are classified into three major groups (Eulgem et al. 2000; Li et al. 2010). The group-I WRKY TFs have two WRKY domains and one C_2H_2 zinc finger. Meanwhile, groupII and groupIII have only one WRKY DBD, but in the case of group-II WRKY

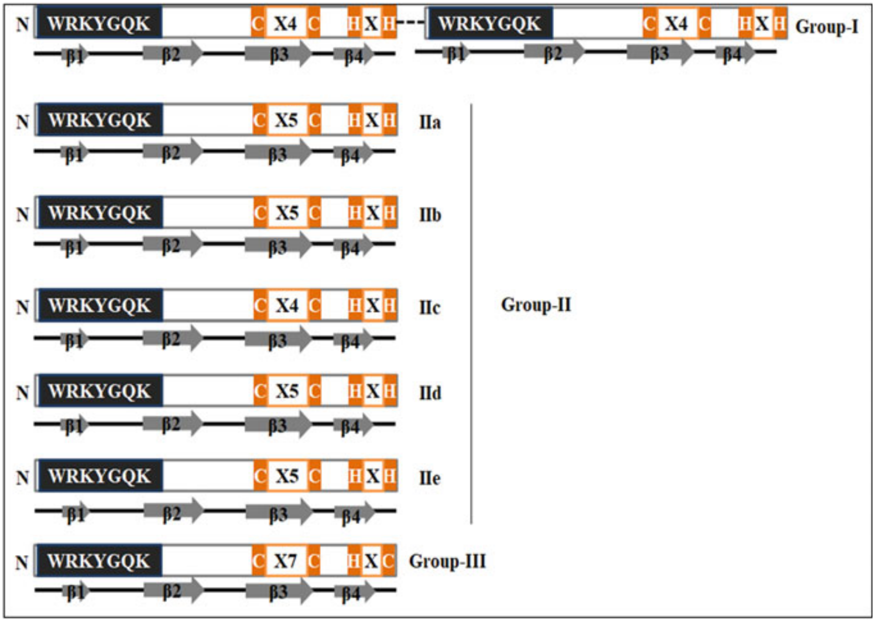

Fig. 6.2 Structural organization of WRKY TFs. The WRKY TFs are classified into three major groups. The N-terminal region have a conserved WRKYGQK motif and the C-terminal have a zinc-finger motif. The lower grey colored arrows indicate four β-sheets. The group-I WRKY TFs contain two WRKY domains and the group-II and III both have only one WRKY domain. However, the group-II WRKY TFs contain C_2H_2 and the group-III WRKY TFs contain C_2-HC zinc finger motif. Here 'X' indicates any amino acid

TFs contain different C_2H_2 zinc fingers, and in group-III WRKY TFs contain C_2-HC zinc finger motifs (Rushton et al. 2010; Phukan et al. 2016). According to the phylogenetic analysis, conserved domain structure, and intron position Zhang and Wang classified the WRKY TFs into five groups, which are group-I, IIa + IIb, IIc, IId + IIe and III (Fig. 6.2) (Zhang and Wang 2005). Based on the insertion position of the intron WRKY TFs are again divided into two categories such as one is an R-type intron (WRKY IIa and IIb subtypes) and another is a V-type intron (WRKY I, IIc, IId, and III subtypes) (Zhang and Wang 2005). Most of the WRKY TFs also have nuclear localization signal (NLS), leucine zippers, serine/threonine-rich region, a proline-rich region, a glutamine-rich region, kinase domains, and TIR-NBS-LRRs. Due to the presence of this structural diversity in the WRKY proteins, they can play multiple functions in the regulation of gene expressions (Chen et al. 2012).

6.9 The Function and Mechanism of WRKY TF in the Regulation of Abiotic Stress Response

The WRKY transcription factors play multiple roles in the regulation of different biotic and abiotic stress-responsive genes (Dong et al. 2003). The molecular mechanism of WRKY TF in biotic stress defense response is already well established. From various studies, it was observed that overexpression of WRKY TFs provides improved stress tolerance against various biotic stress factors (Tsuneaki et al. 2002; Kim et al. 2008; Xing et al. 2008). In *Capsicum annuum* CaWRKY27 positively modulates the resistance mechanism in response to *Ralstonia solanacearum* infection via modulation of salicylic acid (SA) expression. However, in *Nicotiana tabacum,* this resistance developed through jasmonic acid (JA), and ethylene (ET) mediated signaling (Dang et al. 2014). Moreover, in *Arabidopsis*, AtWRKY8 regulates the susceptibility against *Pseudomonas syringae* and *Botrytis cinerea* (Chen et al. 2010a, b). In rice, overexpression of WRKY22 showed enhanced resistance to *Pyricularia oryzae* (Cheng and Wang 2014).

It was observed that WRKY TFs also play crucial roles in different abiotic stress responses including drought, salinity, heavy metals, solar UV-B, nutrient deficiency, freezing, and scorching. Li et al. reported that overexpression of WRKY39, WRKY25, and WRKY26 resulted in improved thermotolerance in plants (Li et al. 2011). In *Dendranthema grandiflorum*, DgWRKY1 or DgWRKY3is involved in improving salt tolerance in tobacco (Jiang et al. 2017). Moreover, transgenic rice overexpressing OsWRKY45 andOsWRKY72 showed improved tolerance to drought and salt stress (Qiu and Yu 2009; Song et al. 2010). WRKY TFs also play an important role in mineral deficiency like in *Arabidopsis thaliana* induced strongly during Pi deficiency (Devaiah et al. 2007).

6.10 Drought Stress

Drought is one of the most severe environmental stress conditions which affects plant growth and productivity in tropical countries. WRKY transcription factor was found to be an important candidate involved in the regulation of drought resistance of plants. For example, in *Arabidopsis thaliana*, the WRKY transcription factor gene *WRKY25* has been shown to regulate drought tolerance by regulating the expression of a set of genes involved in abscisic acid (ABA) signaling and stress-responsive pathways (Doll et al. 2020). Moreover, another *Arabidopsis* WRKY transcription factor, WRKY46, has been shown to play a role in the regulation of stomatal closure under drought stress conditions (Jiang et al. 2014).

In rice, the WRKY transcription factor gene *OsWRKY11* is involved in developing drought tolerance by regulating the expression of genes encoding proteins involved in ABA signaling, antioxidant defense, and stress-responsive pathways. Similarly, the WRKY transcription factor OsWRKY45 has been shown to regulate the expression of genes involved in ABA signaling, as well as genes encoding proteins involved in reactive oxygen species (ROS) detoxification and stress-responsive pathways (Raineri et al. 2015). In *Glycine max,* GmWRKY21 plays a positive role in developing drought tolerance. Overexpression of *GmWRKY21* showed improved drought tolerance and yield under drought-stress conditions (Han et al. 2022). In grapevine and wheat overexpression of VvWRKY52 (*Vitis vinifera*), and BdWRKY36 (*Brachypodium distachyon*) resulted in improved drought tolerance and yield under drought stress conditions respectively. In wheat, TaWRKY44 acts as a positive regulator of drought stress as they, directly and indirectly, activate the cellular antioxidant machinery (Ma et al. 2017).

6.11 Salinity Stress

High salt concentration in the soil leads to osmotic stress in plants. During salt stress, the activity of antioxidant enzymes (superoxide dismutase, catalase, peroxidase) is reduced thus accumulation of hydrogen peroxide (H_2O_2) and malondialdehyde (MDH) increases (Jiang et al. 2017). Under salinity stress, WRKY transcription factors have been shown to activate the expression of genes involved in ion transport, osmoprotection, and stress signaling (Li et al. 2011). For example, some WRKY transcription factors have been shown to activate the expression of genes encoding transporters that enable the plant to take up and accumulate ions such as potassium, which is important for maintaining ion homeostasis under salt stress. Other WRKY transcription factors have been shown to activate genes involved in the biosynthesis of osmoprotectants such as proline and glycine betaine, which help to prevent water loss and stabilize proteins under salt stress (Chen et al. 2012). In *Arabidopsis* overexpression of either AtWRKY25 or AtWRKY33 enhances salt tolerance. TaWRKY10 in *Triticum aestivum* plays a major role during salt stress by regulating osmotic balance. In transgenic rice overexpression of OsWRKY45 and OsWRKY72 resulted in increased salt tolerance (Song et al. 2010). Furthermore, *BcWRKY46* (*Brassica rapa*), *HvWRKY38*(*Hordeum vulgare*), and *ZmWRKY23* (*Zeamays*) genes were constitutively expressed in *Arabidopsis thaliana* plants, which led to increased resistance to high salinity (Wang et al. 2013).

6.12 Heavy Metal Stress

Modern agricultural practices, rapid industrialization, mining, and several other factors result in increased heavy metal contamination in soil and water. Agricultural fields contaminated with heavy metals are responsible for the reduction in crop yield. Heavy metals like cadmium (Cd), chromium (Cr), lead (Pb), aluminum (Al), and mercury (Hg) are toxic to plants even in low concentrations. (Singh et al. 2016). Plants employ different strategies to avoid the negative impact of heavy metal toxicity (Singh et al. 2016). Several transcription factors including WRKY were found to be upregulated in heavy metal stress response. It was observed that the expression of WRKY transcription factors is upregulated in rice under cd stress (Guo et al. 2022). Moreover, maize ZmWRKY4 helps to upregulate the expression of *ZmSOD4* and *ZmAPX* under Cd stress leading to the enhancement of antioxidant enzyme activities (Hong et al. 2017). Overexpression of PyWRKY75 in poplar showed improved Cd tolerance in transgenic plants via increasing chlorophyll content and antioxidant enzymes like superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase (Wu et al. 2022). It was observed that GmWRKY142 induces the expression of the Cd tolerance gene *AtCDT1*, *GmCDT1-1*, and *GmCDT1-2* by directly binding to the W-box region of their promoters (Cai et al. 2020). Plants overexpressing *WRKY13* showed enhanced Cd tolerance and reduced cd accumulation. It was found that in *Arabidopsis* WRKY13 directly binds to the promoter region of *PDR8* (an ABC transporter) and regulates cd tolerance (Sheng et al. 2019).

Furthermore, it was observed that WRKY transcription factors are induced by aluminium (Al) stress. Soybean GmWRKY81 expression was found to be induced and upregulated under Al stress. Overexpression of soybean GmWRKY3 resulted in enhanced Al-tolerance (Shu et al. 2022). Another WRKY family member of *Arabidopsis* AtWRKY47 was found to be involved in the regulation of root growth via modifying the expression of genes associated with cell wall formation including EXTENSIN-LIKE PROTEIN (*ELP*) and XYLOGLUCANENDO-TRANSGLUCOSYLASE HYDROLASES 17 (*XTH17*) which gives Al tolerance. Moreover, overexpression of WRKY47 enhances the Al tolerance in plants (Li et al. 2020a, b).

6.13 UV-B Stress

Depletion of the ozone layer resulted in increasing the amount of UV-B (280–320 nm) irradiation reaching the earth's surface which is potentially harmful to live organisms (Wang et al. 2007b, a). UV-B irradiation can induce different physiological and morphological changes such as short internodes, reduced plant growth, and thickened wax deposition on the surface of leaves (Wang et al. 2007b, a; Chen et al. 2012). It was observed that WRKY TFs play important roles in developing UV-B tolerance in plants (Wang et al. 2007b, a; Zhao et al. 2010). In rice, OsWRKY89 was strongly induced upon UV-B irradiation (Wang et al. 2007b, a). Overexpression of OsWRKY89 showed increased tolerance to UV-B through enhancing the wax and lignin deposition, synthesis of secondary metabolites, and also changing the redox status of the organism. Furthermore, in *Arabidopsis thaliana,* the expression of WRKY36 mRNA was found to be elevated in response to UV-B (Yang et al. 2018). Following UV-B irradiation nuclear UVR8 interacts with WRKY36 and inhibits it from binding to the promoter sequence of *HY5*. As a result, the expression of *HY5*increased leading to the inhibition of hypocotyl elongation (Liang et al. 2018).

6.14 Nutrient Deficiency Stress

Plants require multiple nutrient elements for the maintenance of their normal growth and development. In the absence of any one of the necessary elements, plants showed various developmental abnormalities which ultimately results in yield loss (Datnoff et al. 2007; Chen et al. 2012). Furthermore, it was observed that plants growing under nutrient-deficient conditions are more susceptible to various environmental stresses (Hajiboland 2012). Various reports have mentioned that WRKY transcription factors play a crucial role in nutrient-deficient conditions (Chen et al. 2012; Dai et al. 2016). Phosphorus is an essential macronutrient present in the phospholipids, nucleic acids, and the energy molecule ATP. WRKY transcription factor family plays an important role in Pi starvation (Dai et al. 2016; Rouached et al. 2010; Richardson et al. 2009). The WRKY member AtWRKY75 was found to be involved in the nutrient (phosphate) deficiency response. During Pi deficiency, AtWRKY75 was found to be induced in plants (Devaiah et al. 2007). Moreover, it was observed that AtWRKY6 was also found to be involved in the regulation of phosphate deficiency response. AtWRKY6 negatively regulates *Arabidopsis* PHOSPHATE (PHO1) expression by binding to the W-box position of the AtPHO1 promoter region. It was observed that transgenic *Arabidopsis* overexpressing AtWRKY6 and *Arabidopsis* mutant *atpho1* showed similar phenotypes and were sensitive to low phosphate stress (Chen et al. 2010a, b). AtWRKY42, an interacting partner of AtWRKY6 also binds to the W-box position of the *AtPHO1* promoter and inhibits the *AtPHO1* expression (Chen et al. 2010a, b). Another WRKY family gene of rice, *OsWRKY74* is mainly expressed in the nucleus of the roots and leaves. OsWRKY74 is involved in the modulation of root architecture and activation of Pi-starvation-induced genes. Transgenic rice overexpressing OsWRKY74 shows enhanced tolerance to pi starvation (Dai et al. 2016). WRKY TFs also play an essential role in Iron (Fe) deficient conditions. Fe is a micronutrient essential for several metabolic reactions in plants. Moreover, the excess amount of soluble Fe^{2+}shows a phytotoxic effect. Among the WRKY family members of rice OsWRKY55-like, OsWRKY46, OsWRKY64, and OsWRKY113 are upregulated in an iron-sensitive genotype *BR-IRGA409* under excess iron condition resulting in a repression of the root elongation (Viana et al. 2017). Furthermore, OsWRKY74 also play an essential role in iron (Fe) deficiency condition (Dai et al. 2016). Under Fe deficient condition, WRKY46 regulates root-to-shoot Fe translocation via modulating the expression of VACUOLAR IRON TRANSPORTER–LIKE 1 (VITL1) (Yan et al. 2016). Apart from these, WRKY TFs are also involved in the regulation of genes involved in sugar signaling (Wang et al. 2007b, a; Hammargren et al. 2008; Mangelsen et al. 2010). It was observed that AtWRKY4 and AtWRKY34 regulate the expression of *AtNDPK3a* with the fluctuation of glucose and sucrose levels (Hammargren et al. 2008). Moreover, the AtWRKY45 and AtWRKY65 were found to be involved in the regulation of the expression of genes associated with carbon starvation (Contento et al. 2004).

6.15 Temperature Stress

High and low-temperature stress both can reduce crop yield (Chen et al. 2012). In presence of high-temperature stress, plants showed various morphological and physiological changes like leaf senescence, root growth inhibition, and fruit discoloration (Goraya et al. 2017). WRKY TFs also play an important role in these stress responses. For example, In *Arabidopsis thaliana* overexpressing AtWRKY25 and AtWRKY26 showed enhanced resistance to heat stress (Li et al. 2011). In *Triticum aestivum* transgenic line of TaWRKY33 exhibit enhanced tolerance to heat stress (He et al. 2016). Moreover, in rice OsWRKY11 can bind to the promoter of *HSP101* resulting in increased tolerance to heat stress (Wu et al. 2009). Apart from these, overexpression of AtWRKY39 showed plants with more heat sensitivity (Park et al. 2005).

Low temperature also acts as a negative factor in agricultural crop production. In *Vitis vinifera* VvWRKY24 is involved in the induction of cold stress-responsive genes (Wang et al. 2014). In the case of *Arabidopsis thaliana*, AtWRKY34 expression negatively regulates cold sensitivity (Zou et al. 2010). In transgenic *Arabidopsis*, overexpression of GmWRKY21 showed improved tolerance to cold stress conditions than wild-type plants (Zhou et al. 2008).

6.16 Major Signaling Pathways Associated with the Function of WRKY TF Under Abiotic Stress

Plants have evolved various strategies via which they can modulate or adjust cellular functions according to various environmental and internal signals. WRKY family members act through diverse interconnecting networks to regulate different gene expressions in normal and stressed (both biotic and abiotic) conditions (Banerjee and Roychoudhury 2015). WRKY TFs bind with the cis-acting W-box element to activate or inhibit the transcription of the target gene. WRKY TFs regulate stress responses either by autoregulation or cross-regulation. The process of self or autoregulation is associated with the binding of a WRKY protein to a W-BOX-containing promoter and regulates the expression of stress-related genes. In contrast to this, in cross-regulation, the expression of stress-related genes is regulated by another WRKY TF (Rushton et al. 2012). In *Capsicum frutescens*, CfWRKY6 can activate *CfWRKY40*which results in increased high temperature and humidity tolerance (Li et al. 2020a, b). In *Arabidopsis,* many WRKY TFs such as AtWRKY18, AtWRKY30, AtWRKY40, AtWRKY53, AtWRKY54, AtWRKY60, and AtWRKY70 were found to be interacted with themselves and with each other under stress conditions (Besseau et al. 2012; Banerjee and Roychoudhury 2015). WRKY transcription factors (TFs) play a crucial role in various signaling pathways such as phytohormone signal transduction pathways, ROS signaling, and Mitogen-Activated Protein Kinases (MAPK) cascade in response to abiotic stress.

6.17 Phytohormone Signaling

From various studies, it has been observed that a single transcription factor (TF) may participate in different signaling pathways induced by various biotic and abiotic stress factors. Recent studies on the WRKY TF family in *Arabidopsis* revealed the crucial function of three structurally related proteins such as AtWRKY18, AtWRKY40, and AtWRKY60 in three different phytohormone-mediated signaling pathways of salicylic acid (SA), jasmonic acid (JA), and abscisic acid (ABA) (Chen et al. 2010a, b). Apart from these, two closely related WRKY TFs such as WRKY25 and WRKY33 were found to be involved in both biotic (*Pseudomonas syringae*), and abiotic (salt, cold, and heat) stresses (Zheng et al. 2006, 2007; Li et al. 2009, 2011). It was observed that these two transcription factors act as positive regulators in salt and heat stress responses. WRKY TFs play a major role in regulating plant defense via SA-mediated and also ABA-mediated signaling pathways (Banerjee and Roychoudhury 2015). In *Cucumis sativus,* CsWRKY46 was found to be upregulated during cold stress and in the presence of exogenous ABA (Jiang et al. 2017). Moreover, it was observed that CsWRKY46 is expressed in the nucleus and binds the W-Box region of the promoter of *ABI5* (Zhang et al. 2016).

Interestingly, in cotton GhWRKY91 directly binds with the W-BOX containing the promoter of *GhWRKY17* and regulate the expression under drought stress condition. ABA plays a crucial role as a stress-responsive hormone in stress-signaling pathways (Vishwakarma et al. 2017). Under different stress conditions, the biosynthesis of ABA was enhanced which in turn activates SNF1-related kinases (SnRK2) (Ilyas et al. 2020; Kim et al. 2010; Yu et al. 2016). Recently several studies have revealed that WRKY TFs act as positive regulators of ABA-induced abiotic stress responses such as drought, salt, and heat. It was observed that overexpression of GhWRKY41 showed improved drought and salt tolerance in *Nicotiana benthamiana* by an ABA-dependent signaling pathway. Moreover, overexpression of cotton GhWRKY5 showed enhanced salt tolerance in transgenic *Arabidopsis* via the regulation of jasmonic acid and salicylic acid pathways (Guo et al. 2021). Furthermore, it was observed that the expression pattern of many cotton WRKY TFs such as GhWRKY5, GhWRKY7, GhWRKY27, GhWRKY31, GhWRKY56, and GhWRKY59 was upregulated by one or more treatments of SA, JA, ethylene, ABA, and salt (Dou et al. 2014).

6.18 ROS Signaling

From previous studies, it has been revealed that various stresses are responsible for the enhancement of the production of reactive oxygen species (ROS) in mitochondria, and some of the reactive oxygen species such as H_2O_2also act as signal transduction molecules promoting stress tolerance in plants. Several important enzymes of the zinc-finger protein family such as ascorbate peroxidase (APX), and NADPH oxidases play a crucial role in ROS signaling (Dvořák et al. 2021). Moreover, in mutants of a zinc-finger protein gene, *atzat12* mutant plants showed reduced expression of AtWRKY25 after H_2O_2 treatment indicating obligatory dependency of AtWRKY25 on AtZAT12 (Rizhsky et al. 2004). In *Arabidopsis*, the expression AtWRKY30, AtWRKY48, AtWRKY3, AtWRKY22, and AtWRKY53 were significantly induced by H_2O_2 treatment (Vanderauwera et al. 2005; Chen et al. 2010a, b). Another WRKY TF, WRKY70 was found to be constitutively expressed in *atapx1* mutant plants suggesting its positive role in ROS signaling (Ciftci-Yilmaz et al. 2007). Moreover, it was observed that under light stress the expression of several WRKY TFs (AtWRKY18, AtWRKY25, AtWRKY33, AtWRKY40, AtWRKY46, AtWRKY54, and AtWRKY60) are also enhanced in *atapx1* mutant plants (Davletova et al. 2005). Cotton plants overexpressing GhWRKY6 showed increased SOD and POD activity under salt and oxidative stress (Ullah et al. 2018). It was observed that Tobacco plants overexpressing *TaWRKY10* of wheat showed reduced MDA levels and thereby resist the damage induced by heat stress. Moreover, Babitha et al. reported that AtWRKY28 is involved in conferring resistance to ROS produced by oxidative stress in *Arabidopsis* seedlings (Babitha et al. 2013). However, it was observed that overexpression of GhWRKY17 resulted in reduced levels of SOD, POD, APX, and CAT content under drought stress suggesting a negative role of GhWRKY17 in the production of antioxidant enzymes (Yan et al. 2014). Apart from these, OsWRKY42 also acts as a negative regulator in the ROS signaling pathway, and overexpression of WRKY42 results in a higher accumulation of ROS (Han et al. 2014).

6.19 MAPK Signaling

MAPK signaling pathway acts as a bridge between upstream receptors and downstream TFs through multiple phosphorylation events (Ishihama and Yoshioka 2012). This signaling cascade is mainly consisting of three kinases, a MAPKKK (MAP3K), a MAPKK (MAP2K), and a MAPK which activate each other sequentially via phosphorylation. From previous studies, it has been observed that MAPKs play a crucial role in signal transduction of ABA-dependent stress response (Jeong et al. 2020). In *Arabidopsis,* various MAPKs such as AtMPK3, ATMPK4, and AtMPK6 are activated during both biotic and abiotic stress responses. The N-terminal region of group-I WRKY TFs has a conserved motif, which is activated by a MAPK-dependent phosphorylation event (Ishihama and Yoshioka 2012). Shen et al. (2012) reported that in rice, OsWRKY30 is phosphorylated and activated by MAPK cascade and as a result, the rice seedlings showed enhanced drought tolerance. Moreover, it was observed that Group-I WRKY TFs are activated by MAPK-dependent phosphorylation conferring plant immunity (Eulgem and Somssich 2007). In *Oryza sativa* OsWRKY30 is involved in regulating resistance in drought stress conditions via the MAPK phosphorylation pathway (Danquah et al. 2014). Mutation of a serine residue of the OsWRKY30 resulted in a drought-sensitive phenotype. Apart from these, in response to high-temperature stress, CaMAPK1 interacts with CaWRKY40 in *Capsicum annuum* (Shi 2016). Recently, it was observed that GhWRKY59 is involved in the regulation of the drought tolerance response in cotton plants via activation through the MAPK pathway (Li et al. 2017).

6.20 Future Perspective

In recent years, there has been a significant amount of research on the WRKY TF family, which has led to the discovery of new members and the elucidation of their functions. With the increasing availability of genomic and transcriptomic data, more members of the WRKY family will likely be discovered in the future, and their functions will be further characterized. Moreover, there is growing interest in the use of WRKY TFs for genetic engineering in plants to enhance their resistance to biotic and abiotic stresses, which could help to increase crop yields and improve food security. There is growing interest in using genetic engineering techniques to enhance the expression of these TFs in crops to increase their resistance to stress. This involves overexpressing specific WRKY TFs or manipulating their downstream targets to improve plant growth and yield under stress conditions. To elucidate the role of the WRKY transcription factor, CRISPR/CAS9 strategy could also be used in near future (Phukan et al. 2016). Studying the function of WRKY TFs will also provide new insights into the regulatory mechanisms of plant development and stress responses. This could help to identify key signaling pathways and genes involved in these processes, leading to the development of new biotechnological tools for crop improvement. The availability of genomic data for multiple plant species has enabled comparative genomics studies, which have revealed the evolutionary relationships between different members of the WRKY family. These studies are likely to continue in the future, providing new insights into the evolution and function of these TFs.

6.21 Conclusion

Advanced research in this area is likely to lead to new insights into the regulatory mechanisms of plant development and stress responses, as well as the development of novel biotechnological applications. With the advancement of next-generation sequencing technologies, it is becoming easier and faster to sequence plant genomes and transcriptomes. This has led to the discovery of new members of the WRKY family, and more members will likely be identified in the future. Although many WRKY transcription factors have been identified in plants, their functions are not fully understood. Future studies could investigate the functional characterization of these transcription factors, including identifying their target genes, their role in specific signaling pathways, and their contribution to stress responses. Overall, the future of WRKY transcription factor research holds promise for improving our understanding of plant stress responses and developing strategies for crop improvement under stress conditions.

Acknowledgements The authors gratefully acknowledge Council of Scientific and Industrial Research, Govt. of India, (Ref. No. 38(1587)/16/EMR-II, dated: 17/05/2016 to SR), and SERB, DST, Govt of India (Ref. No. ECR/2016/000539 and Ref. No. CRG/2021/000989-G to SR) for providing financial supports performing research related to the topic discussed in this review. SB is thankful to CSIR, Govt. of India (09/025(0261)/2018-EMR-I) for the research fellowship. AM is thankful to UGC (Ref. No. 221610047029), Govt. of India for the research fellowship. MK is thankful to DST-SERB (Ref No. CRG/2021/000989-G). PR is thankful to UGC (715/(CSIR-UGC NET JUNE 2019)), Govt. of India for the research fellowship. SN is thankful for the DST-INSPIRE (DST/INSPIRE Fellowship/2021/IF200219) fellowship. We apologize to those authors whose work could not be cited due to space limitations.

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Chapter 7
CRISPR/Cas Mediated Genome Editing for Improving Stress Resilience in Plants

Deepu Pandita

Abstract In nature, the plants have to face and fight both the abiotic (cold, heat, drought, salinity, and heavy metals) and biotic stressors (pathogens, including bacteria, fungi, and viruses and insect pests) with colossal effects respectively of 50% and 20% to 40% of global yield loss in agriculture. Clustered Regularly Interspaced Short Palindromic Repeat/Cas (CRISPR/Cas) system has emerged as a pioneering genome editing toolbox due to its simplicity, versatility and adequacy to accomplish transgene free gene manipulations. CRISPR/Cas can be easily programmed to target specific DNA sequences, and it is much quicker and extra efficient than previous gene-editing technologies. One of the most promising applications of CRISPR/Cas in plants is the creation of crops with improved resistance to pests, pathogens, and environmental stressors. In this chapter, we concentrate on understanding the molecular mechanisms of CRISPR/Cas genome editing system, types and applications of CRISPR/Cas for the refinement of stress-related traits in crop plants.

Keywords Genome editing of crops · CRISPR/Cas9 · CRISPR/Cas12 · CRISPR/Cas13 · Abiotic stress · Biotic stress

7.1 Introduction

Abiotic stresses like cold, heat, drought, salinity, and heavy metals are significant factors to decline the growth and development, quantity and quality of crop plants (Ismail and Horie 2017; Shi et al. 2018; Gupta et al. 2020; Chauhan et al. 2020; Tang et al. 2020). Abiotic stresses lead to 50% drop in yield of crop plants (Liu et al. 2022). Secondly, plants are prone to various attacking pathogens, such as, bacteria, fungi, and viruses and insect pests (Wiesner-Hanks and Nelson 2016; Liu et al. 2016; Li et al. 2019b). Biotic stress is accountable for about 20 to 40% of global yield loss in agriculture (Savary et al. 2012; Chen et al. 2019; Mushtaq et al. 2019).

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_7

The CRISPR/Cas consists of two main components: the CRISPR RNA (crRNA) and the Cas protein. CRISPR stands for Clustered Regularly Interspaced Short Palindromic Repeats, and Cas refers to the CRISPR-associated protein. The crRNA is a small RNA molecule that has a specific sequence complementary to the DNA target site that needs to be edited. The Cas protein, on the other hand, is an enzyme that cuts the DNA at the target site specified by the crRNA. The CRISPR associated enzyme known as Cas9 breaks down the target DNA sequence to generate a Double Strand Break (DSB). The two repeated sequences are then used as templates to produce short crRNAs. The cells repair the DSBs by Nonhomologous End Joining (NHEJ) and Homology-Directed Repair (HDR) pathways (Fig. 7.1). The NHEJ pathway generates deletions and insertions at the site of DSBs. The HDR pathway uses homologous donor DNA sequences to generate accurate insertions at the DSB sites (Lin et al. 2014; Arnoult et al. 2017). CRISPR/Cas is a revolutionary genome editing tool that allows researchers to edit DNA sequences with high precision and efficient editing in cells and organisms. One of the main advantages of CRISPR/Cas toolbox is its simplicity and versatility. It can be easily programmed to target specific DNA sequences, and it is much faster and more efficient than previous gene editing technologies. CRISPR/Cas has transformed plant biotechnology by editing of plant genomes through targeted mutations in genes of interest, which can lead to the development of new plant varieties with desirable traits (Pandita et al. 2021; Pandita 2022d, 2022e, 2021b; Pandita and Pandita 2022).

One of the most promising uses of CRISPR/Cas in plants is creation of crops with improved resistance to pests, disease pathogens and environmental/abiotic stress

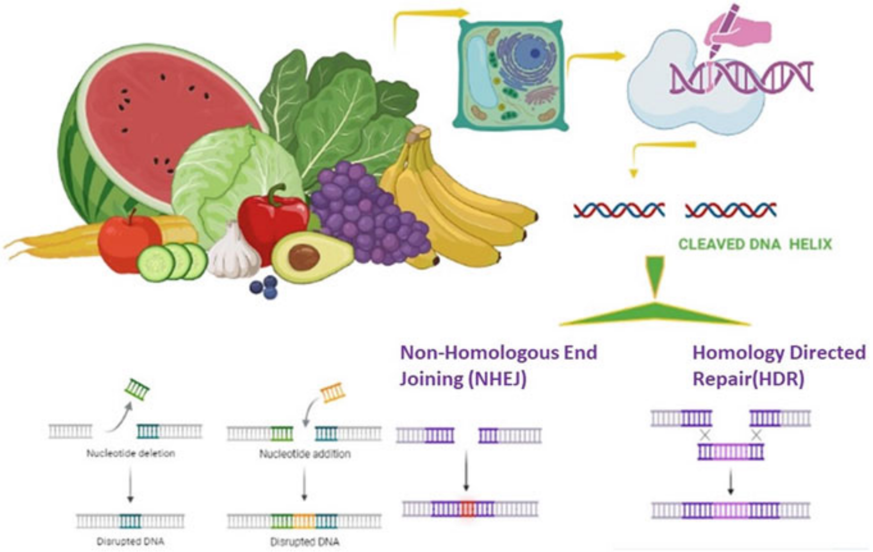

Fig. 7.1 CRISPR/Cas genome editing and repair machinery by NHEJ and HDR. (The figure is generated by BioRender software)

factors such as drought, cold, salinity and heat (Nieves-Cordones et al. 2017; Ji et al. 2018; Oliva et al. 2019; Bouzroud et al. 2020; Pandita et al. 2021; Pandita 2021b, 2022d, 2022e; Pandita and Pandita 2022). Overall, the CRISPR/Cas mediated genome modifications hold tremendous potential for future of plant biotechnology, and is about to play an increasingly important role in efforts to address global food security and other pressing challenges (Pandita et al. 2021; Pandita 2021b, 2022d, 2022e; Pandita and Pandita 2022).

7.2 Basics of CRISPR/Cas System

The CRISPR/Cas system is found in genomes of bacteria and archaea, where it functions as an adaptive defense mechanism against invading bacteriophages or other virulent bacteria. The system works by using RNA-guided nucleases to guide the Cas protein to specific locations in the genome, where it can cleave the DNA and make precise edits (Marraffini 2015). The typical CRISPR/Cas system works in three successive stages:

1. **Adaptation (acquisition)**: The microbes make duplicates of DNA segments acquired from the new spacer DNA fragment sequences from invading viruses or plasmids and make CRISPR arrays (Sander and Joung 2014). The CRISPR arrays are a cluster of short and repetitive DNA sequences. These spacer sequences are then transcribed into crRNAs. CRISPR/Cas9 after recognition with PAM site motif, integrates foreign DNA fragment as spacer sequence inside the locus of CRISPR (Fig. 7.2).

2. **Expression**: Cas protein expresses the nascent transcribed long pre-crRNA into the CRISPR RNAs (crRNAs) and trans-activating crRNA (tracrRNA) (Fig. 7.2). The crRNA associates with a tracrRNA to form a complex that guides the Cas protein to the target DNA site (Garneau et al. 2010; Marraffini and Sontheimer 2010).

3. **Interference**: This is an acquired immunity in bacterial group wherein the Cas protein cuts target viral DNA at the target site resulting in DSBs, which triggers the cell’s DNA repair mechanisms to either remove or replace the damaged DNA sequence (Fig. 7.2) (Xie and Yang 2013).

7.3 Types of CRISPR/Cas Genome Editing System

There are various categories of CRISPR/Cas genome editing systems, each with unique characteristics and applications (Pandita et al. 2021; Pandita 2021b, 2022d, 2022e; Pandita and Pandita 2022). CRISPR/Cas systems have been classified into type 1 and 2 on the basis of Cas genes and interference complex (Chen et al. 2019). The Class 1 (type I, type III, and type IV) makes use of multi-Cas protein complexes

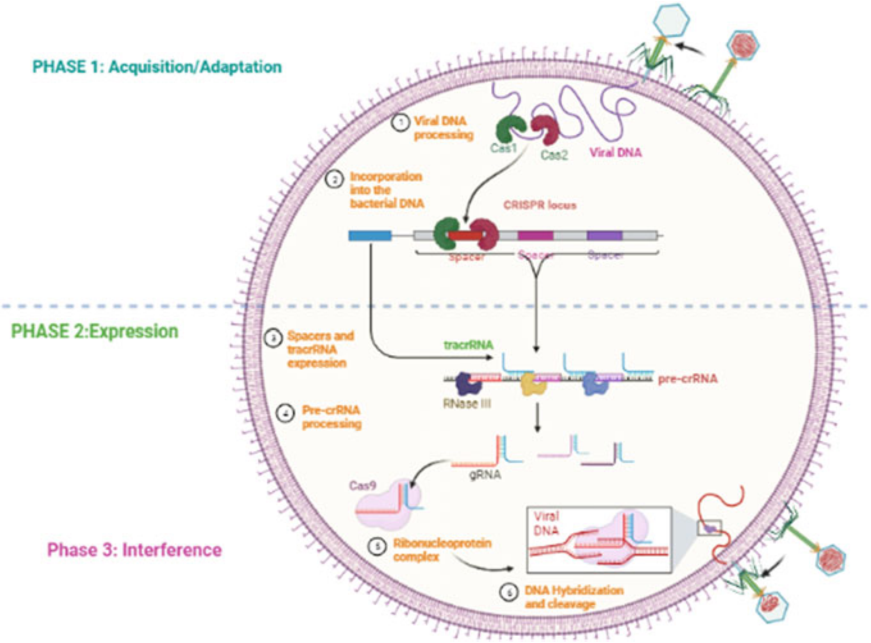

Fig. 7.2 Mechanism of CRISPR/Cas system (The figure is generated by BioRender software)

for interference, whereas the Class 2 (type II, type V, and type VI) makes use of a single protein with the CRISPR-RNA (Koonin et al. 2017). Here are some of the most commonly used types.

7.3.1 CRISPR/Cas9

The type II CRISPR/Cas9, a two-component genome editing tool is a combination of a bacterial defense mechanism (CRISPR) and a protein (Cas9) that can be programmed to cut DNA at a specific location on the basis of RNA-guided DNA interference (Koonin et al. 2017). CRISPR/Cas9 was initially isolated from *Streptococcus pyogenes* (Cong et al. 2013; Hsu et al. 2014) and is the most widely used and well-known type of CRISPR/Cas editing system in plants. The Cas9 protein has two signature endonuclease domains of RuvC and HNH. RuvC domain catalyzes cleavage of non-complementary DNA strand and HNH domain catalyzes cleavage of complementary DNA strand (Jinek et al. 2012; Gasiunas et al. 2012). CRISPR/Cas9 system uses the bacterial protein called Cas9 to cut DNA sequence at a specific location in a precise and efficient manner, guided by a 100- chimeric component nucleotide single-guide RNA (sgRNA) comprising a CRISPR RNA (crRNA), and transactivating CRISPR RNA (tracrRNA) (Hsu et al. 2014) that is designed to bind to a specific target region of DNA sequence of interest in cells and generate a DSB at editing site (Jiang and Doudna 2017). The sgRNA/Cas9 binding followed by cleavage of target DNA depends on presence of Protospacer Adjacent Motif (PAM) sequence (5'-NGG-3') at the downstream of target DNA (Jiang and Doudna 2017). Other PAM sequences are 5'-NNAGAA for CRISPR1 and 5'-NGGNG for CRISPR3 in *S. thermophilus* (StCas9) and 5'-NNNNGATT in *Neisseria meningitidis* (NmCas9) (Gasiunas et al. 2012; Zhang et al. 2013; Müller et al. 2016). The cut generated repairs by Watson–Crick base pairing using the cell's natural DNA repair mechanisms of NHEJ or HDR (Salsman and Dellaire 2017; Chen et al. 2019), either resulting in a specific mutation into the genome or allowing for the insertion of new DNA strand into break site (Fig. 7.1).

CRISPR/Cas9 system has a variety of potential applications in numerous plant species, ranging from model organisms such as *Arabidopsis thaliana* to crops for instance, maize, wheat, rice, barley, grapes, apples, oranges, potato, tomato, soybean, flaxseeds, rapeseed, and watermelon (Jaganathan et al. 2018; Zhang et al. 2018a, b) including the creation of genetically modified crops with desirable traits such as improved yield, resistance to pests and diseases, and tolerance to biotic and abiotic stress by targeted mutations or insertions in the genome. It is simpler, rapid, versatile, inexpensive, better targeting efficiency, multiplex editing and more efficient than previous gene-editing technologies, such as Zinc Finger Nucleases (ZFNs) and Transcription Activator-Like Effector Nuclease (TALEN), with wide applications in improvement of crop plants (Schiml et al. 2014; Xie et al. 2015; Gao et al. 2017; Wang et al. 2018a, b, c; Zhang et al. 2018a, b; Chen et al. 2019).

The restricted application of CRISPR/Cas9 due to its specificity of 5'-NGG-3' PAM sequence has been overcome by SpCas9-NAG and xCas9 with increased PAM compatibility and higher specificity (Wrighton 2018; Hu et al. 2018; Meng et al. 2018). However, there are also concerns about the potential off-target effects CRISPR/Cas9 in plants, which could lead to accidental changes in genome. Researchers are continuing to explore and fully understand the potential applications of CRISPR/Cas9 in plants and to address its potential limitations and long-term effects. Furthermore, regulatory agencies in some countries have different policies regarding usage of genome editing toolboxes in plants, which could limit the adoption of the technology in agriculture. Overall, CRISPR/Cas9 holds tremendous potential for the future of plant biotechnology and has capability to contribute to sustainable agriculture, food security, and environmental conservation.

7.3.2 CRISPR/Cas12

CRISPR/Cas12 is also known as Cpf1 endonuclease derived from *Francisella novicida* (FnCpf1) and its ortholog from a *Lachnospiraceae bacterium* (LbCpf1). This genome editing system uses different protein i.e., Cas12 protein to cut DNA at a specific location, guided by a CRISPR RNA (crRNA). Like Cas9, Cas12 can create a double-stranded break in DNA after recognizing thymidine rich (5'-TTN-3') PAM motif, but it can also cleave DNA in a staggered fashion with sticky end of 4 to 5 5’ nucleotide overhangs, which can lead to different repair outcomes (Zetsche et al. 2015). In CRISPR/Cas12a, Nuclease (Nuc) domain helps RuvC in creating cleavage in both the complementary and non-complementary regions at downstream of PAM (Gasiunas et al. 2012; Schindele et al. 2018). CRISPR/Cas12 has been used in crop plants like Arabidopsis, rice, tobacco, and soybean for genome editing and it offers some advantages over CRISPR/Cas9 (Endo et al. 2016; Tang et al. 2017). One advantage is that Cas12 creates a staggered cut in DNA, which can result in more precise and predictable changes to the genome. Additionally, Cas12 is smaller than Cas9, which makes it easier to deliver into plant cells. Researchers have used CRISPR/Cas12 to create plants with a variety of traits. For example, they have used it to create rice plants that are more resistant to bacterial blight, a devastating disease that can cause significant crop losses. They have also used it to create tomatoes with a longer shelf life, and to modify the flower color of petunias. Like CRISPR-Cas9, there are concerns about the potential off-target effects of CRISPR/Cas12. CRISPR/Cas12 holds tremendous promise for the future of plant biotechnology and has the potential to improve crop yields, reduce pesticide use, and help to ensure food security in scenarios of climate change and other challenges.

7.3.3 CRISPR/Cas13

CRISPR/Cas13 is a type of RNA-targeting genome editing system that is similar to CRISPR/Cas9 and CRISPR/Cas12, but uses a different protein to cut RNA instead of DNA. This system uses the Cas13 protein guided by a CRISPR RNA (crRNA) to bind and cut specific RNA instead of DNA which can be used to manipulate gene expression or knock down RNA transcripts. It has been used for applications such as the detection of viral RNA in diagnostic tests. Although CRISPR/Cas13 has not been as extensively studied in plants as CRISPR/Cas9, it holds potential as a tool for gene regulation and RNA-based therapies in plants. Researchers have used CRISPR/Cas13 to target plant viruses and RNA pathogens, demonstrating its potential as a tool for disease control in agriculture and for knockdown of plant genes by targeting RNA transcripts, opening up new possibilities for gene regulation studies. However, there are still some challenges associated with using CRISPR/Cas13 in plants, such as delivering the protein and crRNA to specific plant tissues and reducing off-target effects. Further research is needed to optimize the technology and address these challenges.

7.3.4 Base Editors

These are a type of CRISPR-based tool that can change individual nucleotides (the building blocks of DNA) without creating a double-stranded break. They use a modified Cas protein fused to an enzyme that can chemically modify a nucleotide, allowing for precise changes to be made to the DNA sequence.

7.3.5 Prime Editors

These are a newer type of CRISPR-based tool that can directly write new genetic information into the genome, rather than relying on the cell's DNA repair machinery to do so. They use a modified Cas protein that can cut one strand of DNA and then use a specially designed RNA molecule to introduce new genetic information at the cut site.

Each type of CRISPR/Cas system has its own advantages and limitations, and researchers choose the most appropriate tool for their specific applications.

7.4 CRISPR/Cas and Abiotic Stress in Plants

Plants face various abiotic stresses like drought, salinity, flooding, high and low temperature extremes through complex signaling pathways. Abiotic stresses harm plant growth and development and downstream cellular responses to stress lead to decline in the grain yield (Lamers et al. 2020; Zhang et al. 2022). CRISPR/Cas genome editing technology has the potential to contribute to improving resilience of plants to abiotic stresses of drought, salinity, extreme temperatures and nutrient deficiency, which are major challenges in agriculture, particularly in the face of climate change (Pandita 2022f, 2023).

One of the main approaches for using CRISPR/Cas to improve plant tolerance to abiotic stress is to directly modify the genes responsible for stress response and tolerance. For example, researchers have used CRISPR/Cas to modify genes involved in water use efficiency, such as aquaporins and stomatal conductance regulators, to increase drought tolerance in plants. The editing outcomes ranged from knockout to other types of modifications. They have also used CRISPR/Cas to modify genes involved in salt tolerance, such as ion transporters and regulatory proteins, to improve plant growth in saline soils. Further, genes affecting plant growth and development, which indirectly affect stress tolerance. For example, CRISPR/Cas can be used to modify genes and microRNA involved in plant hormone signaling, affecting root growth and architecture, or can introduce multiple genetic modifications for more complex traits for resilience to abiotic and biotic stress and thus improve plant nutrient uptake and abiotic stress tolerance along with biotic stress mitigation and contributing to sustainable agriculture and food security in the face of climate change (Pandita 2019, 2021a, 2022a, b, c; Pandita and Wani 2019). The examples highlighting the potential of CRISPR/Cas as a tool for improving plant stress tolerance and addressing challenges of global food security are enlisted in Tables 7.1 and 7.2.

In these studies, CRISPR/Cas was used to modify different genes in plants to improve tolerance to different abiotic stresses. The editing outcomes ranged from knockout to other types of modifications. These examples demonstrate the potential of CRISPR/Cas as a tool for improving stress tolerance in plants and addressing the challenges of global food security. Heat shock protein (Hsp) chaperones protect plant species against abiotic stress with improved membrane stability and detoxification of the reactive oxygen species (ROS) (Xu et al. 2013; Ul Haq et al. 2019). The overexpression of GmHsp90A2 in Soybean roots under heat stress positively regulates thermotolerance by prevention of degradation of chlorophyll and peroxidation of lipids (Huang et al. 2019). CRISPR/Cas9 mediated knockout mutants of GmHsp90A2 showed sensitivity to high temperature stress (Huang et al. 2019), validating regulatory role of GmHsp90A2 in heat stress tolerance. AUXIN REGULATED GENE INVOLVED IN ORGAN SIZE (ARGOS) negatively regulates ethylene signaling whereas the ethylene regulates loss of water (Kawakami et al. 2013). ARGOS overexpression in maize increases yield and tolerance to drought (Shi et al. 2015). CRISPR/Cas9 generated mutant variants of ARGOS8 gene had increased drought tolerance and grain yield traits in maize (Shi et al. 2017).

7.5 CRISPR/Cas and Biotic Stress in Plants

Plants come across biotic stresses such as pathogenic organisms and pests, bacteria, fungi, viruses, and nematodes which cause both the damages to plants and yield losses (Kumar and Verma 2018; Kaur et al. 2022) and are major challenges in agriculture, particularly for food security and sustainable agriculture. Plants fight stressors through various molecular, biochemical, and morphological modes by the modulation of signaling pathways (Nejat and Mantri 2017; Gimenez et al. 2018); such as existence of waxy cuticles and trichomes on leaves (Xu et al. 2011; Javelle et al. 2011), PAMP-triggered immunity (PTI) (Monaghan and Zipfel 2012; Gimenez et al. 2018), effector-triggered immunity (ETI) (Spoel and Dong 2012; Wang et al. 2019), and systemic acquired resistance (SAR) (Fu and Dong 2013; De Vleesschauwer et al. 2014).

CRISPR/Cas genome editing technology has potential to improve resilience of plants to biotic stressors. One of the main approaches for using CRISPR/Cas to improve plant resistance to biotic stress is to modify the genes responsible for plant immunity and defense response. For example, researchers have used CRISPR/Cas to modify genes involved in plant-pathogen interactions, such as disease resistance (R) genes and pathogenesis-related (PR) proteins, to improve plant resistance to various pathogens, including bacteria, fungi, and viruses. CRISPR/Cas has also been used to modify genes involved in plant–insect interactions, such as those encoding

Table 7.1 Some examples of CRISPR/Cas genome editing tool for improving plant abiotic stress tolerance

Crop	Modification of target gene/s	Tolerance to stress	Reference/s
Thale Cress (*Arabidopsis thaliana*)	AtOST2	Drought stress	Osakabe et al. (2016)
	AtAREB1		Roca Paixão et al. (2019)
	AtAVP1		Park et al. (2017)
	AtmiR169a		Zhao et al. (2016)
	AtCBF1, AtCBF2	Cold stress	Chen et al. (2010)
	AtWRKY, AtWRKY4	Salt stress	Li et al. (2021b)
	Atoxp1	Heavy metal stress	Baeg et al. (2021)
Barley (*Hordeum vulgare*)	HvITPK1	Salt stress	Vlˇcko and Ohnoutková (2020)
Rapeseed (*Brassica napus*)	BnaA6.RGA	Drought stress	Wu et al. (2020)
Chickpea (*Cicer arietinum*)	At4CL, AtRVE7	Drought stress	Badhan et al. (2021)
Cotton (*Gossypium hirsutum*)	GhPGF, GhCLA1	Heat stress	Li et al. (2021a)
Maize (*Zea mays*)	ARGOS8	Drought stress	Shi et al. (2017)
	ZmTMS5	Heat stress	Li et al. (2017)
Rice (*Oryza sativa*)	OsMYB30	Cold stress	Zeng et al. (2019)
	OsAnn3, OsAnn5		Shen et al. (2017)
	OsPRP1		Nawaz et al. (2019)
	OsPIN5b, GS3, OsMYB30		Zeng et al. (2020b)
	GS3		Liao et al. (2019)
	OsMYB30		Liao et al. (2019)
	OsERA1	Drought stress	Ogata et al. (2020)
	OsNAC14		Shim et al. (2018)
	OsPYL9		Usman et al. (2020)
	OsSAPK2		Lou et al. (2017)
	OsSRL1, OsSRL2		Liao et al. (2019)
	SRL1, SRL2		Zeng et al. (2019)
	OsDST		Santosh Kumar et al. (2020)
	OsmiR535		Yue et al. (2020)
	OsPUB67		Qin et al. (2020)
	OsHSA1	Heat stress	Qiu et al. (2018)

(continued)

Table 7.1 (continued)

Crop	Modification of target gene/s	Tolerance to stress	Reference/s
	OsPDS		Nandy et al. (2019)
	OsNAC006		Wang et al. (2020a, b)
	OsPYL1/4/6		Miao et al. (2018)
	OsNRAMP5	Heavy metal stress	Tang et al. (2017), Chu et al. (2022)
	OsLCT1		Lu et al. (2017), Chang et al. (2020)
	OsNRAMP1		Chang et al. (2020), Chu et al. (2022)
	OsHAK1		Nieves-Cordones et al. (2017)
	OsARM1		Wang et al. (2017a)
	OsATX1		Zhang et al. (2021)
	OsPRX2		Mao et al. (2019)
	OsRAV2	Salt stress	Liu et al. (2020b)
	OsGT*g*-2		Liu et al. (2020b)
	OsbHLH024		Alam et al. (2022)
	OsNAC45		Zhang et al. (2020a)
	OsDST		Santosh Kumar et al. (2020)
	OsBBS1		Zeng et al. (2018)
	OsNAC041		Bo et al. (2019)
	OsPQT3		Alfatih et al. (2020)
	OsPIL14		Mo et al. (2020)
	OsFLN2		Chen et al. (2020)
	OsAGO2		Yin et al. 2020)
	OsRR22		Zhang et al. (2019), Han et al. (2022)
	OsmiR535		Yue et al. (2020)
Soybean (*Glycine max*)	GmMYB118	Drought stress	Du et al. (2018)
	GmDrb2a, GmDrb2b	Salt stress	Curtin et al. (2018)
	GmAITR		Wang et al. (2021b)
Tomato (*Solanum lycopersicum*)	BZR1	Heat stress	Yin et al. (2018)
	SlAGAMOUS-LIKE 6		Klap et al. (2017)
	SlCPK28		Hu et al. (2021)
	AGL6		Klap et al. (2017)
	SlMAPK3		Yu et al. (2019)

(continued)

Table 7.1 (continued)

Crop	Modification of target gene/s	Tolerance to stress	Reference/s
	SlLBD40	Drought stress	Liu et al. (2020a)
	ALD1, FMO1		Wang et al. (2021a)
	SlARF4		Chen et al. (2021)
	SlGID1		Illouz-Eliaz et al. (2020)
	MAPK3		Wang et al. (2017b)
	NPR1		Li et al. (2019a)
	LBD40		Liu et al. (2020a)
	SlNPR1		Li et al. (2019a)
	HKT1;2 RAD51/54	Salt stress	Vu et al. (2020)
	HAK20		Wang et al. (2020a, b)
	SlHyPRP1		Tran et al. (2021)
	CBF1	Cold stress	Li et al. (2018)
Wheat (*Triticum aestivum*)	TaDREB2, TaDREB3, TaERF3	Drought stress	Kim et al. (2018)
	TaHAG1	Salt stress	Zheng et al. (2021)

plant defense compounds and receptors that are important for insect resistance. In addition to directly modifying defense-related genes, CRISPR/Cas can also be used to modify genes involved in plant growth and development, which indirectly affect plant resistance to biotic stress. For example, researchers have used CRISPR/Cas to modify genes involved in plant hormone signaling, which can affect plant architecture and root exudation, and thus influence plant–microbe interactions and pest resistance. Furthermore, CRISPR/Cas can be used to introduce multiple genetic modifications in a single plant, which can result in more complex traits and greater resilience to biotic stress. For example, researchers have used CRISPR/Cas to introduce multiple disease resistance genes into tomato plants, resulting in improved resistance to several fungal and bacterial pathogens.

There have been numerous examples genome editing of crops by using CRISPR/Cas9 technology. CRISPR/Cas9 targets genes related to building resistance against biotic stressors. The targeted mutation of sugar exporter genes OsSWEET14 and OsSWEET11 by CRISPR/Cas9 in rice improved resistance against bacterial blight disease that can cause significant yield losses (Jiang et al. 2013). Rice *Ethylene Response Factor 922* (*ERF922*) (*OsERF922*), *OsSEC3A* of ethylene signaling pathways, on modulation with CRISPR/Cas9 developed resistance against blast pathogen *M. oryzae* (Huibers et al. 2013; Wang et al. 2016; Ma et al. 2018). CRISPR/Cas9 modified *Pelo*, *Mlo1* genes in tomato, increased resistance to *TYLCV* and powdery

Table 7.2 Some examples of CRISPR/Cas genome editing tool for improving plant biotic stress tolerance

Crop	Target mutation/allele	Trait improvement	Reference/s
Genome Editing of Crops using CRISPR/Cas9			
Arabidopsis thaliana	*eIF(iso)4E*	Turnip Mosaic Virus (TuMV)	Pyott et al. (2016)
	eIF4E1	Clover Yellow Vein Virus (ClYVV)	Bastet et al. (2019)
Apple (*Malus domestica*)	DIPM-1, DIPM-2, and DIPM-4	Fire blight disease (*Erwinia amylovora*)	Malnoy et al. (2016)
Canola (*Brassica napus*)	*BnWRKY11*, *BnWRKY70*	Resistance to sclerotinia stem rot	Sun et al. (2018)
Cotton (*Gossypium hirsutum*)	GhCLA1, GhVP	Resistance to biotic and abiotic stress	Chen et al. (2017)
	Gh14-3-3d	Resistance to verticillium wilt (*Verticillium dahlia*)	Zhang et al. (2018a)
Cucumber (*Cumis sativus*)	eIF4E	CVYV, ZYMV, PRSV-W	Chandrasekaran et al. (2016)
Rice (*Oryza sativa*)	SWEET13	Bacterial blight (*Xanthomonas oryzae* pv. oryzae)	Zhou et al. (2015)
	OsSWEET14	Bacterial blight (*Xanthomonas oryzae* pv. *oryzae* (*Xoo*)	Zeng et al. (2020a)
	SEC3A	Rice blast disease (*Magnaporthe oryzae*)	Ma et al. (2018)
	ERF922	Rice blast disease (*Magnaporthe oryzae*)	Wang et al. (2016)
	eIF4G	RTSV	Macovei et al. (2018)
	Bsr-d1, Pi21, ERF922	Rice blast and bacterial blight	Zhou et al. (2022)
Potato (*Solanum tuberosum*)	P3, CI, NIb and CP; eIF4E; eIF4E1	Potato Virus Y (PVY)	Zhan et al. (2019), Noureen et al. (2022), Lucioli et al. (2022)
Tomato (*Solanum lycopersicum*)	MLO1	Powdery mildew (Oidium neolycopersici)	Nekrasov et al. (2017)
	PL; ACET1a, ACET1b	Fungal disease (Botrytis cinerea)	Silva et al. (2021), Jeon et al. (2020)
	SlPelo and SlMlo1	Tomato Yellow Leaf Curl Virus (TYLCV)	Pramanik et al. (2021)
	PMR4	Powdery mildew (Oidium neolycopersici)	Santillán Martínez et al. (2020)

(continued)

Table 7.2 (continued)

Crop	Target mutation/allele	Trait improvement	Reference/s
	JAZ2	Bacterial speck disease (*Pseudomonas syringae* pv. tomato DC3000)	Ortigosa et al. (2019)
Wheat (*Triticum aestivum*)	TaMLO-A1	Powdery mildew (*Blumeria graminis* f. sp. tritici)	Wang et al. (2014)
	TaEDR1	Powdery mildew (*Blumeria graminis* f. sp. Tritici)	Zhang et al. (2017)
Grapes (*Vitis vinifera*)	WRKY52	Gray mold (*Botrytis cinerea*)	Wang et al. (2018a, b, c)
	MLO-7; VvMLO3	Powdery mildew (*Erysiphe necator*)	Malnoy et al. (2016), Wan et al. (2020)
Watermelon	ClPSK1	Fusarium oxysporum f. sp. niveum	Zhang et al. (2020b)
Genome Editing of crops Using CRISPR/Cas12			
Cotton (*Gossypium hirsutum*)	GhMLO1	Resistance to powdery mildew	Liu et al. (2020b)
Maize (*Zea mays*)	ZmCERK1	Resistance to fungal pathogen	Liu et al. (2021)
Rice (*Oryza sativa*)	OsSWEET13	Resistance to bacterial blight	Li et al. (2019b)
	BUF1 locus	Resistance to *Magnaporthe oryzae* infection	Huang et al. (2022)
	OsOsIF2B	Resistance to rice stripe virus	Zhang et al. (2021)
Tomato (*Solanum lycopersicum*)	SlERF4	Resistance to Botrytis cinerea infection	Zhang et al. (2020b)
	SlMAPK3	Resistance to Botrytis cinerea infection	Zhang et al. (2018c)
Genome Editing of crops Using CRISPR/Cas13			
Rice (*Oryza sativa*)	OsSWEET14	Resistance to bacterial leaf streak	Liu et al. (2020b)
Tomato (*Solanum lycopersicum*)	PDS	Tolerance to high temperature and UV radiation	Wang et al. (2019)
	SlNPR1	Resistance to bacterial spot	Zhang et al. (2018a)

mildew (Pramanik et al. 2021). Similarly various genes were edited to increase resistance against pathogens e.g., DCL2b against ToMV (Wang et al. 2018b), JAZ2 against bacterial speck (*Pseudomonas syringae*) (Ortigosa et al. 2019), MYBS2 against late blight (*Phytophthora infestans*) (Liu et al. 2021), and PMR4 against powdery mildew (Martínez et al. 2020) in tomato. Similarly, *DMR6-1, DMR6-2* (Downy Mildew Resistance 6) gene targeting developed broad-spectrum resistance against *Phytophthora capsici* and *Pseudomonas syringae* in tomato (Thomazella et al. 2016, 2021). Tomelo which is non-transgenic tomato was designed and truncated by CRISPR/Cas9 targeting of *SlMLO1* with use of two sgRNA against *Oidium neolycopersici* which is the causal agent of powdery mildew in tomato plants (Nekrasov et al. 2017).

Erwinia amylovora causes fire blight disease in apple cultivars, and triggers its infection through DspA/E effector which interacts with apple susceptibility protein MdDIPM (Pompili et al. 2020). The knockdown of DspE-interacting proteins of Malus *DIPM-1, DIPM-2*, and *DIPM-4* by CRISPR/Cas9 developed resistance against fire blight in two golden delicious *Malus* × *domestica* susceptible cultivars (Malnoy et al. 2016). *MdDIPM4* knockout has also been produced by CRISPR/Cas9 system (Pompili et al. 2020). *Mildew resistance locus O* (*MLO*) host S gene in plant defense system encodes transmembrane protein (PRR) and *MLO* editing confers resistance to powdery mildew disease (Borrelli et al. 2018). *MLO* gene modification in wheat, tomato, and grapevine by the use of CRISPR/Cas9 developed resistance against powdery mildew disease due to fungi and oomycetes (Malnoy et al. 2016; Nekrasov et al. 2017). *Mildew resistance locus O* (*TaMLO-A1, TaMLO-B1, TaMLO-D1*) were targeted by CRISPR/Cas9 in bread wheat (Wang et al. 2014; Langner et al. 2018). *TaMLO-A1* knockdown wheat developed tolerance to *Blumeria graminis* f. sp. *tritici*, which is causal agent of the powdery mildew disease (Wang et al. 2014). Researchers have developed resistance by CRISPR/Cas in plants against various types of viruses. e.g., resistance to *Beet severe curly top virus* (*BSCTV*), *tomato leaf curl virus* (*TYLCV*), and *bean yellow drawf virus* (*BeYDV*) in *Arabidopsis thaliana, Nicotiana benthamiana* (Baltes et al. 2015; Ali et al. 2015; Hirano et al. 2016), *Merremia mosaic virus* (MeMV), *Cotton leaf curl Kokhran virus* (*CLCuKoV*) and *beet curly top virus* (*BCTV*) (Ali et al. 2016), *Cotton leaf curl Rajasthan virus* (*CLCuRaV*), *Cotton leaf curl Alabad Virus* (*CLCuAlV*), *Cotton leaf curl Kokhran* virus (*CLCuKoV*), *Cotton leaf curl Multan virus* (*CLCuMuV*), and *Cotton leaf curl Bangalore virus* (*CLCuBaV*) (Iqbal et al. 2016), *Cassava brown streak virus* (*CBSV*) (Gomez et al. 2019), *Rice tungro spherical virus* (RTSV) and *Rice tungro bacilliform virus* (RTBV) (Macovei et al. 2018).

While CRISPR/Cas9 has been extensively used for genome editing in crops, CRISPR/Cas12 has also been explored in several plant species. Scientists used CRISPR/Cas12 to edit the OsSWEET11 and OsSWEET13 gene in rice, resulting in improved resistance to bacterial leaf blight. There are examples which demonstrate the potential of CRISPR/Cas13 as a tool for genome editing in crops, similar to CRISPR/Cas9 and Cas12. Some examples of CRISPR/Cas genome editing tool for improving plant biotic stress tolerance are listed in Table 7.2.

7.6 Conclusion

Stressors decline the growth and development, quantity and quality of crop plants. The simplicity, rapidness, versatility, high precision and efficient editing of CRISPR/Cas genome editing toolbox holds tremendous promise for improving tolerance to abiotic and biotic stress factors in plants like Arabidopsis, maize, rice, wheat, barley, grapes, apple, oranges, potato, cucumber, tomato, flaxseed, rapeseed, soybean, chickpea, cotton, watermelon etc. CRISPR/Cas toolbox facilitates designing and tailoring of new plant varieties with desirable traits, contributing to sustainable agriculture and food security in the scenarios of global climate change. However, it is imperative to judiciously assess the potential risks and benefits of this technology and to warrant that any new crops resulting from CRISPR/Cas genome editing are safe for both the human consumption and environment.

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Chapter 8
Impact of Abiotic Stresses on Production of Secondary Metabolites in Medicinal and Aromatic Plants

Josef Jampílek and Katarína Kráľová

Abstract Medicinal plants have been used around the world in folk medicine for generations since ancient times, and today people enjoy using these natural medicines for their healing properties, with some of their pharmacologically active phytoconstituents recently serving as a lead for new drug development. Numerous aromatic plants producing aromatic secondary metabolites (SMs), which are commonly used as culinary herbs and spices, may also exhibit medicinal properties. The final biological effects of medicinal and aromatic plants (MAPs) are determined by the amount and composition of SMs, whose biosynthesis depends on genetic, ontogenetic, morphogenetic and environmental factors. Mild abiotic stresses have been found to stimulate production of SMs in MAPs without adversely affecting plant growth and development and in certain cases may even improve MAP performance. Since MAPs are sessile organisms exposed to various environmental stresses, they have developed effective defense mechanisms allowing protection against the harmful consequences of strong abiotic stresses, especially against the adverse effect of oxidative stress, in which SMs play an important role. This chapter presents a comprehensive overview of the recent findings on the impact of abiotic stresses including drought, salinity, waterlogging, heat, cold, harmful radiation, high soil acidity, elevated levels of ozone and CO_2, heavy metals and agrochemicals (fertilizers and pesticides) on MAPs. The effects of abiotic stresses on the production of SMs in MAPs, including yield and composition of essential oils are highlighted. Responses of MAPs to abiotic stresses of various intensity and corresponding defense mechanisms of MAPs against oxidative stress are discussed. Utilization of in vitro cultures and hairy roots for large-scale production of pharmacologically significant SMs of MAPs using elicitors such as

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_8

metal nanoparticle is presented and advantages of MAPs cultivation in a greenhouse under controlled conditions to achieve high levels of desirable SMs is mentioned as well.

Keywords Abiotic stresses · Aromatic plants · Defense mechanisms · Essential oils · Medicinal plants · Metal nanoparticles · Oxidative stress · Phytoconstituents · Secondaty metabolites

8.1 Introduction

Medicinal plants were used for healing purposes from ancient times and beneficial effects of hundreds of them on human health were listed in Sumerian tablets (300 BC), Ebers Papyrus (1500 BC) or *De materia medica* published by Dioscorides (40–90 AD) (Ahn 2017). In Middle Age, in 1597 healing impacts of approximately 600 medicinal plants were recorded in The Herball or Generall Historie of Plantes by John Gerarde (Singer 1923). While since the late 1970s, the WHO listed 21,000 medicinal plant species (Penso 1980), Schippmann et al. (2002) reported that 52,885 plant species out of 422,000 species of flowering plants growing worldwide are medicinal plant species. On the other hand, according to a report by the Royal Botanic Gardens (KEW, United Kingdom), in 2016, 17,810 plant species were used for medicinal purposes, in addition to 5,538 and 3,649 plant species used as food for human and animals, respectively (Royal Botanic Gardens 2016). Moreover, several medicinal plants producing volatile secondary metabolites (SMs) characterized with distinct fragrance have found utilization in religious ceremonies as ritual plants (Sapkota 2013; Dafni et al. 2020; Jigmei and Yangchen 2022; Jampílek and Kráľová 2022).

Some aromatic plants, which produce aromatic SMs and are usually used as culinary herbs and spices as well as in the food and liqueur industries also show important biological activities, particularly antimicrobial and antioxidant or radioprotective, and can be used for medicinal purposes as well (Christaki et al. 2012; Samarath et al. 2017; Do Nascimento et al. 2020; Nieto 2020; Fierascu et al. 2021; Males et al. 2022; Taban et al. 2022; Jampílek and Kráľová 2022). SMs of medicinal plants also serve as important drug leads for the development of new effective drugs and can be used as structural template in medicinal chemistry (Kayser 2018; Süntar 2020; Chopra and Dhingra 2021; Alam et al. 2022; Jampílek 2022; Jampílek and Kráľová 2022; Nair et al. 2023).

According to Hartmann (2007) "primary metabolism covering the growth and development of an individual is characterized as indispensable, universal, uniform, and conservative, while secondary metabolism covering the interaction of an individual with the environment is needful for survival in the environment and can be described as unique, diverse, and adaptive". While the biosynthesis of SMs in plants is usually relatively low under normal metabolic conditions, it increases significantly when plants are exposed to biotic and abiotic stresses (Ramakrishna and Ravishankar 2011; Kumar and Sharma 2018; Tak and Kumar 2020; Jha and Mohamed

2022; Punetha et al. 2022; Yeshi et al. 2022). Biosynthesis and accumulation of SMs in plants depend on genetic, ontogenic, morphogenetic and environmental factors, whereby change in only one factor can result in modification of the SMs contents (Verma and Shukla 2015). SMs are responsible for the biological activities of medicinal and aromatic plants (MAPs), whereby on molecular level they can target enzymes, mediators, transcription factors or even nucleic acids. Based on chemical structures SMs of plants are classified into several classes including phenolics, alkaloids, saponins, terpenes lipids and carbohydrates, which are indeed primary metabolites but are incorporated among SMs via glycosidation linkages (Hussein and El-Anssary 2018).

Under exposure of plants to abiotic stresses such as drought, salinity, waterlogging, heat, cold, harmful radiation, high soil acidity, elevated levels of ozone, CO_2 or heavy metals or at presence of agrochemicals reactive oxygen species (ROS) causing oxidative stress are produced in excess. Excess ROS causes membrane lipid peroxidation (LPO) resulting in electrolyte leakage, damage of photosystem (PS) II leading to inhibition of photosynthetic electron transport, pigment breakdown, damage of DNA and RNA, inhibition of key enzymes, degradation of proteins and oxidation of amino acids (Manke et al. 2013; Fu et al. 2014; Maleki et al. 2017; Kráľová et al. 2021a, b). Strong oxidative stress due to excess ROS can ultimately result in plant death (Xie et al. 2019; Savchenko and Tikhonov 2021). Moreover, abiotic stresses depending on their intensity and duration can cause considerable losses of crops yields, which is becoming more and more evident nowadays during the ongoing climate change (Kráľová and Jampílek 2021a; Chaudhry and Sidhu 2022; Zandalinas et al. 2022). Against harmful impact of oxidative stress plants developed defense mechanisms involving antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), and glutathione S-transferase (GST), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHR), which can either inactivate the ROS into their intermediates or directly detoxify ROS (Mehta and Gowder 2015; García-Caparrós et al. 2021; Kerchev and Van Breusegem 2021). In addition to antioxidant enzymes, non-enzymatic antioxidants such as glutathione (GSH), carotenoids, phenolic compounds, ascorbic acid, α-tocopherol, flavonoids and alkaloids play an important role in suppressing oxidative stress, neutralize the toxic effects of ROS and stabilize membranes through the modification of cellular metabolic functions by interaction with polyunsaturated acyl groups of lipids (Fu et al. 2014; Waskiewicz et al. 2014; Sharma et al. 2022; García-Caparrós et al. 2021; Kerchev and Van Breusegem 2021).

Injuries caused by excess ROS in MAPs and respective defense mechanisms against oxidative stress are shown in Fig. 8.1. On the other hand, mild abiotic stresses might have beneficial impact on seed germination rate, plant growth and performance, levels of assimilation pigments and photosynthesis efficiency and diminish oxidative stress by reducing levels of harmful ROS via activation of antioxidant defense system and enhance levels of valuable SMs along with increasing yield of essential oils (EOs) and ameliorating their composition, thereby contributing to enhanced tolerance of MAPs against abiotic stresses and improving their nutritional value (Farhoudi et al.

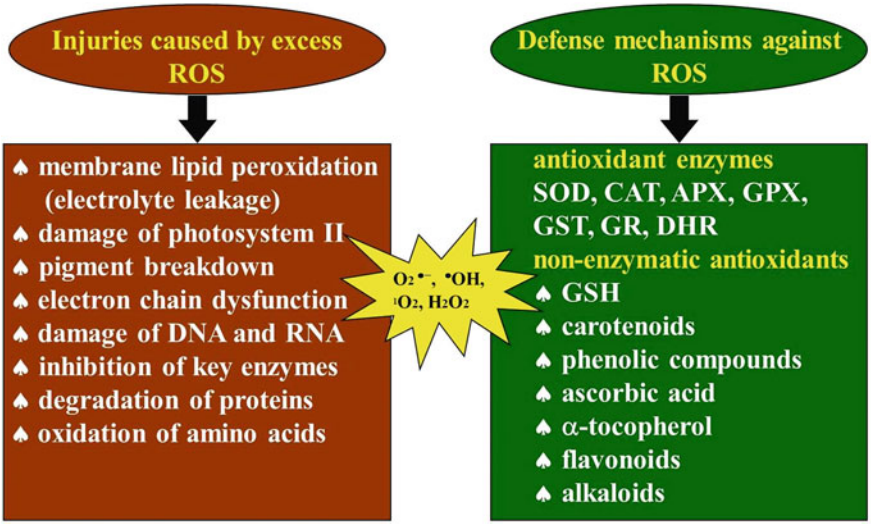

Fig. 8.1 Injuries caused by excess ROS in medicinal and aromatic plants and respective defense mechanisms against oxidative stress

2014; Haddadi et al. 2016; Farsi et al. 2019; Jung et al. 2021; Akbarzadeh et al. 2022; Ansari et al. 2023; Tan et al. 2023), as shown in Fig. 8.2. However, it should be mentioned that even though the levels of some SMs due to exposure of plants to abiotic stresses increase, the content of other one could be reduced resulting in altered composition of EO (e.g., Babula et al. 2015; Azimychetabi et al. 2021). In addition, genes play an important role in plant defense against abiotic stress, and genes involved in SM biosynthesis are upregulated in plants exposed to such stresses (e.g., Liu et al. 2015; Nazari et al. 2017; Hodaeia et al. 2018; Khajavi et al. 2019), which contributes to increased plant stress tolerance. Phytohormones (e.g., abscisic acid (ABA), auxin, jasmonic acid or salicylic acid (SA)) are also linked to plant defense signaling pathways (Wahab et al. 2022) and their exogenous application to plants can stimulate biosynthesis of valuable SMs as well and alleviate harmful impacts of abiotic stresses on plants (Ghasemi et al. 2016a, b; Abdelaal et al. 2020; Otálora et al. 2020; Safari et al. 2020; Azad et al. 2021; Garrido et al. 2022). Plant tolerance to abiotic stresses can also be enhanced by plant growth promoting microbes (Zade et al. 2019; Asghari et al. 2020; Msimbira and Smith 2020; Chiappero et al. 2022).

For large-scale production of pharmacologically important SMs of medicinal plants in vitro cultures and hairy roots are mostly suitable (Sharafi et al. 2013; Asl et al. 2019; Chung et al. 2019; Nourozi et al. 2019a, b; Taghizadeh et al. 2019; Khurshid et al. 2020; Khan et al. 2021) but at cultivation of plants in greenhouse under controlled conditions also high levels of desirable SMs can be achieved (e.g., Zobayed and Saxena 2004; Soltanbeigi et al. 2021). On the other hand, for MAPs growing in field improvement of SMs levels can be obtained by alleviating abiotic stresses

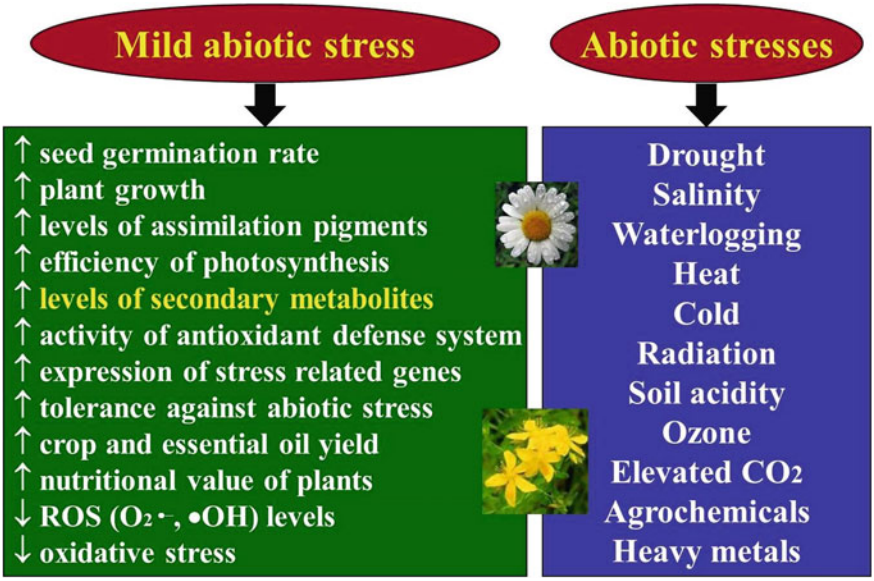

Fig. 8.2 Impact of mild abiotic stresses on medicinal and aromatic plants

showing too strong intensity, for example, using nanopriming (Abbasi Khalaki et al. 2021), pretreatment of plants with UV-B light (Rai et al. 2011), treatment with elevated O_3 concentration (Ansari et al. 2023) appropriate fertilization (Rahimi et al. 2020), irrigation or exogenous application of phytohormones (Ghasemi et al. 2016a; Otálora et al. 2020).

This chapter presents a comprehensive overview of the recent findings on the impact of abiotic stresses including drought, salinity, waterlogging, heat, cold, harmful radiation, high soil acidity, elevated levels of ozone and CO_2, heavy metals and agrochemicals (fertilizers and pesticides) on MAPs. The effects of abiotic stresses on the production of SMs in MAPs, including yield and composition of EOs are highlighted. Responses of MAPs to abiotic stresses of various intensity and corresponding defense mechanisms of MAPs against oxidative stress are discussed. Utilization of in vitro cultures and hairy roots for large-scale production of pharmacologically significant SMs of MAPs using elicitors such as metal nanoparticles is presented and advantages of MAPs cultivation in a greenhouse under controlled conditions to achieve high levels of desirable SMs is mentioned as well.

8.2 Drought Stress

Drought stress is a major environmental stress, which inhibits photosynthesis and respiration of plants, stomatal movement and causes alteration of physiological metabolism resulting in impaired plant growth and reproduction as well as lower crop productivity (Yang et al. 2021; Bandurska 2022). Water deficit activates downstream pathways such as phytohormone homeostasis and their signaling pathways resulting in biosynthesis of protective SMs providing multistress tolerance (Yadav et al. 2021; Bandurska 2022). To cope with drought stress the plants alter cellular osmotic potential and water potential along with activation of their defense systems via enhancing activities of antioxidant enzymes and accumulation of osmolytes such as proline, glycine betaine, phenolic compounds, and soluble sugars as well as phytohormones (e.g., ABA, auxin or jasmonic acid), which are linked to plant defense signaling pathways (Wahab et al. 2022). Under drought stress plants close stomata to prevent water loss. Due to perturbation of the respiratory metabolic pathway under drought stress ROS are generated in excess causing oxidative stress. Increased ROS levels act as an alarm signal and initiate acclamatory/defense responses via signal transduction pathways involving H_2O_2 as secondary messenger. However, at long-term stress when antioxidant system is not able to scavenge excess ROS cellular damage and plant death occurs (Cruz de Carvalho 2008). On the other hand, under low or moderate water deficit stress increased EO yield is observed and biosynthesis of various pharmacologically active SMs, including effective antioxidant compounds is stimulated, even though the levels of other ones can be reduced (Nunes et al. 2014; Nemeth-Zambori et al. 2017; Radwan et al. 2017; Caplan et al. 2019; Farsi et al. 2019; Akbarzadeh et al. 2022). Closure of stomata under water deficit results in considerable reduction of CO_2 uptake and fixation via Calvin cycle decreases accompanied with a strong decrease in the consumption of reduction equivalents ($NADPH + H^+$) and due to their large excess metabolic processes are moved to the production of highly reduced compounds, including isoprenoids, phenols, or alkaloids (Kleinwächter and Selmar 2014).

In *Mentha piperita* plants subjected to full irrigation EO composition and accumulation depended on plant growth stage alterations, whereby the fractions of some monoterpenes such as menthofuran, limonene, and pulegone were reduced as plant matured, whereas menthol, cineole, and neomenthol showed an increase. EO levels of plants subjected to 60% field capacity (FC) (mild water stress) increased, while EO content of those grown under 40% FC (moderate water stress) was greatly reduced in different plant growth stages. Hence, moderate drought stress not only diminished the EO percentage but also altered the EO profile via decreasing menthone and increasing menthofuran contents; increasing drought stress was also accompanied with rising of relative proportions of sesquiterpenes (Abdi et al. 2019a). Comparison of the impact of full irrigation, regulated deficit irrigation (irrigation of the entire root zone) and partial root zone drying (PRD; irrigation only half of the root zone at a time) on *M. piperita* plants showed that the highest EO yield of 23.7 kg/ha as well as the best irrigation water productivity based on oil yield (0.0191 kg/m^3) was obtained using PRD, when plants received 55% of the irrigation volume of the full irrigation treatment (PRD55). Moreover, application of PDR resulted in higher EO ratio and yield also at the second harvest (Akbarzadeh et al. 2022). Similarly, in *M. piperita* plants subjected to PRD55 treatment improved efficiency of EO by 90% and water productivity by 179% compared to full irrigation treatment was observed (Akbarzadeh and Shahnazari 2021). *M. piperita* plants exposed to water deficit (50% irrigation) showed pronounced increase in soluble sugars, while monoterpene concentrations remained relatively constant. Under drought stress the allocation of new vs. old carbon to monoterpenes production, structural growth and storage did not differ each from other in contrast to plants grown under low CO_2 (below ambient CO_2), in which proportionally more newly assimilated C was relocated for monoterpenes production to ensure defense at the expense of growth (Huang et al. 2019). In *M. piperita* plants cultivated under drought stress increased flavonoid contents and total phenolic were detected. Following methyl jasmonate (MJ) treatment of stressed plants SMs such as luteolin, naringenin, coumaric acid, and quercetin were observed, which were not detected at other treatments. Foliar application of 50 μM MJ ameliorated growth characteristics and metabolite profile, including carbohydrates and amino acids in both control and stressed plants (Abdi et al. 2019b). In *M. piperita* plants subjected to 25% FC Rahimi et al. (2018) estimated EO percentage of 1.1%, high levels of H_2O_2 and malondialdehyde (MDA) and high activities of polyphenol oxidase (PPO) and SOD were observed but the total phenol content (TPC) and total flavonoid contents (TFC) were reduced; content of ascorbic acid in drought-stress plants exceeded that of control plants and under 50% FC increased level of flavone was detected (Rahimi et al. 2018). Increasing levels of pulegone and menthofuran and reduction in menthol percentages observed in drought-stressed *M. piperita* plans were associated with upregulation of pulegone reductase and menthofuran synthase and down-regulation of menthol dehydrogenase. Higher EO yield can be induced via increasing limonene synthase gene expression levels, while reduction of menthofuran synthase gene expression levels results in ameliorated quality of EO (Rahimi et al. 2017).

Mentha spicata L plants growing in filed under severe water stress up to their complete maturation were characterized with impaired photosynthesis and modulated stomatal closure, thereby restricting water loss, and at harvest they showed lowered mesophyll conductance. Reduced total biomass, leaf biomass, leaf area index and plant height of drought-stressed *M. spicata* plants resulted in impaired yield of EOs (Marino et al. 2019). Irrigation with untreated municipal wastewater ensured the best quantity of *M. spicata* EO and the best quality and quantity of *Rosmarinus officinalis* EO compared to treatments with treated municipal wastewater, treated industrial wastewater, and untreated industrial wastewater. Under different treatments in the EO of *M. spicata* 5–19 and in the EO of *R. officinalis* 14–23 SMs were detected; predominant compounds in EO of treated plants were D-carvone (57.77–57.44%) and D-limonene (8.70–26.65%) for *M. spicata* and α-pinene (26.12–34.85%), 1,8-cineole (18.95–23.70%), and camphene (9.93–12.80%) for *R. officinalis* (Asadzadeh et al. 2023). *Mentha longifolia* grown without irrigation produced higher EO amounts under drought stress (0.9 ml/100 g plant) compared to irrigated plants (0.6 to ml/

100 g plant), while percentages of limonene and δ-carvone SMs as well as N and K nutrients were reduced; after 3 weeks under water deficit neodihydrocarveol and *cis*-dihydrocarvone contents achieved highest values of 26.4% and 11.43%, respectively (Singh et al. 2022).

Drought plants of *Melissa officinalis* treated with NO showed lower LPO and H_2O_2 levels and electrolyte leakage along with enhanced transcript abundance of Rubisco activase and chlorophyll synthase genes as well as higher free proline levels and relative water content (RWC) (Safari et al. 2022). Lemon balm, marjoram, peppermint and thyme subjected to 40% of soil water capacity (SWC) were characterized with strong reduction of total biomass production and accelerated TPC accumulation in shoots with largest TPC increase observed in lemon balm shoots. Water deficit induced considerable increase of RA (by 23–127%) in thyme, marjoram and peppermint, whereby shoots dry biomass of stressed thyme plants contained till 3.45% RA (Nemeth-Zambori et al. 2017). On the other hand, *Thymus vulgaris* plants subjected to 25% SWC showed pronouncedly higher levels of TPC compared to non-stressed plants but the content of total flavonoids and RA production were not affected (Nemeth-Zambori et al. 2016).

Using the irrigation regimes of 60% and 80% available soil water depletion (ASWD) myrcene levels in treated *Salvia officinalis* plants were higher in spring than in summer and under the irrigation regime of 86.5% ASWD they achieved 4.53%. At application of 1.5 mM and 2.25 mM putrescine, highest borneol concentrations of 1.47% and 1.41% were observed under irrigation regimes of 48.03% and 45.6% ASWD, respectively. Whereas best EO yield characterized with greater quantity and better quality was obtained from plants harvested in summer, putrescine showed only minor impact on EO content and quality but did not affect EO yield (Mohammadi-Cheraghabadi et al. 2023). Beneficial impact of putrescine application on TPC and TFC levels in *S. officinalis* plants under the irrigation regime of 20% ASWD was reported as well (Mohammadi-Cheraghabadi et al. 2021). In *S. officinalis* plants subjected to drought stress the expression of sabinene synthase gene considerably increased but the expression of geranyl diphosphate synthase (gpps) and bornyl diphosphate synthase (bpps) showed a decrease (Hassani et al. 2023). EO profile of sage grown in greenhouse affected by drought stress and various nutrient sources was discussed by Soltanbeigi et al. (2021). Moderate and severe water deficit modulated the expression of some genes involved in biogenic volatile organic compounds as well as EO biosynthesis and metabolic profile of *Salvia dolomitica* Codd plants, and notably increased sesquiterpene levels (Caser et al. 2019). In the EO of sage subjected to drought stress the portion of monoterpenes strongly increased and doubled after two days of treatment; gradual increase of sabinene synthase peaked after 2 weeks (Radwan et al. 2017).

Mahdavi et al. (2020) reported that most deciding metabolites involved in water stress adaptation of *Thymus officinalis* plants are α-phellandrene, *O*-cymene, γ-terpinene and β-caryophyelene. Beneficial impact of 100 ppm SA on the SMs content composition of *T. vulgaris* and *Thymus kotschyanus* plants under well-watered and water stress conditions was observed as well and in *T. kotschyanus* even an increase of thymol content by 93.39% was detected (Mohammadi et al. 2019). Mild and moderate limited irrigations resulted in an increase of EO% in *Origanum majorana* plants but application of MeJA, which had beneficial impact of growth of stressed plants, reduced EO% and yield by 16.9% and 12.0%, respectively, however, it increased oxygenated monoterpenes from 62.73% to 65.44% and decreased the levels of monoterpene hydrocarbons components from 62.73% to 65.44% (Farsi et al. 2019). In *Ocimum basilicum* plants subjected to severe water stress (60% FC) greatest EO content of 1.0% and EO yield of 1.9 g/m^2 was estimated and application of 50 and 100 mg/L SeNPs was able to increase not only the dry matter yields by 14% and 13% but also the EO content by 33% and 36% and EO yield by 52% and 53%, respectively. The highest methyl chavicol and linalool levels were achieved in 80% FC with 50 mg/L SeNPs, while the highest proline (17 μg/g fresh weight) and soluble sugar (6 mg/g fresh weight) levels were observed at 60% FC using 50 mg/L SeNPs (Asghari et al. 2023).

In three levander genotypes drought stress enhanced proline in leaves, antioxidant activity, CAT, peroxidase (POD), and APX activities, MDA levels, TPC, TFC and total sugar content as well as EO%, whereas increasing drought stress resulted in a decrease in monoterpenes and an increase in sesquiterpenes (Shabankareh et al. 2021). Water stressed plants of *Lavandula angustifolia* and *Salvia fruticosa* showed improved EO yield and quality with higher concentrations of phenolic antioxidants and volatile organic compounds (VOCs) from EO of levander cultivated under moderate water deficit and showed pronouncedly higher insecticidal activity against *Tetranychus urticae* (Chrysargyris et al. 2016). In drought-stressed *Artemisia annua* plants with leaf water potential ranging from −0.3248 to −1.22 MPa enhanced proline levels and protein concentration as well as LPO was observed along with increased activities of antioxidant enzymes. Artemisinin content was reduced under water deficit conditions, and it achieved somewhat higher amounts in leaves of severely stressed plants than in moderately stressed ones. In drought-stressed *A. annua* plants glutamine pathway was found to be prevailing, and a diminished expression of catabolic gene expression provided a defense strategy in unfavorable conditions (Soni and Abdin 2017).

Irrigation of chamomile plants at 70% of FC ameliorated plant growth and increased oil production, while under 55% of FC, corresponding to severe drought stress, reduced plant growth, photosynthesis and EO yield. However, drought stress conditions contributed to better quality of EO (Farhoudi et al. 2014). Water deficit greatly stimulated uliginosin B (40- and 6-fold higher levels in the leaves and in the reproductive parts, respectively), 6-isobutyryl-5,7-dimethoxy-2,2-dimethyl-benzopyran (HP1); 5-hydroxy-6-isobutyryl-7-methoxy-2,2-dimethyl-benzopyran (HP3) and TPC without affecting plant biomass of *Hypericum polyanthemum* plants. On the other hand, mild fertilized plants subjected to drought stress showed higher biomass but lower levels of uliginosin B and HP3 than non-fertilized stressed plants and TPC was not altered (Nunes et al. 2014).

In *Camellia sinensis* plants exposed to long-term drought stress of 20 days the accumulation patterns of 116 differentially accumulated metabolites (DAMs) and nine mineral elements (MEs) were found to be pronouncedly affected in leaves, stems and roots. For example, K and Ca levels were clearly changed in all three organs, while the majority of DAM levels as well as levels of the typical N- and C-compounds were enhanced in the stems but reduced in the roots and leaves. Correlation analysis showed association between Mn and flavonoids. Accumulation of function-specialized metabolites and MEs contributing to alleviate oxidative damage under water deficit conditions could be considered as survival strategies in long-term drought stress conditions (Zhang et al. 2020a). Ameliorated expression of key genes in saponin synthesis pathway in *Panax notoginseng* plants grown at 55% and 85% FC resulted in higher levels of saponin compared to water stress of 70% FC, although at 70% FC best agronomic traits at flowering stage of plants were observed (Liao et al. 2017). Treatment of 3-year-old *P. notoginseng* with organic fertilizer using a dose 48 t/ha under drought stress condition of 50–35% FC resulted in dry root yield of 3039.19 kg/ha and 10.85% saponin content (Li et al. 2021a, b).

Water deficit stress diminished biomass and total seed yield of hemp plants but seeds remained filled for effective reproduction and enhanced proline accumulation was observed (Gill et al. 2022). Seven days of drought stress in the early flowering stage of *Cannabis sativa* plants greatly altered the levels of some SMs compared to control plants: cannabigerol (CBG) showed and increase by 40%, while cannabidiol decreased by 70–80% and TPC amount was reduced by 80%. On the other hand, during the initial stage of flowering the production of cannabinoids was not affected by 5 days of mechanical wounding (Park et al. 2022). Using controlled drought stress the drought-stressed hemp plants achieved at harvest enhanced levels of tetrahydrocannabinol acid (THCA) and cannabidiolic acid (CBDA) by 12% and 13%, respectively, compared with control plants along with an increase in yield per unit growing area of THCA by 43%, CBDA yield by 47%, delta(9)-tetrahydrocannabinol (THC) yield by 50%, and CBD yield by 67% (Caplan et al. 2019).

8.3 Salinity Stress

High salinity is one of the major abiotic stresses resulting in major reductions in cultivated land areas and is responsible for considerable losses in crops yields globally, whereby the total area of salt affected soils is approximately 1 billion hectares and shows gradual increase (Pitman and Läuchli 2002; Daliakopoulos et al. 2016; Ivushkin et al. 2019; Mustafa et al. 2019). However, plants can be subjected to salt stress also via irrigation with saline water (Ozturk et al. 2004; Khalid and da Silva 2010; Hussein et al. 2012).

Salinity stress adversely affects the relative growth rate of plants, water relations, transpiration, transpiration utilization efficiency as well as ionic relations and the photosynthetic process resulting in accelerated senescence and yield loss (Negrao et al. 2017; Hameed et al. 2021). Due to increased Na^+ and Cl^- levels in plant cells numerous morphological, physiological, epigenetic and genetic changes in plants can be observed and ROS are generated in excess and excessive uptake of Na^+ and Cl^- results in nutritional imbalance (Hernández 2019; Isayenkov and Maathuis 2019). Salinity results in osmotic stress, which suppresses plant growth and causes perturbation at metabolic level and excess ROS are generated as well (Ahanger et al. 2017; Chiappero et al. 2021). Plants can adapt to salinity via (i) osmotic stress tolerance, (ii) exclusion of Na^+ or Cl^- ion, and (iii) tolerance of tissue to accumulated Na^+ or Cl^- (Munns and Tester 2008). Salt tolerance is controlled by numerous genes involved in different biochemical and physiological mechanisms (Zhang and Shi 2013; Gupta and Huang 2014; Liang et al. 2018).

Physiological, biochemical, and metabolic responses of plants to salinity and drought stresses reflected in altered metabolites including proline, carbohydrates, glycine betaine, γ-aminobutyric acid, and polyamines were described by Goharrizi et al. (2021). However, mild salt stress can also stimulate production of valuable SMs and yield of EO in MAPs (e.g., Zrig et al. 2016; Caliskan et al. 2017; El-Esawi et al. 2017; Wang et al. 2019a; Kulak et al. 2020).

In *M. piperita* subjected to salinity of 120 mM NaCl at 25 °C for 72 h the levels of phenolic compounds, proline and antioxidant activity showed 1.88-, 1.92- and 2.58-fold increases, while exposure to salinity of 120 mM at 35 °C for 72 h resulted in a 3.2-, 1.8-, 4.6- and 9-fold reduction of rosmarinic acid (RA), soluble sugar, chlorophyll (Chl) and K^+/N^+ ratio, respectively. Simultaneous higher expression levels of cinnamic acid 4-hydroxylase (C4H) and hydroxyphenylpyruvate (HPPR) genes suggested the roles of these genes in defense processes and the impact of phenolic compounds on the inhibition of oxidative stress (Gholamnia et al. 2022). Combined treatment of *Mentha* seeds with 10 g/mL of fish flour and 1% or 3% Ca had beneficial impact on crucial enzyme activities related to biosynthesis of phenolic compounds and individual phenolic contents under salt stress and diminished damage caused by salt was reflected in reduced LPO levels, enhanced enzyme activities and higher total flavonoid and phenolic contents (Chitilova and Yucel 2019). Increased vacuolar H^+-ATPase showed positive correlation with the higher salt tolerance in the halotolerate peppermint Keyuan-1 and at exposure of plants to 150 mM NaCl the salt tolerance was achieved via increasing the vacuolar H^+ pumping activity and Na^+ compartmentalization capacity. The activity of a mitogen-activated protein kinase (MAPK) was also considerably enhanced under salt treatment compared to wild type peppermint plants and MAPK protein was found to be responsible for the increased expression of vacuolar H^+-ATPase in the halotolerate plant (Li et al. 2016). Application of vibration frequency (100 Hz) before subjected the *Mentha pulegium* L. seedlings to salinity stress (50–150 mM NaCl) resulted in reduced MDA and H_2O_2 levels, electrolyte leakage, total carbohydrates, and PPO activity, while proline and protein levels as well as APX, POD and SOD activities were induced. Hence, vibration was able to induce more antioxidative enzyme activities (Ghalkhani et al. 2020). Salt stress (30–180 mM NaCl) enhanced MDA and proline accumulation in leaves and roots up to 3–4-fold but practically did not affect leaf Chl levels in *Silybum marianum* Gaertn. and *Mentha haplocalyx* Briq. plants; under salt stress SOD and CAT activities and the soluble protein content in roots (+83%) and stems by (+55%) was increased only in of *S. marianum*, while POD activity increased with increasing salt doses only in *M. haplocalyx*. On the other hand, the presence of 180 mM NaCl resulted in more than 10-fold lower ratios of K^+/Na^+ and Ca^{2+}/Na^+ ratios in both species compared to control plants (Zhou et al. 2021). Combine treatment of *M.*

spicata L plants cultivated in hydroponium with 150 mM NaCl and 60 μM Cu showed adverse impact on morphological characteristics of plants and reduced Chl content as well as levels of polyphenols and antioxidants, thereby affecting EO yield and composition (Chrysargyris et al. 2019).

NaCl (50 or 100 mM) applied as elicitor increased production of phenolic SMs (total phenolics, soluble flavonols, anthocyanins, phenolic acids) in *M. officinalis* L. but did not affect accumulation of photosynthetic pigments and functioning of the PSII; the highest impact on the production of phenolics exhibited 100 mM NaCl (Hawrylak-Nowak et al. 2021). Exogenously applied protective substances such as GSH, proline and SA to salt-stressed *M. officinalis* plants ameliorated the levels of photosynthetic pigments and proline and induced accumulation of phenolic compounds and expression of related biosynthetic genes along with increasing antioxidant capacity and alleviating stress-induced LPO. The contents of total phenolics and flavonoids were strongly correlated with the expression levels of phenylalanine ammonia-lyase (PAL) and chalcone synthase (CHS) genes, which are crucial components of the phenylpropanoid pathway (Safari et al. 2020). A dose of 100 mg/L SeNPs mitigated the negative impact of salinity on *M. officinalis* and the improved salt tolerance of plants was reflected in reduced LPO due to enhanced activities of SOD, CAT and POD. Treatment with SeNPs also increased the transcript levels of PAL and RA synthase genes in salt-stressed plants (Ghasemian et al. 2021).

Treatment with 100 mM NaCl reduced the growth of *S. officinalis* by 61% and the total fatty acids content by 32%. Increasing salinity up to 100 mM resulted in a reduction of polyunsaturated fatty acids and enhancement of monounsaturated fatty acids levels. Main constituents of the EO (α-and β-thujone, 1,8-cineole, camphor, α-humulene, viridiflorol and manool) were present at all salt treatments and maximum yield was observed at 75 mM NaCl (Taarit et al. 2010). The chemical composition of the EO of *S. officinalis* plants treated with various salts (NaCl, KCl, $MgSO_4$, $MgCl_2$, Na_2SO_4, and $CaCl_2$) at doses 50–200 mM was greatly affected by the applied salt and its concentration. α-Pinene and camphor percentages increased under all salt stress and camphene levels were also increased under all stress types except $CaCl_2$ treatment, while β-thujone increased except $MgCl_2$ treatment. In contrast to other treatments, NaCl and KCl reduced the content of α-thujone. Whereas $CaCl_2$ and $MgCl_2$ treatments reduced the percentage of 1,8-cineole, other salt treatments increased it, except of NaCl, which did not affect 1,8-cineole percentage (Kulak et al. 2020).

In *T. vulgaris* plants cultivated 2 weeks under open-field conditions 3-fold higher β-cymene and α-thujene levels were observed compared to shade enclosure conditions, while myrcene levels were four times higher in open field conditions. In thyme plants cultivated under open field conditions and treated with 150 mM NaCl for one month the main constituent of EO, thymol, reached 49% of the total EO and β-cymene showed considerable increase with increasing salinity of the medium. On the other hand, increasing salinity under shade enclosure conditions resulted in reduction of the linalool and β-cymene percentages. The polyphenols and flavonoids contents in thyme leaves of salt-stressed *T. vulgaris* were greatly affected with light intensity as well (Zrig et al. 2016).

In salt-stressed *R. officinalis* L. plants the EO components α-pinene, β-pinene, and cineole were reduced and linalool, camphor, borneol, and verbenone showed strong increase. Biweekly spraying with SA (100–300 ppm) for 8 weeks of *R. officinallis* plants subjected to saline water every 2 days (640, 2,000, and 4,000 ppm NaCl) alleviated adverse impact of salinity stress effects via increasing the total phenolic, Chl, carbohydrates, and proline levels in leaves and reducing Na and Cl levels. In addition, SA promoted the antioxidant enzymes such as CAT, SOD, and APX and increased the non-enzymatic antioxidants (e.g., free and total ascorbate) as well as the levels of APX and 3 SOD genes and expression level of selected genes conferring tolerance to salinity (bZIP62, DREB2, ERF3, and Lop) in salt-stressed plants compared to non-sprayed plants (El-Esawi et al. 2017).

Exposure of *Nepeta racemosa* Lam plants to NaCl increased yield, polyphenol and flavonoid contents, whereas treatment with Na_2SO_4 resulted in yield values, which were comparable to control, enhanced levels of photosynthetic pigments but reduced polyphenol and flavonoid contents (Lungoci et al. 2023).

Salinity did not adversely impact yield or EO contents of *Matricaria recutita* plants and the highest yield and EO content were observed under high-salinity conditions. Pronouncedly higher levels of bisabolol oxide A were detected under high-salinity, in contrast to *cis*-β-farnesene levels, which were much greater under low-salinity. High resistance of *M. recutita* plants to salinity stress was due to avoiding salt accumulation (Hendawy et al. 2019). Comparing responses of various chamomile genotypes reflected in physiological, morphological, and phytochemical characteristics under salinity stress it was found that considering both quantity and quality for the Ahvaz genotype the absence of salt, while for the Isfahan genotype at 6 dS/m, and for the Shiraz genotype 9 and 12 dS/m NaCl was favorable. Isfahan genotype preserved shoot growth and its higher tolerance to 6 dS/m NaCl was associated most likely with POD activity, while with root growth stimulation at 9 dS/m NaCl. Na compartmentation in root at 12 dS/m NaCl ensured the resistance of the Shiraz genotype. Whereas the highest oil and chamazulene content in Isfahan genotype was observed and was not affected by salinity, higher levels of flavonoid compounds were detected in the Shiraz genotype without salt treatment, in the Isfahan genotype treated with 6 and 9 dS/m NaCl and in the Ahavaz genotype at 12 dS/m NaCl (Askari-Khorasgani et al. 2017). Treatment of 14 weeks old *M. recutita* plants with different levels of salinity (50–150 mg/L) and SA (150–450 mg/L) resulted in considerable enhancement of proline levels, photosynthetic pigments and antioxidant activity. Using 150 mg/L NaCl combined with 300 mg/L SA highest amounts of eugenol, ellagic acid, catechin, hesperedin and quercetin were observed, while the highest sinapic acid content (307.1 mg/L) was detected at single treatment with 150 mg/L NaCl. On the other hand, single application of 50 mg/L NaCl and co-application of 50 mg/L NaCl and 300 mg/L SA resulted in maximum levels of chloregenic acid (66.55 mg/L) and caffeic acid (9.93 mg/L) (Fatemeh et al. 2017). According to Baghalian et al. (2008) the irrigation of *M. recutita* plants with saline water (4–16 dS/m) did not affect pronouncedly oil quantity (yield and content), oil quality (chemical composition) and apigenin content in chamomile.

Calendula officinalis plants subjected to salt stress up to 150 mM NaCl for one month showed reduced stem length and fresh weight, unchanged water content and proline levels achieving 9-fold increase. Plants responded to salt stress via the maintenance of K^+ and Ca^{2+} homeostasis and the accumulation of proline acting as osmolyte (Kozminska et al. 2017). Treatment of *C. officinalis* with saline irrigation water (0.39–9.38 dS/m) containing NaCl, $CaCl_2$ and $MgCl_2$ salts resulted in considerable reduction of the flower head yield and total flavonoids and carotenoids levels along with increasing the EO content and its key constituents α-cadinol, γ-and δ-cadinene. Approximately 81 days after bud formation fresh and dry weights of flower heads and EO showed an increase and the content of total flavonoids and carotenoids increased 111 days after bud formation (Khalid and da Silva 2010).

Treatment of *Hypericum pruinatum* plants with of $MgSO_4$, $CaCl_2$ and NaCl salts applied at doses 1–8 dS/m increased the levels of phenolic compounds, namely chlorogenic acid, rutin, hyperoside, isoquercetine, quercitrine and quercetine and the effect was outstanding mainly at higher applied salt doses; phenolic compounds were found to play an influential physiological role in salinity tolerance (Caliskan et al. 2017). NaCl-stress greatly reduced production characteristics of *Hibiscus cannabinus* plants and increased accumulation of H_2O_2, $O_2^{\bullet-}$, MDA, proline, total soluble sugar, and total soluble protein in plants along with increasing the content of antioxidants, including phenolics and flavonoids. Salt stress also induced production of the volatile compounds including heptacosane, 1-octadecanesulphonyl chloride, and tetratetracontane. Biosynthesis of 1-heptacosanol was promoted only at low salinity and disappeared at treatment with high salt concentrations (Birhanie et al. 2022). Investigation of the impact of salt stress on accumulation of bioactive compounds and salt tolerance of *Glycyrrhiza glabra* it was found that higher amounts of glycyrrhetinic acid and glycyrrhizin were produced in treated plants and glycosyltransferases probably greatly contributed to the accumulation of flavonoid glycosides and glycyrrhizin. In the presence of 50 mM NaCl corresponding to the low salt stress best expression levels of bAS and CHS in licorice were observed (Wang et al. 2019a).

In *Lonicera japonica* Thunb plants exposed to salt stress the accumulation of phenolic acids correlated with antioxidant enzyme activity resulting in reduced oxidative damage (Cai et al. 2021) and salt-stress disturbed the phenylpropanoid pathway, monoterpenoid biosynthesis, glycolysis, tricarboxylic acid (TCA) cycle, and alkaloid biosynthesis in *L. japonica* plants (Cai et al. 2020). Current findings related to the roles of SA in salinity tolerance, the responses of plants to salt, and the corresponding mechanisms were overviewed by Hoque et al. (2020). In *Salicornia europaea* exposed to salt stress as key metabolites responding to this abiotic stress sucrose, glucose, proline, quercetin and its derivatives, and kaempferol derivatives are considered, whereby glycolysis, flavone and flavonol biosynthesis, and phenylpropanoid biosynthesis are the most important pathways ensuring enhanced osmotic tolerance and antioxidant activities is salt-stressed plants. Ameliorated salt tolerance under the 50 mM NaCl treatment compared to treatment with 300 mM NaCl is caused by higher accumulation of some saccharides, flavonoids, and phenolic acids. Coumaric, caffeic, and ferulic acids increased considerably in the roots, while quercetin, quercetin derivatives, and kaempferol derivatives showed varied change patterns in the roots and shoots (Duan et al. 2023).

8.4 Waterlogging Stress

A flood is defined as temporary covering by water of land not usually covered by water (EU Directive 2007). A flooding is defined as "the overflow of water from a river, lake or ocean when the water overtops or breaks levees or the accumulation of rainwater on saturated ground in an areal flood" (Folorunso 2021). In contrast to submergence, when the aerial plant parts are completely covered with water, under waterlogging only roots are covered with water (Sasidharan et al. 2017). The roots of plants subjected to waterlogging stress cannot respire because soil profile contains excess water and the amount of oxygen in the pore space for plant roots is insufficient to ensure adequate respiration. Therefore, waterlogging represents serious threat to plants growing in land prone to flooding. Under climate change the global exposure to floods will increase depending on the degree of warming (Parent et al. 2008; Kundzewicz et al. 2010; Ashraf 2012; Hirabayashi et al. 2013).

During waterlogging aerobic respiration of plants is inhibited resulting in limited energy metabolism and suppressed growth and developmental processes. The impact of waterlogging stress on the morphological structure, photosynthesis, respiration, ROS-caused damage, hormone synthesis, and signaling cascades in exposed plants was comprehensively discussed by Arnell and Gosling (2016) and Pan et al. (2021). Anoxia, i.e. total depletion in the level of O_2 in plant tissues, can be one consequence of waterlogging. Survival of plants suffering on anoxia requires reduction of energy requirements of cells and energy production under anoxia declines by 65–97% compared to that observed in air. During prolonged anoxia of several days a part of produced energy is utilized to alleviate acidifying effect on cytosolic pH, even though a cytoplasmic acidosis occurring in some anoxia-intolerant tissues may contribute to their death (Gibbs and Greenway 2003; Greenway and Gibbs 2003).

Flooding usually results in reduced cellular O_2 content, severe reduction of which is observed especially at impaired photosynthesis. Consequently, anaerobic respiration must ensure production of ATP and regeneration of NAD^+. At the developmental level, plants can respond to the low O_2 stress under flooding via altering cellular and organ structure enabling access to O_2 and its diffusion using phytohormones such as ethylene, gibberellin, and ABA (Bailey-Serres and Voesenek 2008). On the other hand, Fukao et al. (2019) in a review paper focused on known or suspected components of submergence/waterlogging stress such as the influence of light/dark cycles, protein isoforms, root architecture, sugar sensing and signaling, miRNA and retrotransposon expression, post-stress molecular events, heavy-metal and salinity stress.

The O_2 sensing mechanism relies on the O_2-dependent destabilization of the group VII ethylene response factors (ERFVIIs), a cluster of ethylene responsive transcription factors; an homeostatic mechanism controls gene expression in plants occurring in hypoxia environment to restrain excessive activation of the anaerobic metabolism, which could be deleterious for the survival of stressed plants (Loreti et al. 2016). Under waterlogging stress all the signaling and physiological pathways are directly or indirectly related to glycolysis, TCA cycle, programmed cell death and ROS removal. Genes responsible for alanine aminotransferase have a decisive role in developing waterlogging-tolerant plants, which are able to control anaerobic fermentation and TCA cycle along with effective utilization of carbons (Bashar et al. 2020).

Mentha aquatica L. plants cultivated under moderately drained and waterlogging conditions induced differently aerenchyma formation in roots, considerably increased growth characteristics, RWC as well as protein content and antioxidant enzyme activity, in contrast to H_2O_2, proline and MDA levels, which were reduced. *M. aquatica* was found to be a waterlogging tolerant plant and waterlogging strongly enhanced activities antioxidant enzymes also in salt-treated plants (Haddadi et al. 2016). *Mentha arvensis* plants exposed to waterlogging stress showed improved adaptive characteristics compared to *M. piperita* plants and were able to exhibit flourished vegetative growth under waterlogged condition. Under waterlogged condition *M. arvensis* was able to withstand 16 days compared to 12 days observed with *M. piperita*. In addition, under waterlogging stress *M. arvensis* reduced its total carbohydrate reserve, while *M. piperita* conserved it and progressively increased its concentration. Lower LPO as well as robust outgrowth of adventitious roots also contributed to improved waterlogging tolerance of *M. arvensis* plants. Moreover, under hypoxia conditions *M. arvensis* plants maintained higher RWC, soluble protein and Chl contents as well as nitric oxide scavenging activity than *M. piperita* plants (Phukan et al. 2014). In *M. pulegium* plants exposed to waterlogging stress leaf RWC, Chl and ascorbate contents as well as SOD, CAT, and PODs activities were lower, while carotenoid contents were higher than in control plants and a 4-fold increase in LPO on the 8th day in stressed plants was observed as well; early MDA accumulation under waterlogging stress can suggest impaired ability for radical scavenging (Candan and Tarhan 2012).

Whereas flooding treatment did not affect stomata, plant growth, water content, fluorescence and gas exchange of *M. officinalis* plants, anthocyanin content in leaves was found to be increased. Lower resistance to flooding showed *O. basilicum* plants because the gas exchange in treated plants achieved only a third of the control plants (Baczek-Kwinta et al. 2008).

Sesamum indicum plants exposed to waterlogging stress during the vegetative stage up to 8 days were characterized with increased LPO and H_2O_2 levels as well as methylglyoxal contents. Prolongation of waterlogging resulted in reduced leaf RWC and proline content, decreased levels of photosynthetic pigments (Chl*a*, Chl*b* and carotenoids), increased levels of reduced (GSH) and oxidized glutathione (GSSG), decreased ascorbate content and declined GSH/GSSG ratio suggesting disruption of redox balance in the cell. Whereas the waterlogging stress resulted in increased activities of APX, MDHAR, and glutathione peroxidase; the activity of dehydroascorbate reductase, GR, and CAT activity in the majority of cases showed a decrease.

Waterlogging also predominantly enhanced glyoxalase II activity, while only slight increase in glyoxalase I activity was observed (Khan et al. 2020a).

Under waterlogging stress, the roots of *Plantago fengdouensis* and *Plantago asiatica* accumulated GSH more effectively in roots compared to leaves and considering free proline levels and CAT, APX, and GR activities especially in root system, *P. fengdouensis* was found to be more tolerant to waterlogging stress than *P. asiatica* (Yang et al. 2015).

In *Chrysanthemum morifolium* seedlings exposed to waterlogging stress Chl content and relative leaf water potential (Ψ) were reduced, while an increase in MDA, GSH and soluble sugar levels was observed. When the waterlogging stress lasted for 4 days it was not possible to restore the physiological and biochemical characteristics of plants (Zhang et al. 2009).

Exogenous melatonin application considerably improved waterlogging tolerance of *Prunus persica* manifested by new leaves, root activity, increased Chl contents as well as by the higher levels of relative Chl content and stomatal aperture compared to untreated waterlogging-stressed plants. In melatonin-treated plants subjected to waterlogging stress the antioxidant function of melatonin was confirmed by higher SOD and POD levels and lower LPO and H_2O_2 levels as well as ethylene content. Melatonin also controlled the anaerobic respiration via increased aerenchyma and the restrained regulation of metabolic enzymes; in addition, melatonin increased the expression levels of Ca^{2+} signaling and hypoxia-related ERF VII transcription factor genes (Gu et al. 2021).

By placing of pots containing *Hypericum brasiliense* plants, which were saturated with water, in other pots filled with water, hypoxia was produced and content of active constituents under waterlogging stress was investigated. It was found that the stress resulted in an increase of the concentration of some SMs in shoots compared to control plants (57.3 vs. 31.5 mg/g for total soluble phenols; 306.4 vs. 82.5 μg/g for 1,5-dihydroxyxanthone; 2.3 vs. 0.3 mg/L for rutin; 4.5 vs. 2.3 mg/L for betulinic acid), while concentration of quercetin decreased (0.4 vs. 1.4 mg/L). On the other hand, higher root concentrations under hypoxia were found for isouliginosin B (39.1 vs. 11.4 μg/L) and betulinic acid (2.7 vs. 1.3 mg/L), in contrast to total soluble phenols (4.5 vs. 5.2 mg/L) and 1,5-dihydroxyxanthone (11.9 vs. 16.5 μg/L), which showed a moderate decrease. Compared to control plants the MDA levels in stressed plants increased both in shoots (8.6 vs. 3.0 mmol/g) and roots (1.1 vs. 0.2 mmol/g). Increased levels of SMs in stressed plants were produced likely as a response to the ROS generation during waterlogging stress (De Abreu and Mazzafera 2005).

Formation of new aerenchymatous adventitious roots (ARs), originating from preformed, dormant primordia on the stem in flooding-tolerant plants, can ensure sustained root function in the hypoxic environment. Flooding resulted in ethylene accumulation in the lower stem region of *Solanum dulcamara* and in a decline of ABA level in both stem and AR primordia tissue. Moreover, flooding and ethylene treatment induced expression of the polar auxin transporter PIN2, whereby silencing of this gene or chemical inhibition of auxin transport suppressed primordium activation also under reduced ABA levels (Dawood et al. 2016).

Ren et al. (2017) investigated the impact of short-term (3 h) and long-term (27 h) waterlogging on *Sesbania cannabina* roots using transcriptome profiling and found reprogramming of the expression of 2719 and 9738 differentially expressed genes (DEGs). Hypoxic stress conditions resulted in promotion of glycolysis and fermentation pathways to ensure ATP production. The expression pattern of 10 unigenes involved in phenylpropanoid biosynthesis, glycolysis, and amino acid metabolism were estimated and the crucial genes and metabolic pathways playing important roles in waterlogging were evaluated.

8.5 Temperature Stress

8.5.1 Heat Stress

Heat stress greatly limits productivity of crops. It can be defined as an increase in temperature lasting a certain period of time, which can cause injury to plants when temperatures exceed the threshold by 10–15 °C (Firmansyah and Argosubekti 2020). Such heat waves during summers cause yield losses in agriculture globally that represents risks for global food security in the future (Wani et al. 2017).

Heat stress-induced changes in the development systems of plants highlighting the morpho-anatomical, physiological, and molecular adaptations were summarized by Ul Hassan et al. (2021). Heat stress downregulates important chloroplast components, thereby damaging the chloroplast, inactivates proteins sensitive to heat (e.g., Rubisco activase), impairs photosynthetic efficiency, eventually also causing cell death (Zahra et al. 2023). High temperature causes alteration in various components of the cell and modifies membrane fluidity, Ca^{2+} ions, cyto-skeleton elements and protein unfolding and can also affect the content and composition of SMs (Asensi-Fabado et al. 2013; Alhaithloul et al. 2020; Park et al. 2022). In response to heat stress strong upregulation of heat shock proteins (HSP) playing crucial in conferring abiotic stress tolerance, improving membrane stability and detoxifying ROS via regulating the antioxidant enzymes system in plants is observed (Firmansyah and Argosubekti 2020). Samtani et al. (2022) discussed the molecular changes observed in cells under rising temperature and their association with thermomorphogenesis and thermotolerance. Regulatory mechanisms of heat stress response and thermomorphogenesis, which is activated under moderately elevated temperatures, below the heat-stress range in plants were highlighted by Zhou et al. (2022). The impact of heat stress on medicinal plants was analyzed by Masarovičová et al. (2019).

As mentioned above, high temperature in the atmosphere causes heat stress for plants accompanied with numerous morphological, physiological and biochemical alterations in plants accompanied with eliciting production of several valuable SMs, and CO_2 plays an important role in the upregulation of atmospheric temperature (Jamloki et al. 2021).

In *M. piperita* plants grown at 25 °C under salinity of 120 mM a 1.88-, 1.92- and 2.58-fold increase in phenolic compounds, proline and antioxidant activity compared to control plants was observed after 72 h treatment. On the other hand, at heat stress of 35 °C under the same salinity level RA, soluble sugar, Chl and K^+/N^+ ratio were found to be reduced 3.2-, 1.8-, 4.6- 9-fold after 72 h treatment. Simultaneously, considerable increase in the expression of HPPR and C4H genes, while pronounced decrease in RAS expression was observed in peppermint plants exposed to simultaneous stresses. The C4H and HPPR genes play a role in defense processes and the effects of phenolic compounds in inhibiting oxidative stress (Gholamnia et al. 2022). Moreover, exposure of *M. piperita* and *Catharanthus roseus* plants to drought and/or heat stress (35 °C) for one and two weeks increased accumulation of osmolytes (proline, sugars, glycine betaine, and sugar alcohols including inositol and mannitol) and tannins, terpenoids, and alkaloids contents, and reduced TPC, TFC and saponin contents; the greatest changes in metabolite levels were observed under exposure to the combined heat/drought stress (Alhaithloul et al. 2020).

Among three investigated medicinal plants, which were exposed to increasing temperatures for 5 days and subsequently exposed to heat stress, *M. officinalis* was more sensitive to heat stress compared to *R. officinalis* and *S. officinalis*. In *M. officinalis* repetition of heat stress reduced RWC and increased α-tocopherol and SA levels, while both other medicinal plants were characterized with ameliorated water contents and reduced jasmonic acid levels in *R. officinalis* and ABA and MDA levels in *S. officinalis* plants previously exposed to high temperatures, suggesting acclimation to stress conditions. Increased α-tocopherol and hormone levels resulted in comparable protective effects in *R. officinalis* and *S. officinalis* plants, which also showed higher resistance under exposure to combine heat and drought stresses than *M. officinalis* plants that died under these conditions (Asensi-Fabado et al. 2013). Treatment with exogenous SA positively affected the EO quantity quality of *S. officinalis* plants due to increased chamazulene and α-(–)-bisabolol levels under normal and heat stress conditions. Whereas Bona cultivar grown under heat stress conditions and treated with 10 mg/L SA showed the highest chamazulene amount of 6.66%, under normal conditions this cultivar achieved the highest α-(–)-bisabolol amount (3.41%) (Ghasemi et al. 2016b). Net assimilation rates and stomatal conductance to water vapor were more affected in *O. basilicum* L. and *S. officinalis* L. exposed to cold–heat consecutive stress than to heat–cold successive stress and emissions of VOCs showed an increase in plants under successive stress compared to control plants. On the other hand, the successive stresses did not affect TPC and TFC compared to plants under only one type of treatment (Copolovici et al. 2022).

In three chamomile cultivars (Bushehr, Bona, Bodegold) cultivated under heat stress conditions considerable decrease in the total Chl content was observed compared to normal conditions in contrast to increased proline content, which was the highest in Bona cultivar. On the other hand, heat stress did not affect pronouncedly the EO content but it was ameliorated by application of exogenous SA (Ghasemi et al. 2016a). The EO of chamomile had a blue to dark blue color likely due to increased levels of phenolics including flavonoids, anthocyanins, and plant steroids (Salamon 2006) Investigation of responses of *C. officinalis* L. to heat stress from

35 to 42 °C showed that increasing incubation temperature and stress duration (0–21 days) resulted in increased electrolyte leakage (Nazdar et al. 2019). Exposure of *Hypericum perforatum* plants to high temperature of 35 °C for 15 days enhanced hypericin, pseudohypericin and hyperforin concentrations in the shoot as well as leaf total POD activity and reduced photosynthetic efficiency of plants compared to plants cultivated at 20 and 25 °C (Zobayed et al. 2005).

The most favorable levels of chlorogenic acid, rutin, *trans*-2-decenal, total phenolic concentrations and the antioxidant capacity of the coriander plants cultivated in hydroponium in plant factory were achieved at combination of photosynthetic photon flux density (PPFD) of 300 μmol/m^2·s and root-zone temperature (RZT) of 30 °C, whereby the response of chlorogenic acid in leaves was more sensitive compared to rutin. On the other hand, considering the plant biomass and water content of leaf and stem, combination of PPFD of 300 μmol/m^2·s and RZT of 25 °C was the most suitable (Nguyen et al. 2019).

Under exposure of *C. sativa* plants to heat stress (45–50 °C) for 7 days the plants were completely wilted regardless of the water supply (1 L/day) and exhibited increased transpiration. From investigated SMs the amount of cannabigerolic acid (CBGA) under heat stress was reduced by 182 μg/g compared to control (206 μg/g) and content of cannabigerol (CBG) was reduced as well. It was supposed that the enzymatic conversion of CBGA to Δ-tetrahydrocannabinolic acid (THCA) and cannabidiolic acid (CBDA) was faster under heat stress resulting in enhanced concentrations of terminal cannabinoid along with depletion of precursor pool. However, while no pronounced difference was estimated in the concentrations of THCA and CBDA, the enzymatic conversion was likely not affected and the biosynthesis of CBGA may have been downregulated upstream in the cannabinoid biosynthetic pathway during the initiation of flowering (Park et al. 2022).

In *Glycyrrhiza uralensis* roots exposed to heat stress of 35, 45 and 55 °C the H_2O_2 content was practically not affected, while at temperatures 35 and 45 °C SOD and POD activities increased and further temperature increase to 55 °C was accompanied with a decrease in SOD activity. On the other hand, CAT activity was not considerably reduced but 1,3-diphosphate glyceric acid levels showed pronounced increase. At 35 °C the activity of PAL was higher than at 45 and 55 °C, whereas changes in L-phenylalanine levels were not observed. Under investigated temperatures the levels of SMs such as celery liquiritin, celery isoliquiritin, glycyrrhizin and isoglycyrrhizin were increased, in contrast to the contents of liquiritin and isoliquiritin, which were reduced. It was concluded that flavonoids and glycyrrhiza antioxidant enzyme activity system exhibit synergistic effect in protecting plants against ROS, whereby flavonoids play a crucial role in the early stage (Gao et al. 2019).

Two-year-old saplings of *Ginkgo biloba* L. exposed to high temperature showed lower photosynthetic rate, leaf water potential (Ψ) and root/shoot ratio and enhanced stomatal conductance and light compensation point were observed; however, only alterations in light saturation point, flavonol glycoside and terpene lactone contents were observed. Heat and drought stresses increased dark respiration rate leading to plant growth inhibition, whereby high temperature affected SMs to greater extent than drought (Zhang et al. 2005).

8.5.2 Cold Stress

Depending on the temperatures and some physiological mechanisms acting in different temperature ranges cold stress in plants can be classified into chilling stress (0–20 °C) and freezing stress (<0 °C). Plant freezing tolerance is associated directly with the capability of plant to suppress the formation of ice crystals in cells. Chilling stress can induce cold acclimation, thereby increasing the freezing tolerance of a plant (Guy 1990; Thomashow 1999). Cold-stressed plants lose water in freezing situation by osmosis and cold stress can result in reduced cell membrane fluidity accompanied with conformational changes in membrane proteins, accumulation of metabolites, and a change of the redox state in the cells. In plants exposed to low temperatures excess generation of ROS causes oxidative stress and cold-resistant plants respond to such conditions by high activity of antioxidant enzymes (Szymańska et al. 2017). Under cold stress plants induce adaptive defenses involving production of osmotic factors to ensure prevention for freezing and reprogramming of transcriptional pathways (Yadav 2010; Takahashi et al. 2013; Masarovičová et al. 2019). Inhibition of the repair of PSII at low temperature stress was observed previously without affecting the photodamage to PSII (Allakhverdiev and Murata 2004). As during cold stress excess ROS generation occurs, the cold-resistant plants usually show high activity of antioxidant enzymes. Consequently, amelioration of the activities of antioxidant enzymes effectively contributes to acquire cold resistance in plants (Szymańska et al. 2017). On the other hand, cold stress also affects plant growth and development, thereby influencing the plant life cycle. Findings related to cold perception and signal transduction from the plasma membrane to the nucleus involving cold sensors, Ca signals, Ca-binding proteins, MAPK cascades, the C-repeat binding factor/dehydration-responsive element binding pathways, and trehalose metabolism were summarized by Guo et al. (2018). Cold acclimation of plants also includes the expression of certain cold-induced genes that function to stabilize membranes against freeze-induced injury (Thomashow 1999). Signaling and response of plants to low-temperature stress was overviewed by Aslam et al. (2022), an overview of cold stress regulation in plants was presented by Manasa et al. (2022), and Bhat et al. (2022) discussed low temperature stress tolerance in legume crops using omics approaches.

The cold tolerant and cold-sensitive plant species exhibit different responses to cold stress. The membranes show crucial role in thermal sensing via activation of mechanosensitive Ca^{2+}-influx channels, when increased Ca level in the cytosol is sensed by some kinases such as Ca-dependent protein kinase and MAPK, which transduce the signals to switch on the transcriptional cascades and in response to cold stress interactive functioning of ICE-CBF-COR genes is involved. In plants exposed to cold stress besides increased activities of enzymatic antioxidants such as SOD, CAT, APX and GR and enhanced biosynthesis of non-enzymatic antioxidant such as GSH and ascorbic acid, which contribute to attenuation of the cold-induced oxidative damage, also synthesis of some cryoprotectants including sugars, proline, glycine betaine, trehalose, and polyamines is activated (Thakur and Nayyar 2013).

Under chilling temperatures (1–10 °C) diverse physiological disturbances in the cells of chilling-sensitive plants can be observed resulting in chilling injury and death of tropical and subtropical plants can be observed (Lukatkin et al. 2012). Under cold stress plant growth process (meristems) is affected long time before photosynthetic carbon gain is affected, thus, plants growing in cold climates are usually not carbon limited (Körner 2016).

Evaluation of the productivity and oil profile of *M. spicata* L harvested during the period from 14 September to 1 November (when already frost was observed) showed that the oil content was high at 14 September but low from 24 October, carvone concentration varied from 42% to 75% and achieved a maximum at the 12 October harvest date, while concentration of limonene was the lowest at 14 September. In the spring of the next year *M. spicata* emerged in late April and was unaffected by the winter or by the early spring frosts suggesting that it can survive as a viable crop at elevation of approximate to 1170 m (Zheljazkov et al. 2012).

Cold treatment at 4 °C of *Ocimum tenuiflorum* plants resulted in almost negligible decrease in eugenol, the major secondary metabolite of the plant after 72 h but some plants died. A comparative differential gene expression study between the common transcripts in cold stress with respect to the control showed that out of the 8 transcripts, 4 transcripts were related to the cold stress response (CDS_30339_Unigene_49530, CDS_5730_Unigene_11635, CDS_8224_Unigene_16350, and CDS_10777_Unigene_20262). As “CDS_8224_Unigene_16350”, a cold responsive calmodulin-like gene (CML), was found to be upregulated in plant leaves treated with cold stress for 72 h, it can be supposed that it can contribute to withstanding of extremely cold sensitive *Ocimum* plant to cold stress (Rastogi et al. 2019).

Exposure of *C. officinalis* to cold stress (4 °C) resulted in enhanced accumulation of osmoprotectants (proline, soluble sugars, glycine betaine and trehalose), phenolics and proteins, and increased antioxidant activities of APX, GR and SOD, while CAT activity showed a decrease. Moreover, under cold stress upregulation of transcript expression of cold-responsive genes (SOD, CAT, APX, GR and DREB1) was observed (Jan et al. 2018). Accumulation of anthocyanins in *Mikania micrantha* during winter was reported as an adaptation strategy of plants to low winter temperatures (Zhang et al. 2019).

Hypericum genus contains many valuable SMs including naphthodianthrones, acylphloroglucinols, flavonoids, and phenylpropanes, whereby chlorogenic acid and flavonoids (amentoflavone, quercetin or kaempferol glycosides) are considered as the most defense-related metabolites ensuring plant tolerance against abiotic/biotic stresses. Species-specific cold-induced phenolic profiles of ten representatives of the genus *Hypericum* from different provenances were investigated, and principal component analysis showed a relationship between the level of defense-related phenolic compounds and interspecies differences in stress tolerance, suggesting that the inherent mechanisms of cold tolerance in *Hypericum* species are related to their origin (Brunakova et al. 2022). Physiological and transcriptomic analysis of *H. perforatum* plants grown at 15 and 22 °C showed that cultivation of plants at lower temperature resulted in increased stomatal density, opening percentages and hypericin content by 1.1- and 1.4- and 4.5-fold compared to plants grown at 22 °C. Moreover, in plants grown 22 °C a total of 1584 DEGs were evaluated (including 749 characterized genes, 421 upregulated and 328 downregulated genes) compared to plants grown at 22 °C, whereby 150 genes were associated with hypericin biosynthesis, plant growth and the stress response (Su et al. 2021). Investigation of 11 candidate reference genes in *H. perforatum* plants exposed to cold and heat stresses showed that the best-ranked reference genes differed between cold- and heat-treated samples and TUB was evaluated as the most stable gene in both experimental conditions., while GSA and GAPDH can be considered as reliable reference genes in cold-treated samples and GAPDH exhibited low expression stability in heat-treated samples. Whereas 26S rRNA and H2A were characterized with the highest stabilities under heat stress, H2A stability in the cold assay was lower. AOX1, AOX2, CAT1 and CHS genes, linked with plant stress responses and oxidative stress showed differential expression profiles over time in treated samples (Velada et al. 2014). Activation of genes coding for enzymatic antioxidant CAT and SOD at both the transcript and protein levels in *H. perforatum* plants exposed to low temperature was reported by Skyba et al. (2012). *H. perforatum* can be considered as frost tolerant plant based on the frost-killing temperature (LT_{50}) of control plants and LT_{50} decreases by >10 °C in cold-acclimated plants. Although the freezing tolerance/avoidance in *H. perforatum* and *H. canariense* (endemic to (sub)tropical Canary Islands and Madeira) under a subfreezing temperature of −4 °C depended on the course of ABA accumulation/depletion, the effect of dehydration or treatment with 76 μM ABA on the level of endogenous ABA was comparable. Even though a 1.6-fold increase in the content of naphtodianthrone and a 1.5-fold increase of ABA was observed in *H. perforatum* plants exposed to −4 °C for 48 h, both dehydration and exogenous ABA did not affect the content of these compounds suggesting that ABA signaling is likely involved into naphtodianthrones biosynthesis under subfreezing conditions and this mechanism could be altered by plant tolerance to cold environments (Brunakova et al. 2015).

Cold acclimation at 8–10 °C for 2 days was reported to mitigate PSII inhibition and oxidative damage in tobacco leaves induced by cold stress of 4 °C, which was reflected in pronouncedly reduced cyclic electron flow as well as proportion of regulatory energy dissipation; under cold acclimation treatment ROS accumulation including $O_2^{\bullet-}$ and H_2O_2 was induced along with increased the activities of SOD, POD, CAT and APX as well as increased accumulation of soluble sugar and soluble protein. Thus, induction of antioxidant enzyme activity, accumulation of osmoprotectats and initiation of photoprotective mechanisms resulted in ameliorated cold resistance of *Nicotiana tabacum* leaves (Wei et al. 2022).

In wild (AGB002) and cultivated genotype (AGB025) of *Withania somnifera* (L.) Dunal plants exposure to cold stress (4 °C) lasting 7 days resulted in increasing accumulation of O_2 and MDA as well as SOD, CAT, APX and GR activities with the prolongation of treatment. At the end of treatment, reduced levels of withanone (WS-2) content in leaves were observed in both genotypes along with a significant increase in leaf withaferin A content, indicating the possible involvement of withanolides in cold protection. Plants of wild genotype AGB002 exhibited higher accumulation of antioxidant enzymes and selected withanolides than AGB025 suggesting their better adaptation to cold stress compared with cultivated genotype AGB025. Increased accumulation of withanolide during cold stress contributed to ROS scavenging (Mir et al. 2015).

Investigation of the impacts of cold on the metabolome and transcriptome of *Fagopyrum tataricum* showed that plants responded to cold stress (4 °C) lasting 8 days with greatly increased content of sugars and their derivatives (e.g., sucrose increased more than 12.4-fold and maltose more than 20.6-fold) and cyanidin 3-*O*-glucoside and cyanidin 3-*O*-rutinoside contents increased more than 11.3-fold and 6.3-fold, respectively, compared to control plants cultivated 25 °C. An increase in some organic acids derived from the TCA cycle compared to control plants was also observed. In contrast, cold-treated plants were characterized with reduced content of some of amino acids and their derivatives. Moreover, most of the phenylpropanoid biosynthetic transcripts were upregulated in cold-treated plants (Jeon et al. 2018).

Prolonged and constant low-temperature stress resulted in a decrease in the content of phenolic substances (caffeic, *p*-coumaric, ferulic and caffeic acid derivatives) and in a decrease in the radical-scavenging capacity in the leaves of both sensitive and more tolerant grape varieties. However, the more tolerant variety showed higher content of phenolic compounds and better radical-scavenging capacity compared to cold-sensitive variety (Krol et al. 2015).

In *Panax ginseng* plants growing for 7 days at 10 °C and then transferred to 25 °C for 28 days plant adventitious roots were stimulated and the accumulation of ginsenosides and the content of total ginsenosides increased 2.53-fold compared to plants grown at 25 °C due to expression of related genes (Wang et al. 2019b).

Flavonoid accumulation in *G. biloba* leaves was affected by day-night temperature. Whereas quercetin, kaempferol and isorhamnetin levels decreased under the 35/30 °C, they increased at 15/10 °C and the highest content of flavonoids was observed under 15/10 °C on the 40th day. Lower temperature also stimulated accumulation of soluble sugars but the accumulation of soluble proteins was not affected by the temperature. ABA was found to function as a stimulator of flavonoid accumulation under high-temperature condition (Guo et al. 2020). Biochemical responses of grape berry flavonoids to high and extreme high temperatures were overviewed by Gouot et al. (2019).

At investigation of cold acclimation and freezing tolerance in three *Eucalyptus* species, *E. grandis* Hill ex Maiden, *E. dunnii* Maiden and *E. benthamii* Maiden Cambage it was found that frost tolerance of *E. benthamii* under control and acclimation scenarios was found to be higher compared to *E. grandis* and *E. dunnii*, likely due to highest accumulation of phenolics, anthocyanins and soluble sugars and lower levels of assimilation pigments and related proteins compared to both other tested *Eucalyptus* species, and metabolic profiles differed among species as well. On the other hand, cold acclimation resulted in increased frost tolerance as well as enhanced levels of osmoprotectants and antioxidant in all 3 species (Oberschelp et al. 2020).

8.6 Radiation Stress

Plants are photosynthetic organisms, which require for their growth and development photosynthetically active radiation (PAR; 400–700 nm) provided by sunlight. However, light can also act as an abiotic stressor affecting plant stress responses (Roeber et al. 2021). Solar radiation comprises also ultraviolet radiation (UV < 400 nm) involving UV-C (200–280 nm), harmful UV-B radiation (280–320 nm) causing severe damaging impact on plant growth and development, UV-A radiation (320–400 nm) as well as far red radiation (FR ca. 700–780 nm) (Nawkar et al. 2013). It should be noted that blue light has shorter waves (ca. 450–495 nm) than red light (ca. 620–750 nm) and therefore carries more energy than red light (UCAR 2023). Stress induced by radiation generates excess ROS and the main targets of radiation in plants are DNA, cell membranes, lipids and proteins and photosynthetic apparatus (Hideg et al. 2013; Nawkar et al. 2013), while excess radiation can also stimulate plant growth and increase stress resistance (Tan et al. 2023). Moreover, ROS such as H_2O_2, $O_2^{\bullet -}$ and $^{\bullet}OH$ can stimulate the antioxidant system of plants and function as signaling molecules (Tan et al. 2023). UV-B and UV-C stress radiation has also been found to induce the biosynthesis of phenolic and flavonoid compounds in plants as well as other valuable metabolites (Rai et al. 2011; Zhang et al. 2017, 2018a; Lv et al. 2021; Rizi et al. 2021; Emus-Medina et al. 2023).

Light intensities above the light saturation point of photosynthesis, i.e., high light (HL) stress, show an adverse impact on plants by causing photoinhibition of PSII, generating excess ROS in PSII and PSI (Szymańska et al. 2017; Singh and Thakur 2018), and also causing specific and dynamic transcriptional changes in gene expression (Li et al. 2018). Under HL stress plants regulate hormones, photosynthesis and the phenylpropanoid pathway and for the high light response both ABA and phytochrome interacting factors are necessary (Huang et al. 2019). Accumulation of plant SMs greatly depends on various environmental factors including light, temperature, soil water content, soil fertility and salinity, and alteration in an individual factor can result in modification of their content (Yang et al. 2018). The impact of UV-B irradiation on the concentration of SMs (alkaloids, terpenes/terpenoids, and phenolics) in medicinal plants along with the fate of the genes and enzymes involved in their biosynthetic pathways was discussed by Takshak and Agrawal (2019). Jung et al. (2020) performed transcriptome analysis of *P. ginseng* response to HL stress. HL stress resulted in a total of 438 highly expressed DEGs from 29,184 representative transcripts, whereby 326 were upregulated and 114 transcripts were downregulated. Majority of upregulated and a considerable number of downregulated transcripts was associated with stress responses and cellular metabolic processes.

8.6.1 Impact of UV-B Radiation

Low dose of supplemental UV-B (+1.8 and +3.6 kJ/m^2·d above ambient) in field conditions did not affect biomass of aromatic herb *Cymbopogon citratus* (D.C.) Staph but increased the levels of carotenoids and phenolic compounds and volatile oils production. In addition, it was found that the low dose of supplemental UV-B radiation increased epidermal transmittance via dense waxy deposition on the adaxial surface of exposed leaves (Kumari and Agrawal 2010). In *Achyranthes bidentata* Blume seedlings exposed to UV-B radiation for 3 and 2 h pronounced increase in oleanolic acid and ecdysterone levels were observed and this increase was due to upregulating the relative expression levels of key enzyme genes involved in biosynthesis of these SMs. On the other hand, under UV-B irradiation Chl*a*, Chl*b* and carotenoid production was reduced (Li et al. 2019). An equal ratio of red and blue light enhanced in vitro cultured *Pfaffia glomerata* biomass and anthocyanin content and 20-hydroxyecdysone production by 30–40% (Silva et al. 2020).

Salvia verticillata plants exposed to UV-B radiation of 10.97 kJ/m^2 per day for up to 10 days showed increased production of phenolic compounds and reduced leaf dry biomass and Chl levels. On the 5th day and recovery time the plants contained 1.34-fold higher total phenol and 2-fold higher flavonoid concentration compared to control and the highest amount of phenolic acids in young leaves. The highest level of antioxidant activity was observed at 5th day of the experiment and antioxidant activity correlated with the amount of phenolic compounds. Moreover, under UV-B irradiation increased the expression of PAL, tyrosine aminotransferase, and RA synthase achieving the highest level in young leaves on the 10th day (Rizi et al. 2021). Exposure of *Salvia miltiorrhiza* hairy root culture to the combined elicitation with UV-B irradiation and methyl jasmonate (MeJA) for 9 days resulted in 4.9-fold increase of tanshinone level over the control (Wang et al. 2016).

Metabolite profiling of *M. officinalis* investigating the recovery of UV-B stressed plants after the removal of UV irradiation showed that the recovery of glycolysis and phenylpropanoid pathway to the original state was rapid, in contrast to TCA cycle and amino acid biosynthesis, which was slow (Kim et al. 2018). UV-B radiation considerably enhanced the levels of rosmarinic and carnosic acids, as well as naringin and carnosol in *Salvia rosmarinus* plant leaves (Luis et al. 2007).

Prunella vulgaris plants, which were in full-bloom stage exposed to UV-B irradiation for two weeks showed considerably higher POD and SOD activities and GSH levels compared to the control plants along with pronouncedly enhanced H_2O_2, MDA and proline levels as well as greatly increased total flavonoids, total phenolics, RA, caffeic acid and hyperoside levels (Zhang et al. 2017). Compared to control plants the soluble sugars and flavonoids contents in an alpine medicinal plant *Sinopodophyllum hexandrum* increased under UV-B irradiation along with increasing expression levels of genes involved in glycometabolism (XET and β-1,3-glucanase) and flavonoid biosynthesis (PAL, C4H, 4CL, CHS1 and DTX41), while podophyllotoxin biosynthesis showed a decrease and genes involved in stress tolerance (MYB, WRKY, APX3 and EX2) were upregulated (Lv et al. 2021).

Exposure of *A. annua* to UV-B radiation (280–320 nm) of 1.44 kJ/m^2 per day for 1 h per day for 10 days induced ROS generation, increased POD activity and ABA content along with stimulated artemisinin in the seedlings. Here, transcriptomic changes during UV-B radiation in *A. annua* were detected. Under UV-B stress 358 transcripts were found to be differentially expressed, 172 of which achieved increased abundance, while abundance of rest 186 transcripts showed a decrease. Considerable upregulation of the expression of crucial enzymes such as amorpha-4,11-diene synthase (ADS) and cytochrome P450 dependent monooxygenase/hydroxylase (CYP71AV1), and related WRKY transcription factors involved in artemisinin biosynthesis was observed (Pan et al. 2014). In vitro propagated *A. annua* plantlets irradiated with a low dose of UV-B light (2.8 W m^{-2}) for a of 3 h resulted in 103% and 100% increased artemisinin and flavonoid yield; UV-B irradiation diminished the levels of Chl*a*, Chl*b* and carotenoids in contrast to UV-B-absorbing anthocyanins and phenolics, which were induced. UV-B radiation resulted in a time dependent increase of $O_2^{\bullet-}$ radical formation. Upregulation of HMGR, DXR, IPPi, FPS, ADS, CYP71AV1 and RED1 gene transcripts involved in stimulated artemisinin production was observed. To the better adaptability of plants to UV-B irradiation lasting 3 h also contributed the differential expression of stress regulated genes (AOX1a, NDB2, UPOX, PAL, LOX) (Pandey and Pandey-Rai 2014). *A. annua* seedlings pretreated for two weeks with short term UV-B (4.2 kJ/m^2 per day) and UV-C (5.7 kJ/m^2 per day) and subsequently transplanted in field achieved increased artemisinin and flavonoid levels at all developmental stages compared to non-irradiated plants, whereby at full bloom stage these SMs increased by 10.5% and 15.7%, respectively. UV-B and UV-C pre-treatments also resulted in increased carotenoid but reduced Chl content and overexpression of genes associated in artemisinin/isoprenoid biosynthesis was observed as well. Under UV-B and UV-C stress the plants reinforced their antioxidative defense system to mitigate the adverse impact of harmful irradiation (Rai et al. 2011).

In higher altitudes atmosphere absorbs less UV radiation, whereby every 1000 m increase in altitude results in an increase of UV levels by 10–12%. In *Arnica montana* plants grown at altitude 2230 m the levels of flavonoids with vicinal free OH groups in ring B were considerably higher compared to flavonoids lacking this feature than in plants grown at altitude of 590 m. Caffeic acid derivatives in plants also greatly increased with the altitude of the growing site, evenly the content of 1-methoxyoxaloyl-3,5-dicaffeoylquinic acid achieved by 85% higher values in higher sites compared to samples from valley sites; higher levels of phenolics exhibiting ROS scavenging activity ensure protection of plants from UV-B at sites with elevated UV-B radiation (Spitaler et al. 2006).

Supplemental UV-B irradiation (3.6 kJ/m^2 per day above ambient) of *W. somnifera* Dunal lasting 40–100 days resulted in reduced withanolide A content but concomitant increase in withaferin A as well as enhanced activities of phenylpropanoid pathway enzymes in leaves and roots, whereby stronger increase was observed in roots; UV-B irradiation generally increased also the levels of other SMs of *W. somnifera* (Takshak and Agrawal 2014).

Under binary stress, namely UV-B irradiation of 1345.00 μW/cm^2 for 1 h and subsequent dark incubation for 72 h, the levels of the strictosidine, ajmalicine, vindoline, and catharanthine alkaloids in leaves of *C. roseus* plants increased by 527.9%, 321.6%, 20.1%, and 19.0%. In addition, in treated plants two-fold higher abundance of 10-hydroxygeraniol oxidoreductase, which is involved in the biosynthesis of indole alkaloid compared to the control was observed and UV-B irradiation also upregulated transcription of mRNA expression levels of genes involved in the indole alkaloid biosynthetic pathway (Zhu et al. 2015).

Exposure of *G. uralensis* plants to UV-B irradiation resulted in upregulation of unigenes encoding crucial enzymes involved in amino acid metabolism and flavonoid biosynthesis and among various flavonoids induced under UV-B treatment particularly levels of some *ortho*-dihydroxylated B-ring flavonoids acting as ROS scavengers were increased (Zhang et al. 2018a).

8.6.2 Impact of Irradiation with Blue and Red Light

Combined treatment with blue (B; 460 nm) and red light (R; 635 nm) applied at a ratio 3B:7R stimulated both the growth and contents of RA and salvianolic acid B in *S. miltiorrhiza* and increased the accumulation of phenolic acids via upregulating the transcription genes SmPAL1 and Sm4CL1 involved in the RA pathway (Zhang et al. 2020b). Treatment with blue, red and far red light stimulated the biosynthetic pathways of cyclic monoterpenes in Japanese mint leaves. Irradiation of plants with blue light lasting 2 weeks resulted in 362% increase of pulegone compared to the control, while menthofuran, menthone, and menthol increased by 285%, 223% and 389%, respectively. Red light irradiation increased pulegone, menthofuran and menthol by 256%, 178%, and 197%, respectively, while menthone and menhofuran contents increased by 229% and 339% under treatment of plants with far-red light. In addition, irradiation with blue light inhibited formation of glandular trichomes (Ueda et al. 2021). Red and blue light also increased accumulation of artemisinin in *A. annua* via stimulating the expression of the genes that were involved in artemisinin biosynthesis, such as amorpha-4,11-diene synthase and cytochrome P450 monooxygenase (CYP71AV1) gene (Zhang et al. 2018b). In vitro derived callus culture of *Eclipta alba* L. exposed to red light achieved pronouncedly higher TPC of 57.8 mg/g and TFC than in callus cultures irradiated with yellow and blue light. Using red light irradiation also highest levels of coumarin (1.26 mg/g), eclalbatin (5.00 mg/g), wedelolactone (32.54 mg/g), demethylwedelolactone (23.67 mg/g), β-amyrin (0.38 mg/g) and luteolin (0.39 mg/g) were observed; in contrast, highest stigmasterol level (0.22 mg/g) was obtained under blue light (Khurshid et al. 2020). Impact of different red light to blue light ratio and photosynthetic photon flux density on the biomass and increasing cannabidiol content in leaves and flowers of *C. sativa* L. was described by Wei et al. (2021).

8.6.3 Impact of Irradiation with Light-Emitting Diodes

Light-emitting diodes (LEDs) can be used to ameliorate the nutritional quality and contents of bioactive compounds in medicinal plants. LEDs need less power, have longer half-life and higher efficacy, enable the use of wider variation in the spectral wavelength than traditional light sources and their use increases plant biomass, nutrient and antioxidant properties. Irradiation of appropriate LED spectral wavelength not only greatly increases activities of antioxidant enzymes in plants, thereby improving the cell defense system and ensuring protection from oxidative damage, but irradiation with LED combinations using different ratios and combination of LEDs with normal light sources can result in increased content of phytochemicals including phenolics, flavonoids, carotenoids, anthocyanins as well (Jung et al. 2021). For example, Loi et al. (2021) discussed the use of LEDs enabling the selection of specific wavelengths and intensities, and thereby targeted accumulation of plant antioxidant compounds including vitamin C, phenols, Chl, carotenoids, and glucosinolates.

Blue and red LED illumination ameliorated growth and SMs in acyanic (green) and cyanic (red) *O. basilicum* L. microgreens. Treatment with predominantly blue illumination increased Chl*a* and anthocyanin levels, Stimulation of the production of phenolics and free radical scavenging activity were ameliorated mainly via predominantly red light in the green cultivar (up to 1.87 fold) and by predominantly blue light in the red cultivar (up to 1.73 fold). Compared to treatment with white light, using predominantly blue illumination resulted in up to 15- and 4-fold higher production of RA and gallic acid. Hence, via tuning of red and blue LED ratios outstanding growth and phenolic contents in both red and green basil microgreens can be achieved (Lobiuc et al. 2017). According to Ahmadi et al. (2022) ameliorated metabolism of RA and amino acids in *M. officinalis* irradiated with light emitting diodes using a combination of blue and red light can be associated with an increase in the biosynthesis of primary metabolites and the increased expression of genes playing crucial role in the production of SMs.

8.6.4 Impact of Shading and Color Nets

Improved biosynthesis of SMs can also be obtained under reduced sunlight or using color nets. Investigation of the impact of shade on important cultivation parameters, including EO yield of MAPs showed that mild shade of 30% exhibited beneficial effects on several species, while at 50% shade no favorable effect was observed (Zubay et al. 2021).

Full sunlight stimulated the expression of flavonoid biosynthesis-related genes and increased flavonoid biosynthesis in *G. biloba* L. Exposure of plants to 76% sunlight treatment resulted in the highest growth of total biomass as well as highest yield of flavonols (total flavonol, quercetin, kaempferol, and isorhamnetin) but the highest content of flavonoids content in leaves was observed under 100% sunlight, suggesting that flavonol production per unit land area is determined by both flavonol content and biomass (Xu et al. 2014). Shading of medical plants by pearl nets (50% shade index) ameliorated phytoconstituents in *T. vulgaris* L., *O. majorana* L., *Origanum vulgare* L., *M. officinalis* L., and *M. piperita* L. plants, and the highest level total phenolic content (TPC) showed extracts from shaded plants of *M. officinalis*. On the other hand, extracts produced from non-shaded thyme and marjoram had been characterized with higher flavonoid contents compared to herbal extracts from shaded plants (Tmusic et al. 2021). Colored shade can affect quality and quantity of the light captured by the plants. *C. officinalis* L. and *Viola tricolor* plants cultivated under the green shade net were characterized with higher anthocyanin and antioxidant activities than yellow and red shade nets (Zare et al. 2019). Using blue net with 50% shading increased plant height, leaf area, Chl content and EO yield in *M. officinalis* plants by 116%, 168%, 42% and 30%, respectively, compared to full sunlight exposure (Oliveira et al. 2016). Investigation of different color shades (40 μmol/m^2·s; blue, red orange, white) on the accumulation of SMs in *Cichorium* leaves immediately after treatment showed that anthocyanin and flavonoid indices, as well as the majority of flavonoids were lower compared but increased when plants subsequently grown one month under higher white light (320 μmol/m^2·s). Pretreatment with orange light increased the levels of isorhamnetin, its derivatives and feruloyl malate and considerably decreased, kaempferol-3-(6″-acetyl)-glucoside levels in *Cichorium* leaves. On the other hand, pretreatment with blue light reduced chlorogenic acid, caftaric acid and isorhamnetin-3-(6″-acetyl)-glucoside contents but increased isorhamnetin-3-glucoside levels and red light resulted in increased levels of quercetin derivatives. It was concluded that low light in the early growth phases caused upregulation of feruloyl malate, caffeoyl malate and kaempferol derivatives and the acclimation of plants to colored light reflected in the induction of specific metabolites suggested that the subsequent biochemical responses were related to the excellent plasticity of phenylpropanoid metabolism (Sytar et al. 2019).

8.7 Soil Acidity Stress

Soils with a pH ≤ 5.5 are considered as acidic soils (Kochian et al. 2004). In soils containing acidic parent materials leaching of minerals in acidic soils results in the loss of essential metal cations (Ca^{2+}, Mg^{2+}, Na^+ and K^+), which are subsequently replaced by H^+ and Al^{3+}. Hence, in acidic soils the availability of plant nutrients, such P and Mo is reduced but the availability of elements such as Al and Mn can achieve toxic levels. Besides such natural acidification of soil use of ammonium-based and urea-based N fertilizers in large amounts contributes to increased soil acidity because transformation of such fertilizers to nitrate is accompanied with increasing H^+ (Ashitha et al. 2021; Hue 2022). Moreover, acid rains, i.e. precipitations resulting in reduction in of soil acidity to pH < 5.6, disturb the balance of C and N metabolism, litter properties, and microbial and enzymatic activities, suppress photosynthesis and impair growth, productivity, and yield of plants (Shi et al. 2021; Prakash et al. 2023).

The effect of pH on the availability of nutrients is influenced both by soils (adsorption of nutrients on soil particles) and plants (through the uptake of biologically available nutrients), and thus also by the solubility of plant nutrients and their concentration in the soil solution in ionic form. Adsorption and mobility of nutrients also depends on soil pH (Barrow and Hartemink 2023; Hartemink and Barrow 2023). Hence, environmental pH govern the availability of mineral nutrients, the structure of the soil microbiome and the composition of natural plant communities and speedy alterations in soil pH have to be accompanied with readjustment of nutrient acquisition strategies associated with dynamic changes in gene expression (Tsai and Schmidt 2021).

EO efficiency of *Salvia hydrangea* DC. ex Benth. plants from Kiasar–Hezarjarib regions, Iran cultivated at two altitudes (1100 and 2000 m) showed positive correlation with the soil factors such as pH, soil electrical conductivity (EC) and saturation percentage as well as Mn and Mg levels, while the common EO composition showed negative correlation with these factors. Naphthalene, 1,8-cineole and camphor were found to be the major compounds of EOs extracted from plants grown at both altitudes. Further main essential constituents in altitude of 1100 m were β-pinene, α-amorphene, bicycleheptan and δ-cadinene, while in altitude of 2000 m these were α-terpineol and ylangene. The EO compositions showed the highest percentage in the altitude of 1100 m (Ebrahimi and Ranjbar 2016).

Chemical and physical soil parameters at the collection sites affected EO constituents of *Salvia desoleana* consisting of 68.2% of monoterpenes, 27.3% of sesquiterpenes and 4.5% of diterpenes. Whereas silt and sand contents correlated with α-pinene and sclareol fractions, the total K_2O correlated to several compounds belonging to the three terpene fractions (Rapposelli et al. 2015).

The total phenolic content in *O. vulgare* plants grown in soils with pH values ranging from 5.75 to 7.80 showed positive correlation with the soil pH ($r = 0.832$), total N ($r = 0.515$), Ca ($r = 0.842$), and Mg ($r = 0.559$), and negatively correlated with soil mobile P. On the other hand, flavonoid content in tested plants correlated with soil mobile P ($r = 0.776$), mobile K ($r = 0.993$), Mg ($r = 0.643$), and Na ($r = -0.843$) (Klimienė et al. 2021). From purple basil plants that were grown in clay, loamy sand and sandy-clay loam soils the highest EO yield was observed in plants grown in the loamy sand soil. The highest concentration of methylcinnamate (46.03%) was observed in loamy sand soils, and the lowest (42.33%) was obtained from sandy-clay loam soils; P_2O_5 and organic matter showed negative correlation with methylcinnamate (Tursun 2022). The mean percentage of EO of *Thymus pubescens* plants cultivated in soils with pH 6–8 showed an increase with increasing soil pH (Dizajeyekan et al. 2016).

R. officinalis grown on calcareous soils (pH > 7) produced high concentrations of monoterpenes such as myrcene and camphor, while α-pinene, β-caryophyllene, and the total sesquiterpene content was higher in plants cultivated on siliceous soils showing higher acidity. On the other hand, alloaromadendrene and δ-cadinene of

Cistus albidus achieved higher levels in plants grown on siliceous soils (Ormeno et al. 2008). The soil pH, total calcium carbonate (CCE), active calcium carbonate (ACCE) and N:P ratio showed positive correlation with EO yield of *R. officinalis*. On the other hand, content of EO in *Thymus algeriensis* was positively affected by pH and N:P ratio but negatively affected by CCE and ACCE (Mehalaine and Chenchouni 2020).

Lippia multiflora plant were cultivated in three sites (Labelekaha, Taoura and Zievogo) in north Cote d'Ivoire (Sudan savanna) in soils with moderate acidity (5.5 < pH < 6) and it was found that at cultivation of plants in down slope position of the landscapes and using fertilization with P the EO contained highest concentrations of geranial, neral, α-phellandrene, *p*-cymene, limonene + β-phellandrene and α-humulene. Besides available P beneficial impact on the concentrations of these volatile SMs showed soil moisture and soil N content (Barthelemy et al. 2014).

Investigation of the impact of pH (5, 5.7, 6 and 7) on the production of SMs in *S. marianum* hairy root cultures showed that maximal level of silymarin 0.26 mg/g d.w. was observed at pH 5 and 25 °C and also the contents of silybin, isosilybin, silychristin, silydianin achieving 0.025, 0.024, 0.061 and 0.095 mg/g d.w., respectively, were higher compared to those grown at higher pH. According to researchers acidic medium likely functioned as inducing signal for lipoxygenase activity resulting in ameliorated silymarin production (Rahimi and Hasanloo 2016).

Investigation of the impact of pH levels on SMs production in submerge root cultures of *Stevia rebaudiana* (Bert.) showed that pH 5.1 was favorable for the improved production of steviosides (79.48 mg/g d.w.) and rebaudioside-A (13.10 mg/g d.w.) contents but reduced the polyphenolics content in adventitious cultures. For dulcoside contents (2.57 mg/g d.w.) in adventitious root cultures and highest levels in total phenolics (70.06 mg/g d.w.) and flavonoids (50.19 mg/g d.w.) pH 5.8 was advantageous (Ahmad et al. 2018a).

Application of lime at doses 2-t/ha ameliorated yield of *Pelargonium capitatum* × *P. radens* plants as well as EO yield and nutrient uptake by plants grown on acidic soils (pH < 5.5). This was evident mainly at the second, third and fourth harvests. Use of liming also resulted in higher cumulative EO yields of all harvests compared to control. Application of lime or an increase in soil pH did not affect oil content (%) and the ratio between citronellol and geraniol, which depended mainly on air temperature fluctuations (Araya et al. 2011).

In field studies performed in growing seasons 2004, 2005, and 2010 *Lupinus angustifolium* plants were cultivated in soils with pH values varying between 5.3 and 6.7 and pH 7.1 and considerably lower alkaloid content was observed in plants grown on soils with a higher pH (pH 6.7 and 7.1 and) than on soils with a lower pH (5.3 and 5.8). For example, in 2010 alkaloid content in plants grown on soils with pH 5.3 and 6.7 achieved 0.0687% and 0.0355%, respectively. Moreover, genotypic differences in the response to different pH values in the soil were observed as well (Jansen et al. 2012).

In *Crocus sativus* plants cultivated in loam–clay–sand soils (pH 738–7.50) high values of picrocrocin (134.33 mg/kg) and kaempferol-3-sophoroside-7-glucoside (11.29 mg/kg) but low values of safranal (2.20 mg/kg) were observed (Chaouqi et al.

2023). The pH of medium greatly affected the release of alkaloids from roots of *Datura stramonium, C. roseus*, and thiophenes from roots *Tagetes patula* cultured in vitro and reduction of pH ranging from 4.8 to 7.0 to pH 3.5 resulted generally in increases of SMs ranging from 4- to 20-fold; particularly high increase (ca. 400-fold) was observed for ajmalicine (Sáenz-Carbonell et al. 1993). Investigation of the impact of medium pH in hairy root cultures of *W. somnifera* (pH 4.0–6.5) on withanolide A production showed that its highest levels were observed when a pH 6.0 medium was used (Praveen and Murthy 2012).

Investigation of SMs of *Curcuma longa* and *Zingiber officinale* plants grown at various altitudes and soil characteristics showed that curcuminoid, the secondary metabolite of turmeric, was affected by altitude, soil pH, soil texture as well as soil available P, while gingerol and shogaol, the SMs of *Z. officinale*, were affected by altitude, soil pH, soil organic matter, soil texture (silt and sand), and soil P; more SMs were observed in plants grown in the highlands compared to those from lowlands (Setyawati et al. 2021).

The caffeine content in leaves of *Coffea arabica* trees grown in soils pH of which ranged from 4.107 to 4.705 remained relatively constant and correlation between the pH of the soil and leaf caffeine content was not observed (Lochner 2016). Investigation of the impact of combining levels of watering (5–100% FC) and soil pH (3; 7 and 11) on EO concentration in *Chrysopogon zizanioides* L. Nash plants showed that the highest levels of terpenoid compounds (47.36%) were produced at soil pH 3 and watering level of 25%, and the highest levels of fatty acid compounds (38.51%) were observed at pH 3 and watering level of 100% (Taufikurahman and Fatimah 2023).

8.8 Stress Induced by Ozone

Ozone (O_3) is a highly reactive gas occurring in both stratosphere and troposphere, which is harmful for living organisms. Whereas stratospheric O_3 is formed via interaction of UV radiation originating from sun with molecular O_2, the tropospheric O_3 is formed predominantly via photochemical reactions between man-mad VOCs and nitrogen oxides (NO_x) (Yu et al. 2021). The “ozone layer”, occurring ca. 6–30 miles (10–50 km) above the Earth’s surface, diminishes the portion of noxious UV radiation reaching the Earth’s surface (EPA 2021). Due to its powerful oxidative potential O_3 induces generation and accumulation of ROS such as H_2O_2 and/or O_2 and adversely affects physiological and biochemical processes in plants, causing denaturation of lipid membranes, impairment of photosynthesis alteration of stomatal conductance, and disrupts plant cellular organelles (Langebartels et al. 2002; Rai and Agrawal 2012; D’Angiolillo et al. 2015; Masarovičová et al. 2019; Morales et al. 2021). Even though long term exposure to O_3 negatively affects the overall yield performance, O_3 stress can also have beneficial effect of the content of valuable SMs in medicinal plants, can modify EO content and composition and volatile emissions of medicinal plants reflected in enhanced synthesis of antioxidant substances including carotenoids, phenolics, flavonoids and other SMs ensuring protection against damaging effects of O_3 (Pellegrini et al. 2018; Döring et al. 2020; Deepti et al. 2022; Ansari et al. 2023). The impact of O_3 on growth, development and reproductive processes in medicinal plants, including their natural products, was summarized by Deepti et al. (2022). Effects of toxic gases O_3 and CO_2 on plant SMs were discussed by Kumar et al. (2017a, b) and Risoli and Lauria (2022) discussed application of ozonated water for elicitation of plant defense response and stimulation of plant metabolism, especially secondary metabolism.

M. spicata subsp. *glabrata* exposed to 100 ppb O_3 for 21 days, 5 h per day in fumigation chambers showed reduced EO yield by 18%; the content of major SMs of EO of ozonated plants compared to control showed a decrease for piperitenone oxide (92.6% vs. 89.4%) and β-caryophyllene (3.9% vs. 2.6%), while it increased germacrene D (2.5% vs. 5.3%). Moreover, percentage of germacrene D also increased in VOC emissions of treated plants (+112%), while the emission rates of myrcene or sabinene were not greatly affected and those of α-pinene, limonene, 1,8-cineole, *E*-ocimene and β-caryophyllene decreased under O_3 exposure in contrast to β-pinene and *E*-β-farnesene, which showed an increase (Nali et al. 2006).

Exposure of *M. officinalis* L. leaves to 80 ppb O_3 for 5 h resulted in ameliorated synthesis of SOD, ascorbic acid, phenols and total carotenoids as well as RA (prevalent phenolic compound of lemon balm). Despite of increased antioxidant capacity throughout the recovery phase (12–48 h from the beginning of the exposure) leaf surfaces of treated plants were damaged (Döring et al. 2020). Under in vitro exposure of *M. officinalis* to O_3 (200 ppb, 3 h) great increase in LPO was observed along with pronounced rising of lutein, neoxantin, violaxantin, anteraxantin carotenoids, while β-carotene levels showed a decrease. Compared to control plants the total VOCs emission considerably increased in O_3 treated plants compared to control plants achieving 7.6% increase of neral and 4.2% increase of allo-aromandendrene after the recovery period of 3 h, and the content of non-terpenoid compounds also showed a powerful increase. Under exposure to O_3 volatile products of the lipoxygenase pathway (LOX products) *E*-2-hexanal, *E*-3-hexenol, *Z*-3-hexenol-acetate and *E*-3-hexenol-acetate originating from free fatty acids released by phospholipases from membranes in response to O_3 were increased as well and an association between volatile LOX products and membrane degradation was observed (D'Angiolillo et al. 2015). In aseptic shoot cultures of *M. officinalis* treatment with 200 ppb O_3 for 3 h resulted in activation of enzymes involved in phenolic metabolism, increased lignin levels suggesting development of cellular barriers and an accumulation of phenolic compounds as well as an increase of antioxidant capacity were observed. At O_3 treatment RA levels were approx. fourfold higher compared to control plants and the production of SMs depended on the time of exposure and the concentration of the stressor (Tonelli et al. 2015).

Leaves of *S. offic*inalis plants exposed to O_3 (120 ppb) (5 h per day) for 90 consecutive days were characterized with impaired photosynthetic activity, loss of photosynthetic pigments Chl*a* and Chl*b* starting from 30 days from the beginning of treatment and cellular water deficit at the end of the experiment, suggesting oxidative stress in the chloroplasts. During O_3 treatment increased the levels of antioxidant compounds such as phenols (especially caffeic acid and RA), and water-soluble carbohydrates in plants due to activation of an adaptive survival mechanism under oxidative stress (Pellegrini et al. 2015). Investigation of phenolic and VOCs profiles of *S. officinalis* leaves exposed to 120 ppb O_3 (5 h/day) for 36 consecutive days showed an overall increase of phenolic compounds, reduction of volatile monoterpene emissions and enhanced levels of sesquiterpenes in both leaves and EOs, and plant leaf extracts exhibited improved antioxidant capacity. However, with prolongation of O_3-treatment the plants were not able to activate secondary metabolism (Marchica et al. 2021). The use of reflectance spectroscopy for early detection of *S. officinalis* responses to O_3 was reported by Marchica et al. (2019). Under exposure of *S. officinalis* to 120 ppb O_3 for 36 days (5 h/day) SA content showed +150% increase and SA accumulation started before the production of ethylene. However, the synthesis and/or regeneration of antioxidants such as ascorbate and GSH were not able to ensure protection of membranes from LPO (Marchica et al. 2022).

Suspension cell cultures of *H. perforatum* treated with 60–180 nL O_3/L produced considerably more hypericin compared to control and its content in cells exposed to 90 nL/L O_3 in late exponential phase for 3 h was even fourfold higher compared to control (Xu et al. 2011). In three-month old *H. perforatum* L. plants exposed to 110 ppb O_3 for 5 h increased H_2O_2 levels (+35%) but unchanged levels of ascorbate and approx. twofold higher reduced/oxidized glutathione ratio was observed compared to control. After 24 h of exposure, the levels of H_2O_2 considerably decreased and accumulation of total phenols, flavonoids and anthocyanins (+45%, +58% and +2%, respectively) was observed along with ameliorated antioxidant potential. The pool of soluble phenolics, which were involved in detoxification mechanisms, was found to be altered in both three and six months old plants (Pellegrini et al. 2018).

Comparison of the impact of elevated O_3 level (63.6 ppb) and ambient O_3 level (43.3 ppb) on different developmental stages of *Sida cordifolia* L. (Bala) plants cultivated in field showed that treatment with elevated O_3 concentration resulted in increased trichome density (+83.56%), reduced levels of photosynthetic pigments, induction of flavonoids and proline (non-enzymatic antioxidants) and increased levels of enzymatic antioxidants (as ascorbate peroxidase, CAT, POD, GR, and PAL) at all growth stages along with increased contents of lignin, tannin, saponin, alkaloids in leaves and roots, and phytosterol in roots. On the other hand, an increase in total phenolics and thiols as well as phytosterol in leaves was observed at 90 days after treatment (DAT) and SOD was induced only at 30 DAT (Ansari et al. 2023).

In *Capsicum baccatum* red pepper fruits exposed to 171.6 $\mu g\ O_3/m^3$ for 62 days in an open-top chamber capsaicin levels were reduced by 50% in the pericarp, but they were not affected in the seeds. Treatment with O_3 also resulted in an increase of the total carotenoid content (+52.8%) and total phenolic compounds (+17%) in the pericarp and 87% decrease of the total antioxidant potential in seeds. The contribution of seeds to the total radical-trapping antioxidant potential and total antioxidant reactivity was higher than that of the pericarp and O_3 treatment adversely affected the ferric-reducing antioxidant power of the seeds and diminished $NO^{\bullet}$ scavenging activity in the pericarp (Bortolin et al. 2016).

Leaves of *G. biloba* trees exposed in open-top chambers to double O_3 concentration compared to ambient air contained elevated levels of terpenes, but decreased concentrations of phenolics. Diminished synthesis of phenolics can result in reduced resistance of *G. biloba* to O_3 and other environmental stressors, while increased levels of terpenes can improve the antioxidant effectiveness in leaves at the end of O_3 fumigation (He et al. 2009). Leaves of four-year-old *G. biloba* trees exposed to twice ambient O_3 concentration in open-top chambers reduced the concentrations of the isorhamnetin aglycon by 7%, while increased the concentration of quercetin aglycon by 6% (Huang et al. 2010). NO was found to be crucial for O_3-induced flavonol accumulation in *G. biloba* cells exposed to O_3. Under O_3 exposure considerably increased activity of nitrate reductase (NR) activity was observed and it was stated that NR-mediated NO signaling is involved in O_3-induced flavonol production of *G. biloba* cells (Xu et al. 2012).

8.9 Stress Induced by Elevated CO_2

CO_2 is a greenhouse gas, which absorbs and emits radiant energy within the thermal infrared range in the atmosphere, thereby contributing to global warming. Due to its stronger absorption band for infrared heat it is responsible nowadays for approx. 72% of the anthropogenic greenhouse effect, whereby the global temperature increase correlates with the total amount of CO_2 emitted into the atmosphere (Rogelj et al. 2015; Kráľová and Jampílek 2021a). On the other hand, CO_2 is indispensable for photosynthesis and greatly affects not only biomass but also SMs of plants (Saravanan and Karthi 2014; Kumar et al. 2017a; Masarovičová et al. 2019; Kaundal and Kumar 2020). CO_2 plays a crucial role in the upregulation and management of atmospheric temperature and rapidly elevating CO_2 levels resulting in temperature increase in the atmosphere can affect morphological, physiological, and biochemical characteristics of plants and elicit manifold SMs in medicinal plants (Walia et al. 2022a). Current status of medicinal plants in perspective of environmental challenges and global climate changes, focusing on elevated CO_2 levels, extreme temperatures, changes in precipitation regimes as well as increased occurrence of harmful pests and pathogens, was comprehensively discussed by Ahmadi-Lahijani and Moori (2022). In contrast to elevated O_3, which decreases terrestrial C and N pools and fluxes, elevated CO_2 increases them and therefore, simultaneous increases in CO_2 and O_3 levels result in negation or even overcompensation of adverse effects of elevated O_3 on ecosystem functions and carbon and nitrogen cycles (Xia et al. 2021).

M. officinalis cultivated at 1050 ppm CO_2 showed increased height, EO yield and final yield by 24.3%, 26.3% and 65.3%, respectively, compared to plants grown under 380 ppm CO_2, while the stomatal conductance and EO percentage showed a decrease by 35.2% and 53%, respectively. Moreover, application of fertilizer intensified the effect of elevated CO_2 (Shoor et al. 2012).

Under exposure of *Salvia sclarea* plants to elevated temperature (2.5–3.0 °C above ambient) total dry biomass production, number of leaves/plant and leaf area/plant increased by 162.4%, 58.0% and 64.9%, respectively, compared to plants grown under ambient condition, while violaxanthin and neoxanthin metabolites decreased by 23% and 18% and de-epoxidation state increased by 16% over ambient. Exposure of plants to elevated CO_2 (550 μmol/mol) increased the total dry biomass production by 21.4% but decreased number of leaves/plant and leaf area/plant by 16.8% and 30.9% compared to ambient CO_2 levels (390 μmol/mol) and an increase in GSH content (+18.3%) and induction of antioxidative enzymes was observed as well. Considerably higher contents of linalyl acetate and linalool, which are constituents of EO, were detected at treatment with elevated temperature compared to that of elevated CO_2 (Kumar et al. 2017a).

Compared to *T. vulgaris* plants grown under ambient CO_2 concentration, the plants cultivated at elevated CO_2 (500 μmol/mol) concentrations showed increased SOD activity in July, and unchanged activity or reduced SOD activity in August and September; activities of GPX and CAT in leaves were not altered or decreased in the investigated period. Under 500 μmol/mol CO_2 the activity of GR and GSH content increased and in exposed leaves considerable increase in EO yield, with minor increments in phenolic components and decrements in mono- and sesquiterpene components was observed along with reduction of thiobarbituric acid reactive substances (TBARS) levels. Consequently, ROS formation under elevated CO_2 was reduced (Vurro et al. 2009).

In Turkish's purple basil showing as main components methyl *Z*-cinnamate and linalool temperature increase from 26/16 to 29/19 °C increased total phenylpropanoid content. Methylcinnamate content was not greatly affected but linalool content showed a decrease and the yields in RA and caffeic acids were highest at lower temperatures. Under both investigated temperatures the total phenylpropanoid content was reduced with increasing CO_2 concentration from 400 to 800 ppm in contrast to linalool, which showed an increase (Tursun and Telci 2020).

Combined treatment with elevated CO_2 and elevated temperature of *Valeriana jatamansi* Jones lasting 2 years showed favorable impact on plant biomass as well as on the content of major EO compound patchouli alcohol. Fertilization improved the growth and biomass of plants, while it reduced the content of patchouli alcohol (Walia et al. 2022b). Treatment of *V. jatamansi* for 4, 12 and 16 months with elevated CO_2 (550 ± 50 μmol/mol) pronouncedly increased stem (15.3–15.6%), root (3.2–72.5%), and total biomass (7.7–52.7%) of plants, while elevated temperature (2.5 ± 0.5 °C above ambient) increased these characteristics by 15.0–45.3%, 11.6–55.5% and 12.4–47.9%, respectively; the above treatments also resulted in advanced phenological stages by 1.2–3.9 days (Kaundal and Kumar 2020). On the other hand, content of EO from rhizomes and roots of *V. jatamansi* after 12 months of exposure to elevated CO_2 and elevated temperature increased by 17.7% and 4.3%, respectively, compared to ambient conditions, and pronouncedly higher levels of patchouli alcohol, bornyl acetate, β-patchoulene, germacrene D, monoterpene hydrocarbons and oxygenated sesquiterpenes were detected as well (Kaundal et al. 2018). *V. jatamansi* is a medicinal plant containing more than 30 compounds in its EO with patchouli alcohol (36.6–52.8%) as a major compound. EO content was found to be higher during winter season compared to other seasons and antioxidant activity of EO (IC_{50} = 117.5–227.6 μL/

mL) also varied among seasons, maximum antioxidant activity being observed in spring season (Rawat et al. 2017).

Considerably increased levels of hypericin and psendohypericin and enhanced biomass were detected in *H. perforatum* plants grown in an in vitro bioreactor in a closed controlled environment system with CO_2 enrichment than in plants cultivated in the greenhouse or in vitro-grown plants (Zobayed and Saxena 2004). *H. perforatum* plants grown under photosynthetic photon flux of 600 μmol/m^2·s with 1500 μmol/mol CO_2 for 45 days achieved 29-, 30- and 4-fold greater fresh and dry mass, and the number of stem nodes as well as 30- and 41-fold greater hypericin and pseudohypericin contents compared to control (Mosaleeyanon et al. 2005). Whereas treatment of *H. perforatum* plants in a western Himalayan region with vermicompost resulted in higher biomass (8.50%) and higher hypericin (20.65%) content compared to control, exposure of plants to elevated CO_2 (550 ± 50 μmol/L reduced hypericin content by 22.00%, and combine exposure to elevated CO_2 and elevated air temperature (2.5 ± 0.5 °C above ambient) reduced it by 19.30% compared to ambient. On the other hand, combined treatment lasting 140/280 days showed beneficial impact on plant height (+8.49%/6.90%) and plant dry mass (+35.70%/55.20%) compared to ambient conditions (Sharma et al. 2020).

Papaver setigerum DC plants grown under 600 μmol/mol CO_2 were characterized with considerably higher leaf area and above ground biomass and increased amount of alkaloids compared to plants grown under 300 μmol/mol CO_2, the highest increase in alkaloids levels of wild poppy being observed with an increase in CO_2 from 300 to 400 μmol/mol (Ziska et al. 2008). The production of TP and TF in *Labisia pumila* Benth. varieties *alata*, *pumila* and *lanceolata* grown under elevated CO_2 of 1,200 μmol/mol combined with nitrogen fertilization (0–270 kg N/ha) decreased with increasing N fertilizer dose in the order leaves > roots > stems (Ibrahim et al. 2010). Also Dong et al. (2018) overviewed beneficial impact of elevated CO_2 on nutritional quality of vegetables, including increased contents of TF, TF and ascorbic acid. *Gynostemma pentaphyllum* plants grown two months under elevated CO_2 (720 μmol/mol) and temperature regime 28/23 °C (day/night) showed pronouncedly higher biomass and increased leaf Chl content compared to plants cultivated at 360 μmol/mol CO_2 and temperature regime of 23/18 °C. In addition, elevated CO_2 enhanced the level of total sugars and gypenoside A, while reduced the total antioxidant capacity and main antioxidant compounds in plant organs. In plants cultivated under elevated CO_2 and temperature lower levels of TP and TF in leaves, stems, and inflorescences were observed (Chang et al. 2016).

Beneficial impact of elevated CO_2 (600 and 900 ppm) on growth of *C. roseus* as well as phenolics, flavonoids, tannin and alkaloid levels was observed by Saravanan and Karthi (2014). Elevated CO_2 of 560 ppm exhibited beneficial impact on growth and alkaloids production in *C. roseus* plants and diminished the level of oxidative stress compared to plants grown under 375 ppm CO_2. Under limited N the positive impact of elevated CO_2 was lower compared to plants fertilized with 50 and 100 kg N/ha, respectively. Whereas addition of 100 kg N/ha promoted growth of *C. roseus* plants under elevated CO_2, production of alkaloids was not affected (Singh and Agrawal 2015).

Treatment of ginger plants with 800 μmol/mol CO_2 considerably increased anthocyanin, rutin, naringenin, myricetin, apigenin, fisetin and morin contents in plants compared to plants grown under 400 μmol/mol CO_2. The combined treatment of plants with elevated CO_2 and SA increased anthocyanin and flavonoid contents in plants compared with single treatment. Enhanced production of these SMs can be associated with increased chalcone synthase activity at high CO_2 levels (Ghasemzadeh et al. 2012). In *Z. officinale* Roscoe plants grown under elevated CO_2 (800 μmol/mol) plant biomass, total soluble carbohydrates (TSC) as well as TF and TP showed considerable increase. The TF and TP in the plant organs decreased as follows: rhizomes > stems > leaves and the levels of these SMs depended on individual cultivar. TSC and TP content were positively correlated in both tested *Z. officinale* cultivars and the antioxidant activity showed an increase in ginger seedlings cultivated under elevated CO_2 (Ghasemzadeh and Jaafar 2011).

In suspension cultures of *P. ginseng* CA Mayer roots grown 45 days at 2.5% CO_2 the TP and TF levels increased by 60% and 30%, respectively, compared to control; high CO_2 concentration also promoted the activities of glucose-6-phosphate-dehydrogenase, shikimate dehydrogenase, PAL, cinnamyl alcohol dehydrogenase, caffeic acid peroxidase and chlorogenic acid peroxidase and contents of total protein, non-protein thiol and cysteine increased by 45%, 30% and 52%, respectively, compared to control (Ali et al. 2005). On the other hand, based on the results of meta-analysis of 1026 experimental observations Loladze et al. (2019) reported that elevated atmospheric CO_2 reduced the levels of plant carotenoids.

8.10 Stress Induced by Agrochemicals

Agrochemicals whether in bulk or nanoform are frequently used to improve yield of crops. For normal physiological and metabolic processes of medicinal and aromatic plants both macro and micronutrients are indispensable. Yield and composition of essential elements considerably depends on the availability of micronutrients, which can be applied via foliar or soil treatment. The amount and the composition of EO in aromatic plants is greatly modified by the content of micronutrients in soil but micronutrient management need to consider beside required fertilizer amount needed to compensate micronutrients deficiency also their possible toxicity. The toxicity of micronutrient fertilizers can be reduced using their nanoformulations (Kumar et al. 2022). Whereas application of fertilizers ensures required nutrition of plants resulting in ameliorated growth and development of plants (Jampílek and Kráľová 2017a, 2019; Zhang 2017; Kráľová and Jampílek 2022; Shokouhifar et al. 2023), pesticides are designed to protect plants against weeds, insects or harmful bacteria and fungi causing plant diseases (Jampílek and Kráľová 2015, 2017b, 2018, 2020a, b; Jampílek et al. 2020; Kráľová and Jampílek 2023a), and in such way ensure healthy development of plants. However, the presence of such agrochemicals in soil can also affect the yield and composition of EOs in medicinal plants (Radušienė et al. 2019; Jervekani et al. 2020; Rahimi et al. 2020; Pirmani et al. 2022). Imbalance of micronutrients in soil was also reported to modify the yield and composition of EO in aromatic plants (Kumar et al. 2022).

8.10.1 Applications of Fertilizers

M. piperita plants cultivated under mild an severe water deficit stress corresponding to 40% and 55% depletion from the available water achieved maximum EO content (0.97%) under mild drought stress, while the best antioxidant activity as well as SOD activity was observed with unfertilized plants (characterized with 25% depletion from the available water) and plants fertilized with urea (140 kg/ha). On the other hand, antioxidant features, total phenol, and RA content in plants grown under water deficit in soils treated with vermicompost showed a decrease (Mirzamohammadi et al. 2021). Nitrogen fertilization enhanced EO yield of Greek oregano (*O. vulgare* ssp. *hirtum*) (Link) Ietswaart (Karamanos and Sotiropoulou 2013) and increased the levels of phenolic compounds (e.g., thymol and carvacrol) in *Origanum syriacum* L. var. *aegyptiacum* Tackh (Omer 2008). Secondary metabolites RA, ursolic acid (UA) and oleanolic acid (OA) in *P. vulgaris* plants were strongly reduced under drought-stress. Treatment with NPK fertilizer mitigated the adverse impact of water stress on plants via pronounced improving or vegetative dry weight, reproductive dry weight as well as yields of mentioned SMs, suggesting that combined application of NPK fertilization and rightly timed exposure of *P. vulgaris* plants grown in arid and semi-arid regions to water stress results in increased total yields of RA, UA and OA (Chen et al. 2011). The top linalool content in *Coriandrum sativum* EO was achieved using chemical fertilizers and vermicompost × humic acids at the flowering onset stage (Rasouli et al. 2022).

Investigation of inorganic (Steiner solution at 75% nutrient concentration) and organic fertilizes (humic acids and an organic fertilizer containing biosynthetic amino acids) on biomass and EO production of *M. recutita* plants cultivated in hydroponia containing two types of substrate (one from volcanic rock and another from a mixture of soil, compost and perlite (50:20:30)) showed that inorganic fertilizer and harvest days have had beneficial impact on the morphological characteristics but did not affect the total yield of EO. On the other hand, treatment with humic acids was found to enhance α-bisabolol yield (Juarez-Rosete et al. 2012). Application of 5 kg/m^2 poultry manure and water depth equivalent to 150% evapotranspiration was fond to be favorable for the production of EO and flavonoid content of chamomile cultivated in the city of Presidente Prudente, SP, Brazil (Aleman and Marques Patricia 2016).

Foliar application of N and nano-chelate nitrogen (NC) (N + NC) was found to alleviate negative impact of water stress on the grain yield, biological yield and EO yield of *C. officinalis* plants compared to control plants. In addition, NC foliar application and *Azotobacter* inoculation exhibited synergistic effect on the content of proline enzymes and antioxidant activity and combined treatment of foliar application of N + NC along with inoculation of seeds with *Azotobacter* was favorable not only for morphological characteristics but also for EO yield and proline content (Pirmani et al. 2022). The marigold plants treated by chemical phosphorus fertilizer irrigated at 80% FC achieved EO yield of 997.75 kg/ha compared to 597.24 kg/ha observed with control plants (Rahimi et al. 2020).

In *Coreopsis tinctoria* plants grown in hydroponium at the presence of different N levels (0.625–5.0 mM) low and moderate N levels affected enzyme activities related to C and N metabolism, stimulated the accumulation of carbohydrates, diminished the levels of N metabolite and improved the internal C/N balance. Whereas the flavonoid content in roots and stalks was relatively stable, in leaves achieved maximum at low and moderate N levels. Close positive correlation of flavonoids with carbohydrates and negative correlation with N metabolites was observed suggesting that C and N metabolism can alter the distribution in flavonoid biosynthesis pathways (Li et al. 2021b).

Nitrogen fertilization of bush tea (*Athrixia phylicoides* DC.) ranging from 150 to 225 kg N/ha resulted in considerable quadratic response of total polyphenols, total flavonoids, total tannins and total antioxidants in plant leaves and twigs, even though minimum inhibition concentration and minimum microbicide concentration of bush tea extract were not ameliorated (Tshivhandekano et al. 2017). On the other hand, N deficiency pronouncedly suppressed growth and photosynthesis of *S. rebaudiana* plants but enhanced contents of steviol glycosides (SGs) in leaves, achieving 49.97%, 46.64% and 84.80% increase for rebaudioside A, stevioside, and rebaudioside C, respectively. N-deficiency upregulated many genes, including those involved in phenylpropanoid biosynthesis, flavonoid biosynthesis and starch and sucrose metabolism and it was concluded that stimulation of SGs production may be associated with alteration of carbon metabolism and induction of certain transcription factors under N-deficiency (Sun et al. 2021).

Nitrogen fertilizer (30 kg N/667 m^2) ameliorated not only the stomatal conductance, leaf intercellular CO_2 concentration, transpiration rate, net photosynthetic rate, Chl and starch contents as well as yield of *Nelumbo nucifera* but the DEGs also enhanced the biosynthesis of SMs and phenylpropanoid biosynthesis (Zhao et al. 2022). Whereas soil-application of 45 kg N/ha and 26 kg P/ha was found to be optimum dose for increasing shoot and root length, leaf area, fresh and dry weight of shoot and root, total Chl and leaf-N, P, and K content, nitrate reductase, carbonic anhydrase activity, and total alkaloid content in *W. somnifera*, the dose of 30 kg N/ha ensured the best for root length, fresh and dry weights and root-yield per plant. N and P fertilizers did not affect carotenoid content, while N application did not affect leaf-P content (Nasir and Khan 2012).

Mineral nitrogen fertilizer containing 33% NH_4^+ applied on *H. pruinatum* plants at doses 30–120 kg N/ha increased accumulation of naphtodianthrones and emodin, and did not affect phloroglucinol derivatives but the accumulation of major phenolics, such as catechin, chlorogenic acid, hyperoside, quercitrin, isoquercitrin and total phenolic content showed considerable reduction with increased N doses. Antioxidant activity of plant extracts was mostly related to hydroxycinnamic acids and flavonoids (e.g., quercetin, isoqercitrin and hyperoside). Even though plants treated with high N doses exhibited lower antioxidant activity compared to non-fertilized samples, the highest antioxidant capacity was observed in samples showing greater abundance of phenolics (Radušienė et al. 2019).

Growth characteristics, Chl content, RWC, and yield of *Crocus sativus* plants grown under drought stress was reduced, while the levels of proline and soluble carbohydrates as well as content of crocin, picrocrocin, and safranal showed an increase. However, mineral nutrition deficit diminished saffron growth characteristics, yield, and content of SMs both at 100% FC and 66% depletion of soil water. While the greatest plant growth was observed at fertilization with 25% of chemical fertilizer and 75% chicken manure, quality of saffron was the highest at application of 3-fold higher amount of chemical fertilizer than chicken manure (Aboueshaghi et al. 2023). Saffron plants cultivated in loam–clay–sand soils were characterized with high levels of crocins and kaempferol-3-sophoroside-7-glucoside but low content of safranal. The plants cultivated in soils rich in organic matter, P and K contained high contents of crocins and kaempferol-3-sophoroside-7-glucoside but low values of safranal, and clays containing low Fe amounts exhibited beneficial impact on the coloring strength of saffron (Chaouqi et al. 2023).

Comparing the impact of NH_4NO_3 fertilizer doses (0.19–2.0 mM) applied via irrigation in 2-days intervals for 15 days on one-year-old seedlings of *Cyclocarya paliurus* plants it was found that flavonoid contents in roots and stalks were reduced but in leaves showed a maximum at 0.63 mM NH_4NO_3 and flavonoid level correlated with flavanone-3-hydroxylase activity. The partitioning of C among primary and secondary metabolisms was assumed to be responsible for flavonoid biosynthesis (Deng et al. 2019).

8.10.2 Applications of Pesticides

Pesticides applied at sub-lethal doses were reported to affect secondary metabolism of higher plants as well. Alachlor suppressed flavonoid synthesis at a step late in the biosynthetic pathway, and glyphosate inhibited synthesis of all cinnamate derivatives by inhibiting 5-enolpyruvylshikimate-3-phosphate (EPSP) synthase, and inhibition of EPSP synthase resulted in the high levels of shikimate, benzoic acids and benzoic acid derivatives. On the other hand, the sulfonylureas and *p*-nitro-substituted diphenylether herbicides can enhance terpenoid stress metabolite (Lydon and Duke 1989).

Bensulide, linuron, and benfluralin herbicides increased content of monoterpenoids including camphor and β-pinene in *S. officinalis* plants but reduced the levels of 1,8-cineole and 3-isothujone. Treatment with 200 and 400 ppm negatively affected growth and EO yield of *S. officinalis* (El-Keltawi and Croteau 1987). Reduced levels of secondary compounds due to treatment with herbicides can be associated with herbicide-reduced carbon fixation and subsequent carbon flow into the secondary metabolic pathways. Jervekani et al. (2020) investigated the effect of light-dependent herbicides oxadiargyl, bentazon, oxyfluorfen, metribuzin, and phenmedipham + desmedipham on growth and EO content of *S. officinalis* and found that EO content generally increased with increasing herbicide rate; the use of high concentration of oxyfluorfen resulted in the highest EO content. Foliar spraying of *S. officinalis* with 500 ppm L-phenylalanine under inoculation of the plant roots with *Pseudomonas fluorescent* bacterium increased the contents of oxygenated monoterpenes in the EO of sage (Samani et al. 2019). Treatment with bensulide, linuron, and benfluralin herbicides increased the content of monoterpenoids (e.g., camphor and β-pinene) in *S. oflcinalis* but decreased 1,8-cineole and 3-isothujone levels (El-Keltawi and Croteau 1987).

Treatment with linuron was reported to double the content of azulene only in *M. recutita* L. (Maas 1978). Sublethal treatment of *Abutilon theophrastic* Medic with glyphosate resulted in strongly increased levels of shikimate and protokatechuate, while hydroxybenzaldehyde and *p*-coumarate levels showed a decrease. During recovery from herbicide treatment rapid loss of protokatechuate along with rapid increase in other phenolic acids was observed (Becerril et al. 1989).

D. stramonium contains as SMs tropane alkaloids atropine and hyoscyamine and the narcotic cocaine. Tropane alkaloids are synthesized by the condensation of tropine and tropic acid, a phenylalanine-derived intermediate. Treatment of plants with glyphosate and chlorsulfuron resulted in reduced levels of phenylalanine as well as tropinone, φ-tropine, and tropine contents but in 3-fold enhanced levels arginine and ornithine. Moreover, application of 1 μM chlorsulfuron and glyphosate reduced the expression of putrescine *N*-methyltransferase mRNA transcripts in *D. stramonium* roots. These results suggest that these herbicides likely reduce the overall tropane alkaloid biosynthesis in this plant (Deng 2005). Herbicide 2-methyl-4-chlorophenoxyacetic acid (MCPA) reduced the alkaloid content of horsetail *(Equisetum pulustre* L.) by 90% in contrast to 2,4,5-trichlorophenoxyacetic acid (2,4,5-T), which markedly increased toxic alkaloid concentrations in *Delphinium burbeyi* Huth (Williams and Cronin 1963).

Variations of metabolites of *Lonicerae japonicae flos* including chlorogenic acids, iridoids and organic acid-glucoside due to treatment with imidacloprid, flonicamid and acetamiprid insecticides were reported by Pan et al. (2021).

8.11 Heavy Metal Stress

Plants require for their growth and development metal macronutrients K, Ca, Mg as well as micronutrinets Fe, Mn, B, Zn, Cu, and Mo and also some other metals/metalloids such as Ni, V, Na, Co, Al, Se, and Si were found to improve plant growth when applied at low doses (Marschner 1995; IFA 2020; Kráľová and Jampílek 2022, 2023b). However, application of higher doses of metal nutrients, whether as ions or nanoparticles (NPs), similarly to application of toxic metals such as Cd, Hg or As, generate oxidative stress in plants, thereby affecting the processes at molecular, biochemical and morphophysiological levels (Masarovičová et al. 2010; Kráľová et al. 2019, 2021; Hafeez et al. 2023). Higher concentrations of metals cause injury to plant photosynthetic apparatus resulting in inhibition of photosynthetic electron transport, reduced concentration of Chl and carotenoids as well as net photosynthesis, cause LPO and membrane injury and impaired plant performance and plant growth. Moreover, ROS generated in excess have influence on the expression of many genes that control number of processes including growth, cell cycle, programmed cell death, responses of plants to abiotic and biotic stresses, as well as systemic signaling. Even though plants can use numerous defense mechanisms to reduce negative effects of toxic metals including reduced heavy metal uptake by plants, sequestration into vacuoles, or binding by phytochelatins (Shahid et al. 2015; Ghori et al. 2019), to avoid adverse impact of ROS and protect plant cells from oxidative damage plants use antioxidant defense systems able to scavenge ROS. On the other hand, exposure of plants to metal stress results in enhanced production of valuable SMs and contributes to ameliorated nutritional quality of plants.

A number of medicinal plants produce SMs showing high pharmacological effectiveness, and therefore, increased production of SMs under controlled metal stress would be desirable considering that under such conditions not only increased yield of EOs but also improved composition of SMs in EOs can be achieved.

Enhanced accumulation of some SMs under Cd stress was observed in *M. piperita* (Azimychetabi et al. 2021), *H. perforatum* (Babula et al. 2015), *O. basilicum* (Gheshlaghpour et al. 2021; do Prado et al. 2022), *Centella asiatica* (Biswas et al. 2020) and *M. recutita* (Zarinkamar et al. 2021). Precursors of herniarin, *Z*- and *E*-2-β-D-glucopyranosyloxy-4-methoxycinnamic acids in *M. recutita* increased at doses 3, 60 and 120 μM Cd, although herniarin levels were not affected (Kovacik et al. 2006) but high Cd concentration reduced EO yield in *M. officinalis* (Kilic and Kilic 2017).

Application of 600 Pb/kg soil increased hypericin content in *H. perforatum* (Zarinkamar et al. 2013), treatment of *Mentha crispa* with 900 mg Pb/kg soil resulted in 2.3-fold increase in carvone content (Sá et al. 2015), and 0.04 mM Pb considerably enhanced caffeic and RA contents in *O. basilicum* plants cultivated in hydroponium (do Prado et al. 2022).

Ni stress enhanced the content of soluble phenols, sum of flavonols and catechin in *H. perforatum*, *H. olympicum*, and *H. orientale* (Kovacik et al. 2022), caused ca. 4-fold increase in chlorogenic acid at treatment of *M. recutita* plants with 120 μM Ni (Kovacik et al. 2009) or enhanced content of menthone and menthyl acetate in *M. piperita* exposed to 20 mg Ni/kg soil (Nabi et al. 2020). Whereas exposure of *Anethum graveolens* and *Pimpinella anisum* plant to 2 mM Zn increased the content of phenols, flavonols and flavones, in exposed *Foeniculum vulgare* plants these SMs showed a decrease (Majdoub et al. 2017); enhanced levels of steviol glycosides were observed at treatment of *S. rebaudiana* with 6 ppm Zn (Baroni-nezhad et al. 2021). Increased content of α-pinene and camphene was detected in *M. piperita* plants sprayed with 0.5 g/L Cu (Lafmejani et al. 2018a), content of some SMs increased in *M. spicata* plants exposed in hydroponium to 60 μM Cu (Chrysargyris et al. 2019) and levels of steviol glycosides were enhanced in *S. rebaudiana* plants treated with 10 ppm Cu (Baroni-nezhad et al. 2021); enhanced content of steviol glycosides was also detected in *S. rebaudiana* plants treated with 2.5 ppm Fe (Baroni-nezhad et al. 2021). Treatment with low Cr(VI) concentrations increased content of hypericins in *H. perforatum* plants; *M. aquatica* plants exposed to Mn achieved higher levels of anthocyanins and flavonoids compared to control (Nazari et al. 2017), and exposure of *O. basilicum* plants to 0.04 mM Al resulted in enhanced levels of caffeic acid and RA (do Prado et al. 2022), while treatment with metalloid Si (2 mM) increased estragole and eugenol contents (Gheshlaghpour et al. 2021). Beneficial impact on EO yield and composition was also observed in *M. officinalis* plants sprayed with combination of metal nutrients (Fe + Mn + Zn + Cu) (Yadegari 2017). Multiples of SMs content compared to control in selected medicinal plants exposed to various metals is summarized in Table 8.1.

Production of SMs can also be enhanced using metal/metal oxide NPs acting as elicitors. Even though these NPs have the same chemical composition than respective microscale metal/metal oxides, they show distinct physical and chemical properties due to their nanoscale size and frequently can ensure the same required biological effect using lower dose compared to bulk compound (Jampílek and Kráľová 2015, 2017b; Kráľová et al. 2019, 2021). The impact of metal-based NPs on plants depends besides the size of NPs also on their concentration, zeta potential, and shape and as well as on the exposed plant species (Ahmad et al. 2022).

Metal-based NPs similarly to bulk metals generate ROS, whereby at low NPs concentrations plants increase the activities of antioxidant enzymes as well as concentrations of non-enzymatic antioxidants such as GSH, ascorbic acid, phenolics, flavonoids carotenes or alkaloids (Kráľová and Jampílek 2021b; Rivero-Montejo et al. 2021). Effective accumulation of industrially important flavonoids at application of nanosized metal elicitors, inducing stress and activating plant defense can be achieved using in vitro cultures (Khan et al. 2021). Stimulation of SM production in plant tissue cultures using AgNPs and CuNPs as elicitors was overviewed by Zaeem et al. (2022).

In cell suspension cultures of *Carum carvi* treatment with 50 mg/L AgNPs increased *p*-cymene and carvone contents compared to control, while treatment with 100 mg/L AgNPs increased the production of thymol and carvacrol (Dehghani-Aghchekohal et al. 2022). Beneficial impact of CuNPs on the content of total phenolics, anthocyanins, flavonols and flavonoids, thymol and carvacrol in *Zataria multiflora* Boiss was reported by Asadollahei et al. (2022). In cell suspension cultures of *H. perforatum* plants treated with AgNPs accumulation of bisxanthone, gancaonin O and fusaroskyrin increased 540-, 214- and 98-fold, while hyperxanthone C was most induced by AuNPs, apigenin by CuNPs, dihydroxydimethoxy-xanthone I by CuO NPs, gallic acid by ZnO, emodin by PdNPs, emodin anthrone by CeO_2 NPs and quercetin by TiO_2 NPs (Kruszka et al. 2022). Higher geranyl acetate, geranial, neral, and geraniol compounds were observed in *Dracocephalum moldavica* plants treated foliarly with 80 mg/L CuONPs than at application of 160 mg/L chelated-Cu (Nekoukhou et al. 2023) and spraying of dragonhead plants with 160 mg/L ZnONPs increased the levels of neral, geraniol and geranial more than treatment with the same dose of ZnS fertilizer (Nekoukhou et al. 2022).

Zn NPs elicited higher levels of trigonelline in hairy roots compared to control (Tariverdizadeh et al. 2021) and at application of 100 mg/L of ZnO NPs to *Hyoscyamus reticulatus* L. hairy roots significant increase of hyoscyamine and scopolamine levels was observed after 48 and 72 h (Asl et al. 2019). Approximately fivefold

Table 8.1 Enhanced production of secondary metabolites (SMs) of medicinal plants elicited by heavy metals

Plant	Metal elicitor	Cultivation mode	Elicitor dose	SMs	SM content compared to control	Refs.
Anethum graveolens	Zn	Addition to soil	2 mM	Phenols	1.10	Majdoub et al. (2017)
				Flavonols and flavones	1.27	
				Dihydroflavonols and flavanones	0.48	
Centella asiatica	Cd	Addition to soil	200 mg/kg	Carotenoids	0.76	Biswas et al. (2020)
				TPC	1.42	
				TFC	1.46	
				Asiaticosid	25.50	
				Asiatic acid	14.50	
				Madecassoside	49.63	
				Madecassic acid	14.06	
				Total centelloside	18.54	
Centella asiatica	Pb	Addition to soil	400 mg/kg	Carotenoids	2.07	Biswas et al. (2020)
				TPC	1.25	
				TFC	1.29	
				Asiaticosid	2.76	

(continued)

Table 8.1 (continued)

Plant	Metal elicitor	Cultivation mode	Elicitor dose	SMs	SM content compared to control	Refs.
				Asiatic acid	2.07	
				Madecassoside	1.60	
				Madecassic acid	2.79	
				Total centelloside	2.48	
Foeniculum vulgare	Zn	Addition to soil	2 mM	Phenols	0.84	Majdoub et al. (2017)
				Flavonols and flavones	0.76	
				Dihydroflavonols and flavanones	1.03	
Hypericum perforatum	Cd	Grown in hydroponium	10 µM	Hypericin	0.96	Babula et al. (2015)
				Hyperforin	1.45	
				Hyperoside	1.57	
				Gallic acid	1.15	
				Chlorogenic acid	1.32	
				Quercetin	1.19	
				Epicatechin	1.72	
				Total soluble phenols (shoot)	1.27	
				Total soluble phenols (root)	1.14	

(continued)

Table 8.1 (continued)

Plant	Metal elicitor	Cultivation mode	Elicitor dose	SMs	SM content compared to control	Refs.
Hypericum perforatum	La	Grown in hydroponium	10 μM	Hypericin	0.66	Babula et al. (2015)
				Hyperforin	1.30	
				Hyperoside	0.71	
				Gallic acid	0.55	
				Chlorogenic acid	1.09	
				Quercetin	0.51	
				Epicatechin	2.73	
				Total soluble phenols (shoot)	1.34	
				Total soluble phenols (root)	0.30	
Hypericum perforatum	Pb	Addition to soil	600 mg/kg	Hypericin	≈3.36	Zarinkamar et al. (2013)
Hypericum perforatum	Cr(VI)	Grown in hydroponium	0.01 mM (7 days)	Hypericin	1.38	Tirillini et al. (2006)
				Pseudohypericin	1.05	
				Protopseudohypericin	2.35	
				Total hypericins	1.38	
			0.01 mM (7 days)	Hypericin	1.00	
				Pseudohypericin	1.40	
				Protopseudohypericin	4.79	

(continued)

Table 8.1 (continued)

Plant	Metal elicitor	Cultivation mode	Elicitor dose	SMs	SM content compared to control	Refs.
				Total hypericins	1.25	
Hypericum perforatum	Ni	Grown in hydroponium	1 µM	Chlorogenic acid	0.95	Kovacik et al. (2022)
				Catechin	1.29	
				Rutin	0.94	
				Quercetin	0.98	
				Biapigenin	1.13	
				Amentoflavone	2.92	
Mentha aquatica	Mn	Grown in hydroponium	160 µM	Carotenoids	1.06	Nazari et al. (2017)
				Anthocyanins	1.43	
				Flavonoids	1.73	
Mentha crispa	Pb	Addition to soil	900 mg/kg	Carvone	2.31	Sá et al. (2015)
				Dihydrocarveol	0.53	
				Borneol	1.09	
				β-bourbonene	0.50	
				β-cariophyllene	0.64	
				Germacrene D	0.33	
Mentha piperita	Cd	Addition to soil	20 ppm	α-pinene	1.46	Azimychetabi et al. (2021)
				Sabinene	1.75	
				1,8-cineole	1.12	
				Menthone	0.92	

(continued)

Table 8.1 (continued)

Plant	Metal elicitor	Cultivation mode	Elicitor dose	SMs	SM content compared to control	Refs.
				Menthofurane	1.26	
				Menthol	0.93	
				E-caryophyllene	1.72	
				Monoterpene hydrocarbons	1.09	
				Sesquiterpene hydrocarbons	5.63	
				Oxygenated monoterpenes	0.97	
Mentha piperita	Cu	Foliar spraying	0.5 g/L	α-pinene	1.05	Lafmejani et al. (2018a, b)
				Camphene	1.21	
				Sabinene	0.83	
				Limonene	0.81	
				Germacrene D	1.06	
				Carvacrol	0.81	
				Borneol	0.70	
				Pulegone	1.09	
				Cavrone	0.63	
Mentha spicata	Cu	Hydroponically grown	60 μM	α-pinene	1.00	Chrysargyris et al. (2019)
				Sabinene	1.02	
				Limonene	1.19	

(continued)

Table 8.1 (continued)

Plant	Metal elicitor	Cultivation mode	Elicitor dose	SMs	SM content compared to control	Refs.
				1,8-cineole	0.99	
				β-caryophyllene	1.23	
				Carvone	0.97	
				Pulegone	1.25	
				Monoterpene hydrocarbons	1.15	
				Sesquiterpene hydrocarbons	1.15	
				Oxygenated monoterpenes	0.97	
Ocimum basilicum	Cd	Addition to soil	50 mg/kg	Estragole	1.13	Gheshlaghpour et al. (2021)
				Eugenol	1.25	
Ocimum basilicum	Al	Grown in hydroponium	0.04 mM	Caffeic acid	1.04	do Prado et al. (2022)
				Rosmarinic acid	0.75	
				TPC	0.85	
				TFC	0.65	
Ocimum basilicum	Pb	Grown in hydroponium	0.04 mM	Caffeic acid Rosmarinic acid TPC TFC	3.40 8.58 1.06 1.06	do Prado et al. (2022)
Ocimum basilicum	Cd	Grown in hydroponium	1.20 mM	Caffeic acid	3.8	do Prado et al. (2022)

(continued)

Table 8.1 (continued)

Plant	Metal elicitor	Cultivation mode	Elicitor dose	SMs	SM content compared to control	Refs.
				Rosmarinic acid	7.2	
				TPC	1.14	
				TFC	1.05	
Pimpinella anisum	Zn	Addition to soil	2 mM	Phenols	1.32	Majdoub et al. (2017)
				Flavonols and flavones	1.51	
				Dihydroflavonols and flavanones	1.72	
Stevia rebaudiana (Bert.)	Cu	Addition to soil	10 ppm	Steviol glycosides	1.48	Baroni-nezhad et al. (2021)
Stevia rebaudiana (Bert.)	Fe	Addition to soil	2.5 ppm	Steviol glycosides	1.18	Baroni-nezhad et al. (2021)
				Rebaudioside A	1.25	
Stevia rebaudiana (Bert.)	Zn	Addition to soil	6 ppm	Steviol glycosides	1.17	Baroni-nezhad et al. (2021)

higher levels of hyoscyamine and scopolamine compared to control were observed in genetically transformed root culture of *H. reticulatus* treated with 900 and 450 mg/L FeNPs after 24 and 48 h exposure period (Moharrami et al. 2017). Foliar treatment of *Leonurus cardiaca* plants with 250 mg/L FeNPs greatly increased soluble sugar, total phenolics and hyperoside content compared to control (Jafari and Hatami 2022).

Treatment of *Nigella arvensis* plants with NiO NPs increased glaucine and quercetin amounts in plant organs compared to control (Modarresi et al. 2020) as well as phenol content (Chahardoli et al. 2020), while application of Al_2O_3 NPs resulted in enhanced levels of total phenols, saponins and iridoids (Chahardoli et al. 2020). *V. tricolor* L plants treated with 10 mg/L AgNPs showed considerably higher levels of rutin, apigenin, and quercetin than the control plants (Hassanvand et al. 2021). Foliar treatment of *Tanacetum parthenium* plants with TiO_2 NPs (up to 1000 ppm) increased the levels of main SMs in EO with the exception of parthenolide (Shahhoseini and Daneshvar 2023) and foliar spraying with TiO_2 NPs also increased the levels of phenolic compounds in *Ziziphora clinopodioides* Lam (Asadi and Cheniany 2022).

Multiples of SM content compared to control in selected medicinal plants (*Artemisia absinthium* L, *Artemisia annua* L, *Dracocephalum polychaetum* Bornm., *Dracocephalum moldavica* L., *Hypericum perforatum* L., *Hypericum triquetrifolium* Turra, *Linum usitatissimum* L., *Mentha piperita* L., *Momordica charantia* L., *Ocimum basilicum* L., *Salvia officinalis* L., *Salvia miltiorrihiza* Bunge, *Stevia rebaudiana* L. and *Withania somnifera* L. Dunal) elicited by various metal/metal oxide NPs is shown in Table 8.2.

8.12 Conclusion

Medicinal plants have been used by humans for medicinal purposes since ancient times, while aromatic plants were indispensable as spices in the preparation of dishes due to the valuable SMs contained in these plant species. SMs provide defense of MAPs against the adverse impact of abiotic stresses that generate excessive ROS, resulting in oxidative stress adversely affecting development and growth of plants. Enzymatic/non-enzymatic pathways to scavenge ROS are activated in MAPs exposed to abiotic stresses, and the expression level of genes involved in SM biosynthesis increases, and plant protection against oxidative damage is also enhanced. In addition to antioxidant activity, numerous SMs of MAPs also exhibit other interesting biological activities such as antibacterial, anticancer, etc., and may serve as a leads for development of new drugs. Stimulation of the biosynthesis of many SMs in MAPs exposed to mild stress contributes to increasing the nutritional value and medicinal properties of these plants. Increasing SM production in MAPS by controlling and optimizing internal and external factors can thus be used to design smart biotechnologies enabling the production of high-quality drugs. In particular, cultivation of medicinal plants under controlled conditions in vitro using tissue cultures or hairy

Table 8.2 Enhanced production of secondary metabolites (SMs) of selected medicinal plants elicited by various metal nanoparticles

Plant	NPs of elicitor	Cultivation mode	Elicitor dose	SMs	SM content compared to control	Refs.
Artemisia absinthium L	Cu	Seeds inoculated on MS medium	30 μg/mL	TPC TFC	≈1.65 ≈1.14	Hussain et al. (2017)
Artemisia absinthium L	Ag	Seeds inoculated on MS medium	30 μg/mL	TPC TFC	≈0.66 ≈0.87	Hussain et al. (2017)
Artemisia absinthium L	Au	Seeds inoculated on MS medium	30 μg/mL	TPC TFC	≈0.75 ≈0.65	Hussain et al. (2017)
Artemisia absinthium L	TiO_2	Irrigation of plants	20 mg/L	Artemisinin	0.62	Bami et al. (2022)
Artemisia annua L	Co	Cell suspension culture (24 h)	5 mg/L	Artemisinin	2.25	Ghasemi et al. (2015)
Artemisia annua L	Ag-SiO_2	Hairy root culture	900 mg/L 3 d 20 d	Artemisinin	 1.71 3.90	Zhang et al. (2013)
Dracocephalum polychaetum Bornm	Fe_3O_4	Cell suspension culture	100 ppm	Narengin Rutin Quercetin Apigenin Rosmarinic acid Thymol Carvacrol	2.02 3.15 6.29 4.81 3.18 5.07 3.22	Taghizadeh et al. (2019)
Dracocephalum moldavica L	TiO_2	Irrigation of hydroponically grown plants	100 mg/L	Geraniol Geranial (*E*-citral) *Z*-citral	1.41 1.05 1.07	Gohari et al. (2020)

(continued)

Table 8.2 (continued)

Plant	NPs of elicitor	Cultivation mode	Elicitor dose	SMs	SM content compared to control	Refs.
Dracocephalum moldavica L	TiO_2	Spraying of plants grown in pots	30 ppm 30 ppm 100 ppm	Rosmarinic acid Ellagitannin Chlorogenic acid Caffeic acid	1.23 1.40 1.22 1.41	Kamalizadeh et al. (2019)
Hypericum perforatum L	ZnO	Cell suspension culture	100 ppb	Hypericin Hyperforin	3.80 13.36	Sharafi et al. (2013)
Hypericum perforatum L	Fe_2O_3	Cell suspension culture	100 ppb	Hypericin Hyperforin	5.40 12.02	Sharafi et al. (2013)
Hypericum triquetrifolium Turra	Fe_3O_4	Spraying on the leaves	150 ppm	Hyperocyte Quercitrin Kaempferol Hyperforin Pseudohypericin Hypericin	1.40 1.44 1.82 1.21 1.14 0.90	Bal et al. (2022)
Linum usitatissimum L	Ag	Cell suspension culture, 20 days	30 µg/L	Secoisolariciresinol diglucoside	10.0	Zahir et al. (2019)
				Lariciresinol diglucoside	2.8	

(continued)

Table 8.2 (continued)

Plant	NPs of elicitor	Cultivation mode	Elicitor dose	SMs	SM content compared to control	Refs.
				Dehydrodiconiferyl alcohol glucoside	5.0	
				Guaiacylglycerol-coniferyl alcohol ether glucoside	1.75	
Linum usitatissimum L	ZnO	Cell suspension culture	60 mg/L	Total lignan	≈1.59 1.50	Karimzadeh et al. (2019)
Linum usitatissimum L	ZnO	In vitro culture (MS medium)	500 mg/L	Secoisolariciresinol diglucoside	1.28	Zaeem et al. (2020)
				Lariciresinol diglucoside	1.35	
				Dehydrodiconiferyl alcohol glucoside	1.60	
				Guaiacylglycerol-β-coniferyl alcohol ether glucoside	1.54	
Linum usitatissimum L	TiO_2	Cell suspension culture	150 mg/L	Total lignan	1.50	Karimzadeh et al. (2019)
Mentha piperita L	Cu	Foliar spraying		Menthone Menthol Menthofuran	1.25 1.15 1.65	Lafmejani et al. (2018a)

(continued)

Table 8.2 (continued)

Plant	NPs of elicitor	Cultivation mode	Elicitor dose	SMs	SM content compared to control	Refs.
Mentha piperita L	Fe	Foliar application, 3 times	0.5 g/L 0.5 g/L 1.5 g/L	Menthone Menthol Menthofuran	1.65 1.30 2.50	Lafmejani et al. (2018b)
Mentha piperita L	Fe_2O_3	Irrigation of plants	30 μM	Menthone Menthol Menthofuran Linalool Pulgeone Isoborneol	0.90 0.85 4.02 0.76 2.70 1.50	Askary et al. (2016)
Mentha piperita L	TiO_2	Foliar spraying	150 mg/L	Menthol Menthone Menthyl acetate	1.09 1.32 1.11	Ahmad et al. (2018b)
Momordica charantia L	Ag	Cell suspension culture	5 mg/L	TPC	1.40	Chung et al. (2019)
				TFC	1.56	
				Flavonoids	1.52	
				Hydroxybenzoic acid	1.23	
				Hydroxycinnamic acid	1.15	

(continued)

Table 8.2 (continued)

Plant	NPs of elicitor	Cultivation mode	Elicitor dose	SMs	SM content compared to control	Refs.
Momordica charantia L	Zn	Foliar spraying	20 ppm	Carotenoids	2.55	Sharifi-Rad et al. (2020)
				Anthocyanins	1.11	
				TPC	1.19	
				TFC	1.45	
Ocimum basilicum	CuO	Callus cultures	10 mg/L	Rosmarinic acid	1.54	Nazir et al. (2021)
				Chicoric acid	1.42	
				Caffeic acid	2.42	
				Cyanidin	4.70	
				Peonidin	4.92	
Ocimum basilicum	MgO	Callus cultures	10 mg/L	Rosmarinic acid	1.48	Nazir et al. (2021)
				Chicoric acid	1.24	
				Caffeic acid	1.55	
				Cyanidin	1.50	
				Peonidin	1.17	
Ocimum basilicum	Fe_2O_3	Foliar treatment	200 mg/L	Soluble phenolic metabolites	≈1.70	Ghaffarzadeh et al. (2022)
Ocimum basilicum	Se	Foliar treatment	100 mg/L	1,8-cineole	1.02	Asghari et al. (2023)
				Linalool	1.01	
				Methyl chavicol	1.07	
				α-bisabolol	1.00	
				Caffeic acid	1.10	
				Chlorogenic acid	1.16	
				Rosmarinic acid	1.06	
				Quercetin	1.31	
				Cinnamic acid	1.20	
				Apigenin	1.18	

(continued)

Table 8.2 (continued)

Plant	NPs of elicitor	Cultivation mode	Elicitor dose	SMs	SM content compared to control	Refs.
Salvia officinalis L	Ag	Foliar spaying	100 mg/L	Rosmarinic aid	≈11.0	Farida et al. (2020)
Salvia officinalis L	TiO_2	Sprying of the 4 months old plants	200 mg/L	TPC TFC *p*-cymene 1,8-cineol *cis*-thujone Camphor	1.63 1.72 1.61 2.23 1.88 1.31	Ghorbanpour (2015)
Salvia miltiorrihiza Bunge	CeO_2	Soil applicaion	500 mg/L	Rosmarinic acid (root) Tanshinon (root)	1.59 1.25	Paryan et al. (2020)
Stevia rebaudiana L	Ag	Callus culture	45 mg/L	Stevioside	1.36	Golkar et al. (2019)
Stevia rebaudiana	CuO	Leaf regenerants tissue culture	20 mg/L	Rebaudioside A Stevioside	1.50 1.94	Ahmad et al. (2020)
Stevia rebaudiana L. Bertoni	ZnO	Tissue culture grown shoots	0.1 mg/L 1.0 mg/L	Rebaudioside A Stevioside TPC Stevioside TPC	1.35 1.53 1.42 1.60 1.63	Javed et al. (2017)
Stevia rebaudiana L	ZnO	Leaf regenerants tissue culture	2 mg/L	Rebaudioside A Stevioside	1.49 1.27	Ahmad et al. (2020)

(continued)

Table 8.2 (continued)

Plant	NPs of elicitor	Cultivation mode	Elicitor dose	SMs	SM content compared to control	Refs.
Stevia rebaudiana L	ZnO	Hydroponic cultivation	75 mg/L	TPC TFC	1.61 1.88	Velazquez-Gamboa et al. (2021)
Stevia rebaudiana L. Bertoni	TiO_2	Spraying of soil cultivated plants (3 × in 3 weeks)	60 mg/L 200 mg/L	Stevioside	≈1.64 ≈1.77	Rezaizad et al. (2019)
Stevia rebaudiana L	Fe	In vitro culture	45 µg/L 135 µg/L	Rebaudioside A Stevioside TPC TFC	≈2.13 ≈2.21 2.0 4.0	Khan et al. (2020b)
Stevia rebaudiana L	Mg	In vitro culture, MS medium		Stevioside	1.11	Desai Heta et al. (2017)
Withania somnifera L. Dunal	Zn-Ag (0.95:0.05) (0.75:0.25)	In vitro culture (MS medium; 1 month)	20 mg/L	Wihtanolide	≈14.08 ≈5.60	Singh et al. (2019)
Withania somnifera L. Dunal	Ni	In vitro culture (MS medium; 1 month)	20 mg/L	Wihtanolide	≈7.90	Singh et al. (2019)
Withania somnifera L. Dunal	CdSe QDs	In vitro culture (MS medium; 1 month)	20 mg/L	Wihtanolide	≈3.75	Singh et al. (2019)

roots can provide constant levels of desirable SMs and can be used for their large-scale production, and these SMs can be used in medicinal preparations and dietary supplements. Even for plants grown in greenhouses, mild stress conditions can be optimized by manipulating lighting, temperature, water regime, etc. For example, the use of LED light irradiation with appropriate wavelengths combined with optimal temperature will result in multiple stresses contributing to the most efficient stimulation of the biosynthesis of desirable SMs, thereby eliminating secondary risks for humans and animals. In field conditions, where plants are exposed to harsh environmental conditions, increased SM biosynthesis can be achieved, e.g., by applying appropriate fertilizers or by an irrigation regime that ensures that the resulting intensity of abiotic stress is not too high, leading to reduced growth and SM levels in MAPs. In the current period of ongoing climate changes, it is advisable to prefer the cultivation of MAPs that are tolerant to abiotic stresses, which can be achieved both by breeding and genetic modification of plants. The development of "omics" technologies such as genomics, transcriptomics, proteomics and metabolomics allows the rigorous study of the temporal and spatial patterns of biosynthesis and accumulation of SMs in individual plant organs, tissues and cells, as well as the relevant molecular regulatory mechanisms at different growth stages and stress conditions, and allow to achieve remarkable theoretical information useful in the improvement of MAPs varieties and SM biosynthesis, as well as the yield and composition of EOs.

Acknowledgments This work was supported by projects APVV-22-0133 and VEGA 1/0116/22.

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Chapter 9
Seed Bio-priming: An Emerging Tool Towards Improved Germination and Agricultural Sustainability

Mina Bayanati, Behnam Asgari Lajayer, Abdel Rahman Al-Tawaha, and Tess Astatkie

Abstract Global agriculture will face two major challenges in the future, population growth and climate change. Low crop yields are often attributed to environmental stresses. Drought stress is one of the most important factors limiting crop production. Seed priming is one of the simplest and most effective methods that can reduce germination time and establish uniform seed setting. Priming using different materials can have different results. Seed bio-priming is mainly used for legumes that have the ability to coexist with nitrogen-fixing bacteria. However, different studies have been conducted to apply this feature on other crops, particularly cereals. Drought stress can affect seed germination and seedling establishment. Some species of *Azetobacter*, *Azospirillium* and *Pseudomonas* are the most important types of plant growth-promoting rhizobacteria (PGPR) that are active in the root environment (rhizosphere). The application of bio-priming can decrease the negative effects of water deficiency and can have positive effects on seed germination indices.

Keywords Seed bio-priming · Drought stress · Germination · Seed vigor

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Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_9

9.1 Introduction

The main goal of seed enhancement technology is to increase the ability of seeds to withstand different environmental challenges. Various methods are used to ensure high seed yield, and most of these methods have commercial applications. Important methods of seed empowerment include seed hydration, biological seed treatments, and seed coatings (Tabatabaei 2013). However, in these methods, direct manipulation of seed embryo is not performed. Another way of empowering seeds is to propagate somatic embryos, and then coating and marketing as synthetic seeds. Methods to increase physiological seed efficiency, such as priming, are used to improve physiological performance during germination or at the early stages of seedling growth. Seed priming technique is treating seeds with an aqueous solution (somatic and non-somatic) before sowing so that the seeds can absorb water but do not germinate. The main goal of seed priming is to increase germination rate, and to facilitate a faster and more uniform emergence, especially in stressful conditions such as cold, humidity, and excessive germination temperatures, which may induce secondary dormancy or soil structure conditions that lead to post-planting sealing. Seed improvement treatments are used worldwide to improve germination uniformity and to reduce the germination time (Lutts et al. 2016).

Seed priming can be done using different methods such as hydropriming, osmopriming, solid matrix priming, hormone priming, and steam priming. The process of soaking (hydropriming) and moistening the seeds in water and drying them before they complete their germination is called hydropriming, and in fact this priming method is very simple, economical and environment friendly (Arif et al. 2014; Khalid et al. 2019). This technique does not use any chemicals and it uses only distilled water for priming the seeds. One of the disadvantages of this method is that some seeds, sometimes, do not absorb water evenly, which causes non-uniformity and inactivation of physiological processes necessary for synchronization and improvement of seed efficiency. Hydropriming is effective in reducing the risks of seedling establishment in drought stress conditions and allows the seeds to have a uniform growth in irregular rainfall conditions, minimizes the use of chemicals, and improves seed vigor and seedling growth.

The process of osmopriming involves soaking seeds in solutions with high osmotic potential and ventilation. Osmotic solutions include polyethylene glycol, potassium nitrate, magnesium sulfate, calcium chloride, sodium chloride, potassium dihydrogen phosphate, glycerol, mannitol and other high molecular weight salts. Osmopriming is one of the most widely used seed priming techniques (Guzman and Olave 2006). In solid matrix priming method, seeds with substances that have a high contact surface, different particle sizes, and seeds that are insoluble in solid-state are mixed with low chemical activity (Pandita et al. 2010). These seeds have moisture absorbing materials including vermiculite, zeonolite, and microcell, which have high matrix potential and low osmotic potential.

In steam priming method, the seeds are not directly placed in the solution, but the moisture is given to the seeds in a vapor state, and the seeds are rotated regularly inside a wheel so that the steam reaches all parts of the seeds. The incorporation of plant growth regulators during pre-soaking, priming and other pre-planting treatments have improved the seed performance of many vegetative plants. Effects on important metabolic regulatory systems are associated with hormonal and seed viability changes. The regulators involved in seed germination and stress response are auxin and abscisic acid. Hormones can be beneficial for the growth and function of some types of crops that grow under stress (Iqbal and Ashraf 2006; Ulfat et al. 2017).

A considerable number of bacterial and fungal species of soil have synergetic associations with plants and have valuable effects on growth. Growth promoting bacteria are among the microorganisms around plant roots that improve plant growth. These bacteria are able to have a positive effect on plant growth through various mechanisms such as nitrogen fixation, production of growth-promoting hormones, and supplying nutrients required by the plant. Seed bio-priming warrants the survival and growth of plants before reaching maturity. It also increases the yield of the produced plant by increasing the nutritional value of the product. In this chapter, we aim to present a brief overview of the role of microorganisms to improve the germination of seeds.

9.2 Role of Bio-priming in Germination

Currently, one of the biological methods used to increase the quantity and quality of production in sustainable and organic farming systems is using effective soil microorganisms that can increase the growth and the yield of crops. Among these organisms, a notable group of bacteria in the rhizosphere increases plant growth and yield through different mechanisms. These bacteria are naturally present in soils but since their number and density are low in the soil, inoculation of plant seeds with these bacteria can bring their population to the desired level and thus lead to their beneficial effect in the soil (Seyed and Khavazi 2011). Inoculation of seeds with live bacteria, including plant growth-promoting rhizobacteria (PGPR), is called bio-priming, which can promote the growth and productivity of plants through various mechanisms (Mahmood et al. 2016). Some benefits of biopriming are introduced in the Fig. 9.1.

Bio-priming is a new seed treatment technique that improves seeds by combining two aspects: biological inoculation of seeds with beneficial organisms and physiological (water absorption). Seed bio-priming involves coating the seed with some beneficial and hydrated bacteria. Microorganisms in seed inoculation increase the yield of plants, especially if the microorganisms used in seed inoculation are established in the root zone of plants and coexist with the plant. Bacteria stimulate plant growth, effective nutrient uptake, root growth and development, increase competitiveness with other plants, and resistance to various stresses. Also, mycorrhiza fungi have a

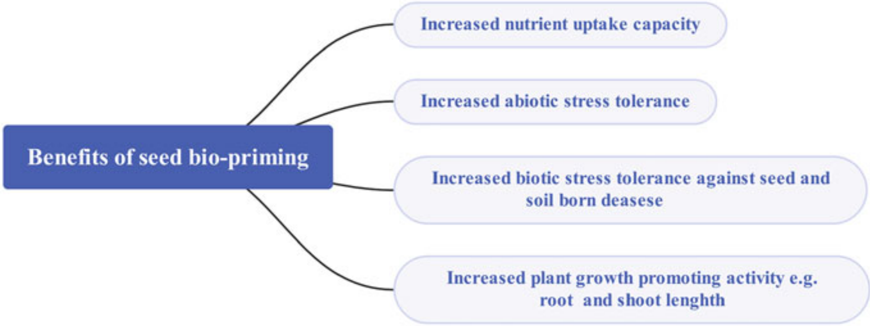

Fig. 9.1 Some physiological benefits of seed bio-priming on plants

multifunctional purpose on the canvas of cropping systems that causes: (1) improved physical quality of soil (through the spread of fungal filaments), (2) improved chemical quality of soil (by increasing the absorption of nutrients), and (3) improved biological quality of soil (through soil food network) (Cardoso and Kuyper 2006).

Sustainability of agricultural systems is one of the most important issues all over the world, mainly on soil quality. Organizational operations based on the use of organic matter improve the stability of agricultural systems through improvements in the physical, chemical, and biological properties of soil (Sayyari-Zahan et al. 2015). Bacteria stimulate plant growth and development via direct and indirect mechanisms (Vessey 2003). Bacteria eliminate harmful effects of some pathogens through various mechanisms, including induction of resistance to the pathogen production in the host plant, production of cell wall degrading enzymes plant pathogenic fungi, antibiotic production, competition with harmful species for root occupation, systemic resistance in plant and increasing plant resistance to non-living stresses (Van Loon 2007). Providing synthetic compounds to the plant via bacteria facilitates the absorption of nutrients, the production of vitamins, atmospheric nitrogen fixation, the dissolution of minerals such as phosphorus and potassium, and the production of siderophore for iron solubilization, synthesis phytohormones including auxin, cytokinin and gibberellin to improve various stages of plant growth and synthesis of enzymes that affect plant growth and development, including the direct involvement of PGRP on the plant (Gray and Smith 2005).

A positive effect of bio-priming with growth-promoting bacteria and azospirillium, phosphobacteria, and mycorrhizal fungi was reported to improve germination rate, seed vigor and initial seedling length in *Sesamum indicum* plant (Suma et al. 2014). Treatment of corn seeds with growth stimulating bacteria increased germination of corn by 20% and caused significant increase in dry weight and wet weight of stems and roots by 7% (Bakonyi et al. 2013).

9.2.1 *Physiology of Priming*

Seed priming triggers germination related functions during the initial stage of germination before the radical protrusion and leads to higher, sooner and coordinated germination compared to unprimed seeds. Increased germination rate will usually be accompanied by increased seedling vigor index, germination potential, root properties, photosynthetic efficacy, plant performance, and other growth and developmental attributes in plants (Zheng et al. 2016; Hussain et al. 2016). It has been documented that the higher rate of germination in primed seeds is largely related to a significant increase in enzyme activation, time of imbibition, change of metabolites during imbibition, and osmotic adjustment (Hussain et al. 2015; Lechowska et al. 2019). Furthermore, seed priming induces the synthesis of some important enzymes such as α-amylase and increases the soluble sugar levels during germination process (Anaytullah and Bose 2007). On the other hand, the antioxidant defense system in seedlings emerge from primed seeds due to increased activities/levels of glutathione reductase (GR), catalase (CAT), peroxidases (POD), superoxide dismutase (SOD), and ascorbic acid (AsA), and regulation of stress protein like aquaporins (AQP), dehydrins (DHN), and late embryogenesis abundant (LEA) proteins (Anaytullah and Bose 2012; Chen and Arora 2013).

In general, seed germination has three stages. The first phase of germination (stage I) is the absorption of water by the process of imbibition. In terms of water uptake and time, this phase is similar in both primed and unprimed seeds. The second stage (stage II or lag phase) of germination, which is a hydration process in unprimed seeds is done without any special control. Compared with unprimed seeds, hydration treatment in primed seeds permits imbibition and induction of the pre-germinative metabolism (“start”), but radicle emergence is disallowed, which is characterized by increased stage II. The last stage (stage III or radical protrusion phase) signifies the germination and post-germination phase, which is similar both in primed and unprimed seeds (Rajjou et al. 2012).

Other biochemical and molecular changes during the above three phases include: the initiation of priming memory, change of DNA and mitochondria, respiration, energy metabolism, antioxidant system, gene transcription and translation, cell cycle initiation, and induction of stress response gene such as LEA, DHY, AQP, and hormone signaling in stage I. Also, in stage II, new mRNA is caused by the priming memory upon second rehydration and synthesized proteins. After the mobilization of stored nutrition, radical cell elongation events occur, and lastly, radicle emerges from ruptured seed coat in stage III (Chen and Arora 2013).

Regardless of the changes mentioned above, the higher activities of many enzymes for metabolism of proteins (proteases), carbohydrates (α and β-amylases), and lipids (isocitratelyase) involved in mobilization of stored reserves in seed has been showed in primed seeds (Sisodia et al. 2018). These enzymes have an important role in the breakdown of large molecules and lead to better seedling growth (Varier et al. 2010).

Other compounds that have a significant role in kinetic exchange of water are aquaporins (AQPs). AQPs in primed seeds, due to faster imbibition compared with unprimed seeds, improve water uptake (Kubala et al. 2015). The higher activity of AQPs has been attributed to their higher expression genes (SoPIP2;1) in primed seeds (Chen and Arora 2013). An enhanced capacity of seeds to absorb, and transmembrane transport of water to different plant tissues through the regulation of AQPs has been reported. AQPs are involved in water absorption and supply. It is also assumed that they are one of the mediators in accelerating the germination of primed seeds and can also be effective in resisting environmental stresses (Chen and Arora 2013; Wojtyla et al. 2016).

The role of hormones such as gibberellin (GA) and abscisic acid (ABA) in germination cannot be ignored. Generally, GA as growth promoter and ABA as growth retardant have antagonistic roles. There is an interaction between GA and ABA, which is controlled by the genes involved in this interaction, the biosynthetic genes of these hormones, as well as proteins related to metabolism of germination and stress (van der Geest 2002; Weiss and Ori 2007). Weitbrecht et al. (2011) reported that accumulation of ABA during embryogenesis inhibits vivipary and modulates seed maturation, while GA biosynthesis signaling is generally reduced in mature seeds but increased during germination.

9.3 Improvement of Germination Indices by Microorganisms

Currently, a seed pretreatment technique is commonly used as an agent to improve germination. Seed pretreatment is a strategy to increase the rate, speed, and uniformity of seed germination under adverse environmental conditions (Ansari et al. 2012). Biological treatments stimulate plant growth by producing plant hormones such as auxin, gibberellin and cytokinin, as well as amino acids and siderophore.

According to a study by Younesi et al. (2013), the average germination rate of alfalfa cultivars increased in response to bacterial pretreatment and reached its highest level in the combined pretreatment of *Azetobacter, Azospirillum* and Pseudomonas, which was 49% different from the control (untreated) seeds. Batista et al. (2021) also reported that the application of growth-promoting bacteria increased germination, seedling strength, root length, surface area, and root density. The stimulating effect of seed germination inoculated with different isolates of various species of pseudomonas on the seeds of witch hazel species was also reported. Inoculation of peanut seeds with two strains of *Pseudomonas* fluorescent led to an increase in germination rate of 49–93%. In another study, it was reported that corn seeds inoculated with trichoderma and grown in soil without fertilizer increased by 25%. The inoculation also increased the yield and quality characteristics of the plant. Bacteria of the genus *Azotobacter*, *Azospirillum* and *Pseudomonas* are the most important bacteria that increase the growth of the active plant in the root environment. In addition to nitrogen fixation and solubilization of soil phosphorus, these bacteria affect the growth and yield of crops by producing significant amounts of substances and growth-promoting substances, especially auxins, gibberellins and cytokinins.

Bacteria of the genus *Azotobacter* and *Pseudomonas* and bacteria of the genus *Azospirillum* have a cooperative relationship with the host plant (Hamidi et al. 2018). In a study on the effect of different strains of *Azospirillum* under salinity stress, it was shown that salinity resistance and yield increased compared to the control treatment (Saatovich 2006). It has also been reported that pretreatment of rice with Azotobacter has significantly increased performance (Piao et al. 2005). Kokalis-Burelle et al. (2006) reported that growth-promoting bacteria under salinity stress increase plant germination rate, growth, and yield. Another report showed that growth-promoting bacteria increase seedling vigor, shoot and root length, and seedling dry weight in rice (Ng et al. 2012).

Among the growth promoting bacteria, Azotobacter and a mixture of *Azotobacter* and *Azospirillium* significantly increased germination parameters compared to the control treatment on Melon (*Cucumis melo*) (Nastari Nasrabadi et al. 2019). Azotobacter are the first soil bacteria to stabilize nitrogen and heterotrophs. Due to the aerobic nature of these microorganisms, they cannot tolerate anaerobic conditions and therefore are found in abundance in the rhizosphere. Different species of this genus include *Azotobacter chroococum*, *A. agilis*, *A. vinelandii*, *A. beijerinckii*, *A. nigricans*, *A. paspali*, *A. armenicus*, *A. salinestris* (Mrkovacki and Milic 2001). Azotobacter bacteria have unique properties such as cyst formation that show their resistance to environmental stress (Aasfar et al. 2021). Mia et al. (2009) reported that dual seed inoculation of Chickpeas with Azotobacter and *Rhizobium leguminosaurum* gave the highest amount of nitrogen (N) and phosphorus (P) in the shoots. Various studies have shown that the main reason for the effective coexistence between rhizobium bacteria and legumes is the secretion of plant hormones especially auxin (IAA) that increases the growth of the root (Kloepper 1978).

9.4 Bio-priming Plays an Imperative Role in Drought Stress

The application of biological fertilizers as an alternative to chemical fertilizers with the aim of increasing soil fertility and crop production is considered as sustainable agriculture. On the other hand, water shortage is one of the most important causes of crop yield reduction in arid and semi-arid regions and calls for the development of strategies to increase seed resistance such as seed bio-priming to drought stress (Fig. 9.2).

Plant growth begins with seed germination, and in order for it to survive, the sprout must be able to adapt to environmental conditions and settle in the soil. Germination begins with the absorption of water by dry seeds and ends with the elongation of the embryonic axes (Kabiri and Naghizadeh 2015; Vasconcelos et al. 2017). Drought stress also affects various aspects of plant growth (morphology, physiology and anatomy) and causes many changes such as reduced or delayed germination, reduced shoot growth and reduced biomass and growth rate (Pohl et al. 2008). Drought

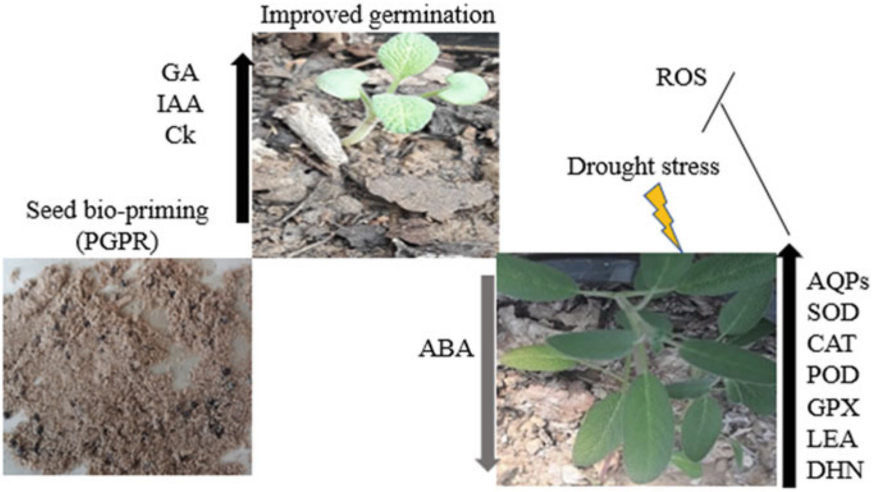

Fig. 9.2 Seed bio-priming causes changes in the antioxidant system and hormonal plant, and enhances tolerance to drought stress

stress may completely prevent seed germination. Therefore, germination rate and seedling establishment under stress conditions play an important role in increasing plant growth. Drought stress often reduces seed germination in field conditions and leads to reduced seed establishment. Germination and seedling establishment are critical stages in the plant life cycle.

Temperature and humidity are the most important environmental factors controlling germination. In many species, the percentage and rate of germination is controlled by temperature (Tabatabaei 2013; Kebreab and Murdoch 2000). Other important benefits of priming that have been mentioned in various sources include breaking seed dormancy, stronger growth of seedlings obtained from primed seeds, increasing competitiveness against weeds, faster flowering and ripening, and superior yield (Harris et al. 2001).

Drought stress affects germination by limiting water uptake by seed, movement and transfer of seed stocks, or by having a direct effect on organic structure and fetal protein synthesis. Decreased germination rate under drought stress can be due to the direct effect of slower decomposition of cotyledon endosperm by slower transfer of decomposed material to seedlings (Shahbazi et al. 2016).

Lack of water in the plant leads to plasmolysis of the plant cell, closing of the pores to prevent evaporation and perspiration, and thus stop photosynthesis and increase light respiration. On the other hand, the amount of ethylene increases and as a result the plant growth decreases (Saharan and Nehra 2011). In response to water shortage, the plant increases the production of osmolytic substances such as proline, glycine, betaine, mannitol and sorbitol, and is maintained through the osmotic potential in the plant (Dimkpa et al. 2009). Reducing the harmful effects of water deficiency necessitates the identification of drought tolerance mechanisms in plants, which in addition to identifying the effect of environmental stresses on plant growth, newer methods can be achieved to deal with these stresses. Patten and Glick (2002) reported that stimulating rhizosphere bacteria growth causes plants to tolerate drought stress by developing the plant's root system, increasing nutrient uptake, improving soil structure, increasing water holding capacity, and increasing the expression of genes responsible for drought resistance.

Pseudomonas bacterial application in lettuce plant neutralizes or reduces drought stress by improving the antioxidant status and improving plant growth under stress conditions (Grover et al. 2011). In wheat, it has been reported that growth-promoting bacteria produce hormones such as auxin that make the plant hardy to drought stress (Yazdani Biuki et al. 2010). By inoculating Rhizobium strains with ACC deaminase production on wheat growth under drought stress, Khosravi et al. (2011) found that inoculation with KYA40 strain increased shoot dry weight. Mastouri et al. (2010) reported an increase in the germination and growth of tomato seedlings induced by inoculation with Trichoderma under drought stress. Seed treatment with growth-promoting fungi also improved germination and growth in plants such as *Oryza sativa* (Cortés-Rojas et al. 2021), *Zea mays* (Singh et al. 2020), and *Nicotina tobacum* (Lee and Kim 2019).

In addition to the positive effects of bio-priming in inducing drought resistance in products, Hasanuzzaman and Fotopoulos (2019) investigated the effects of salinity on most important cultivated crops and the potential role of PGPR bio-priming seed in inducing salinity tolerance, and reported that improved drought tolerance can be achieved by introducing drought tolerant genes such as TaEXPR23, TaCP, TaABC1, WRKY2 and modifying their expression by modern wheat cultivars. By identifying drought-related genes, efforts can be made to improve drought-tolerant wheat cultivars and to study molecular pathways associated with this stress. Table 9.1 lists a number of key genes whose expression levels change under environmental stress.

9.5 Conclusion and Future Studies

In general, it can be said that drought stress is one of the most important abiotic stresses that affects the physiological parameters and growth of plants. Conducting research on the effect of drought stress on physiological parameters and growth of plants, strategies to reduce its effect, for example by priming seeds with different materials are necessary because the most sensitive stage of plant life is germination. If the plant can successfully pass these stages, it is likely to survive and establish. Therefore, it is necessary to study the range of tolerance of plants to drought stress under the influence of priming with microorganisms on germination traits. Currently, the role of molecular and bioinformatic studies along with physiological measurements is well known; however, little information is available on the process of molecular changes due to seed priming. Molecular studies especially RNA- seq and metabolomics during seed priming are needed to identify new genes expressed and their signaling network during germination, especially under stress.

Table 9.1 Induced key genes under environmental stress by seed priming

Gene	Function	Stress	Priming
SOD, CAT, APX, GR ANS, OPX	Encoding non-enzymic and enzymic	Salinity, drought	Spermine and spermidine (Paul and Roychoudhury 2017) Melatonin (Heshmati et al. 2021)
BADH1 P5CS PDH	Osmolyte	Salinity, drought	Spermine and spermidine (Paul and Roychoudhury 2017) Calcium compounds (Singh et al. 2020)
NCED3	ABA-biosynthetic enzyme	Salinity	Spermine and spermidine (Paul and Roychoudhury 2017)
TRAB1, WRKY71	Transcription factor	Salinity, drought	Spermine and spermidine (Paul and Roychoudhury 2017)
SAMDC SPDS SPMS DAO PAO	PA-metabolizing enzymes	Salinity, drought	Spermine and spermidine (Paul and Roychoudhury 2017)
NAC, TCS	GA-pathway	Drought	Uniconazole (Zhou et al. 2021)

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Chapter 10
Effects of Drought Stress on Agricultural Plants, and Molecular Strategies for Drought Tolerant Crop Development

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Abstract In natural environment, plants are subjected to encounter various kinds of abiotic stresses. Drought stress is the inevitable factor that onsets without the identification of any borders or without any warning. It is the most significant environmental stress brought on by fluctuations in temperature, light intensity, and low rainfall. It deteriorates plant biomass production, quality, and energy, leading to adverse effects

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_10

on the growth and production of plants. Abiotic stress causes physical damage, physiological and biochemical disruptions, and molecular changes. Depending on the species, plants have developed a variety of intricate resistance and adaptive mechanisms, including physiological and biochemical responses, to deal with this stress. Plants have acquired a variety of strategies to deal with drought stress, including altered stomatal conductance and distribution, altered growth pattern and structural dynamics, reduced transpiration loss, increased root length, accumulation of compatible solutes, increased transpiration efficiency, osmotic and hormonal regulation, and delayed senescence. Breeding strategies, molecular and genomics perspectives, emphasizing the alteration of omics technology metabolomics, proteomics, genomics, transcriptomics, genomics, and phenomics that improve plant stress tolerance, and marker-assisted selections are the major drought stress alleviation measures. Additionally, CRISPR-Cas method has opened up new dimensions and promises in developing drought tolerant plants. In the present chapter, the evidence on plant responses to drought stresses are explained and their possible defense measures are discussed.

Keywords Drought stress · Phytohormone · Drought tolerance · Mitigation · Genetic improvement · Molecular breeding

10.1 Introduction

During the growth and development phase, plants inevitably face several stresses which may be due to agricultural and natural conditions. Among all the stresses the plants face, drought is one of the most severe environmental stresses affecting the plants' productivity and growth. The plant body mass comprises about 80–95% of water which plays an important role in several physiological processes (Abbasi and Abbasi 2010; Brodersen et al. 2019). Due to the rapid growth in population and increasing demand for food, drought stress has become problematic in the field of agriculture (O'Connell 2017). Drought condition is very unpredictable, it depends on various factors such as water holding capacity around the rhizosphere, uneven distribution of rainfall, and evapotranspiration, while in some cases it has been found that plants are not able to uptake water from the soil, even there is enough moisture present near the root zone (Seleiman et al. 2021). Such a phenomenon is called physiological or pseudo-drought (Salehi-Lisar and Bakhshayeshan-Agdam 2020). When plants face such evolving conditions, it becomes necessary to enhance the ability of plants to withstand drought. In order to improve water-use efficiency, mere physical adaptations of roots and leaves may prove insufficient. This is where

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molecular signals come into play, particularly a specific gene encoding regulatory proteins that govern the expression of numerous other genes. These molecular signals engage in crosstalk through various regulatory mechanisms, enabling the plant to respond effectively to drought conditions (Shahid et al. 2020; Yadav et al. 2020). Here, the fundamental reactions of agricultural plants to drought stress are addressed, as well as the management strategies are discussed which can be followed in order to reduce the negative consequences of this abiotic stress.

10.2 Environmental Factors Responsible for Drought Stress in Plants

The ongoing increase in air temperature and atmospheric CO_2 levels is anticipated to intensify global climate change, leading to significant alterations in rainfall patterns and distribution (Yang et al. 2019; Yin et al. 2018). While insufficient rainfall is typically the primary factor contributing to drought stress, the situation can be exacerbated by the evaporation of water from soils. This evaporation is primarily influenced by high temperatures, intense light, and dry winds, and it can intensify an ongoing drought event (Cohen et al. 2021). The effects of global climate change often led to widespread drought stress across large regions on a global level. In addition to drought, salinity stress is also recognized as a major factor contributing to water deficits in plants (Adnan et al. 2020; Mostofa et al. 2018; Tariq et al. 2020). There are several factors that are responsible for drought stress in plants.

10.2.1 Global Warming

Certain consequences arising from climate change may have positive impacts on agricultural productivity. One such example is the potential increase in photosynthesis rates observed under elevated CO_2 levels. Consequently, the higher concentrations of CO_2 in the atmosphere could potentially enhance grain yields in the future (Brown et al. 2018). Usually, climate change brings about adverse consequences for both natural and agricultural ecosystems. Rising air temperatures can lead to the melting of glaciers, which in turn poses a risk of flooding agricultural lands, particularly those with low or negligible slopes (Cook et al. 2014). Furthermore, the diminishing glaciers are resulting in the reduction of water reservoirs, thereby restricting the availability of water for crops. This trend is progressively worsening over time. In fact, numerous rain-fed agricultural regions worldwide have been experiencing reduction in annual accumulated precipitation because of global warming (Sultan et al. 2019). The impact of global warming extends beyond water loss in the soil, affecting water loss at the plant level as well. Increased temperatures resulting from global warming led to significant transpiration of internal water within plants, intensifying the pre-existing water deficit challenges in diverse agricultural systems worldwide. If the anticipated rise in air temperature reaches approximately 2 degrees Celsius above present levels by the end of this century, an estimated one-fifth of the global population will face severe water deficits, highlighting the extensive impact of such conditions (Ray et al. 2019).

10.2.2 Irregular Rainfall

Areas reliant solely on rainfall for crop production are anticipated to face greater stress compared to regions that have access to irrigation systems such as canals and rivers. In rain-fed areas, drought episodes are closely linked to the distribution of rainfall throughout the year, leading to heightened risks of water stress occurring periodically over specific timeframes (Konapala et al. 2020). The prominent human activities of industrialization, deforestation, and urbanization have significant impacts on rainfall patterns, thereby influencing the availability of water to plants. These activities play a role in climate change, ultimately affecting the overall water availability for plant growth and development (Fatima et al. 2020). During the summer season, various factors contribute to the exacerbation of drought stress on plant growth and development. These include increased atmospheric water demand by plants, higher rates of evaporation and transpiration, and reduced availability of rainfall. The distribution and intensity of rainfall within and across years significantly influence both the management of water resources for plants and the occurrence of drought stress in most scenarios (Karandish and Šimůnek 2017; Seleiman et al. 2021).

10.2.3 Change in Monsoon Patterns

In numerous regions across the world, the monsoon system serves as a crucial source of rainfall, particularly during the summer season. The occurrence of the monsoon is closely tied to temperature, as it acts as the primary driving force behind its formation and dynamics (Ali and Anjum 2016). If current conditions persist, it is anticipated that rain-fed areas will experience a substantial decline of approximately 70% in summer precipitation levels by the beginning of the twenty-second century (Yu et al. 2013). Estimations suggest that the linear rise in atmospheric CO_2 concentration will contribute to increased rainfall, posing adverse effects on crop production. This rise in rainfall levels is anticipated to result in widespread flooding and significant economic losses within the agriculture sector of densely populated countries (Guo et al. 2015; Reddy 2015). In such scenarios, the variability in monsoon rainfall plays a crucial role and will continue to influence the moisture levels of the rhizosphere. This, in turn, significantly impacts plant productivity in specific regions of the world, primarily through changes in the intensity, occurrence, and duration of rainfall. Notably, the shifts in monsoon patterns have led to extreme variations between dry and wet seasonal rainfalls, resulting in significant food insecurity for approximately two-thirds of the global population (Prakash et al. 2020). In addition to the inherently random and unpredictable nature of rainfall patterns, recent climate changes have further contributed to the potential shortening or lengthening of the rainy season. This variability can exacerbate existing and future scenarios, leading to challenges of both water deficit and water excess in certain climatic zones. Given the agricultural context, it is imperative to adapt crop production practices to align with the behavior of the monsoon season and transition towards sustainable crop production methods. Implementing proper management techniques and effective crop planning are two key strategies to address the quantitative shifts experienced during monsoon patterns, whether they involve water deficiency or excessive rainfall (Seleiman et al. 2021).

10.3 Impact of Drought Stress on Plants

Plants that are under drought stress may experience severe effects on their growth, development, and overall health. The plant undergoes changes such as reduction in turgor pressure, closure of stomata during the day, disruption of water potential gradients, change in membrane integrity, leaf rolling, and a decrease in cell development and growth, which are vital for maintaining life processes (Zargar et al. 2017). The drought stress affecting the plant is briefly mentioned and is shown in Fig. 10.1: water deficiency, reduced photosynthesis, stomatal closure, oxidative stress, nutrient imbalance, reduced growth and development, increased susceptibility to diseases and pests, stem extension, and root proliferation (Fig. 10.1).

10.3.1 Water Deficiency

Water scarcity is a major environmental barrier to plant growth and development. The most obvious effect of drought stress is the limited availability of water in the soil. Water is necessary for several physiological functions of plants, such as photosynthesis, nitrogen intake, and transpiration. Drought stress leads to water deficit in plant tissues, disrupting these essential processes. Water scarcity outbreaks are due to the occurrence of less or the absence of rainfall resulting in low soil moisture content and low water potential in aerial parts of the plant such as leaves and stems (Ristvey et al. 2019). In arid environments, the rate at which water is lost by transpiration from leaves outpaces the rate at which water is absorbed by roots. Seed germination is one of the most important phases in the life cycle of a plant, and is highly responsive to its existing surrounding environment (Bahrami et al. 2012). For the success or failure of plant establishment in soil, the prime requirement for germination is the presence of water (Hasanuzzaman et al. 2013).

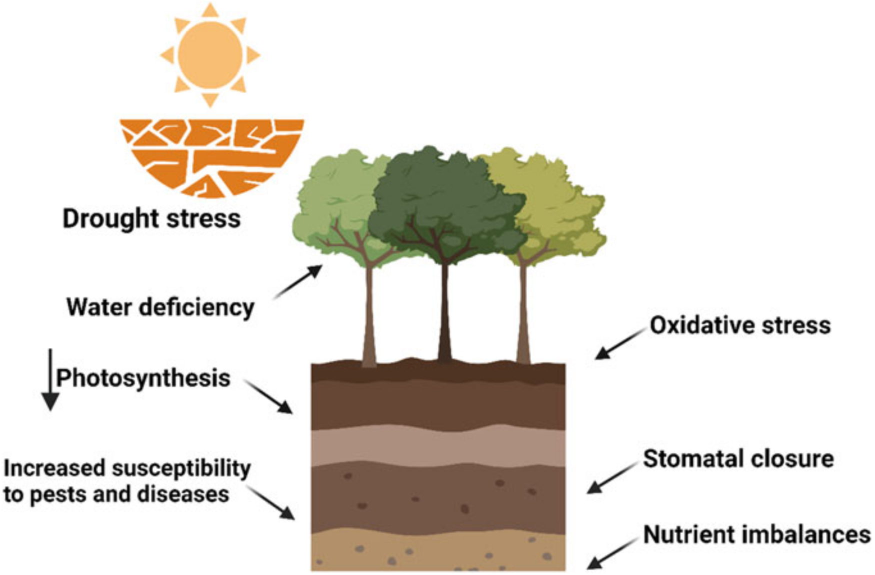

Fig. 10.1 Impact of Drought stress on plants. Image created with BioRender.com (https://biorender.com/)

10.3.2 Reduced Photosynthesis

Photosynthesis is one of the main processes affected by water stress. Leaf photosynthetic products are the material basis of plant growth. (Yang et al. 2021). Drought stress negatively affects photosynthesis, the process by which plants convert light energy into chemical energy. Insufficient water reduces the availability of CO_2, leading to decreased photosynthetic rates. By lowering both leaf area and photosynthetic rate per unit leaf area, drought stress is known to limit photosynthesis. Continued photosynthetic light reactions during drought stress under limited intercellular CO_2 concentration result in the accumulation of reduced photosynthetic electron transport components, which can potentially reduce molecular oxygen, resulting in the production of reactive oxygen species (Basu et al. 2016).

10.3.3 Stomatal Closure

Plants close their stomatal aperture as the first response at the onset of drought to maintain the leaf water potential (Laxa et al. 2019). To conserve water during drought, plants often close their stomata (small openings on the leaf surface that regulate gas exchange). Stomatal closure or metabolic impairment is the major cause of a decreased photosynthetic rate (Basu et al. 2016). Stomatal closure reduces the uptake of carbon dioxide (CO_2) required for photosynthesis and limits the release of oxygen (O_2). Stomatal closure limits leaf absorption of CO_2 and prevents transpiration water loss due to turgor pressure and/or reduced water potential (Yang et al. 2021). This can significantly impair a plant's ability to produce energy and growth. This results in reduced plant productivity, stunted growth, and decreased crop yields.

10.3.4 Oxidative Stress

Most abiotic stressors lead to an increase in ROS production. Reactive oxygen species (ROS) are frequently produced by various plant species growing under different conditions under drought stress (Hasanuzzaman et al. 2012; Hasanuzzaman et al. 2013). During normal circumstances, plants synthesize reactive oxygen species (ROS) as the by-product of different vital physiological phenomena such as photosynthesis and photorespiration (Corpas et al. 2020). These reactive species involved in cellular regulation, act as secondary messengers and as a signaling molecule for different metabolic pathways, including seed germination, senescence, plant growth and development (Gonzalez-Gordo et al. 2020) The production of dangerous ROS like $O_2{}^{*-}$, H_2O_2, $^1O_2$, and OH^* beyond the plant's scavenging capacity and causing oxidative stress (Li et al. 2010). According to many researches, chloroplast photochemistry alterations result in an excessive synthesis of highly reactive ROS species (Hasanuzzaman et al. 2020). These detrimental ROSs that are produced cause damage to the cell's proteins, lipids, carbohydrates, and nucleic acids as well as alter cellular homeostasis, which can sometimes result in cell death. So, oxidative stress leads to disrupting normal cellular functioning, impairing plant growth and development.

10.3.5 Nutrient Imbalances

A nutritional imbalance can have an impact on several biological processes. Mineral nutrients help to synthesize vital organic molecules like amino acids and proteins in plants. Mineral uptake by plants is a very effective process due to the large surface area of the roots and their ability to absorb inorganic ions at low concentrations in the soil solution (da Silva et al. 2011). Drought stress affects nutrient uptake by plants. Water deficit situations usually reduce the overall soil nutrient accessibility, root nutrient translocation and ultimately lessen the ion contents in various plant tissues (Kheradmand et al. 2014). The decline in the K was attributable to reduced K mobility, declined transpiration rate, and weakened action of root membrane transporters (Hu and Schmidhalter 2005; Hu et al. 2013.) The stomatal guard cells experience an ionic imbalance between K+ , Cl, and H+ due to drought. This ionic imbalance dominates the turgor pressure in the guard cells, which subsequently controls the closing of the stomata. The strict regulation of stomatal conductance under water deficiency enables plants to minimize water loss through evaporation or transpiration

(Mukarram et al. 2021). Nutrient imbalances can result in nutrient deficiencies or toxicities, thus further affecting plant health and productivity.

10.3.6 Reduced Growth and Development

Cell growth is considered one of the most drought-sensitive physiological processes due to the reduction in turgor pressure (Anjum et al. 2011). Meristematic cell divisions produce daughter cells, and the resulting tremendous proliferation of the new cells is what leads to growth. Under severe water deficiency, cell elongation of higher plants can be inhibited by interruption of water flow from the xylem to the surrounding elongating cells. Drought stress causes impaired mitosis; inhibits cell expansion and division, leading to reduced plant growth (Taiz and Zeiger 2010). It affects the development of leaves, stems, and roots, resulting in smaller plant size, decreased biomass, and shorter root systems. In addition to reducing the production of flowers and fruits, drought stress can also result in early leaf senescence (yellowing and shedding).

10.3.7 Increased Susceptibility to Pests and Diseases

Plants are drought susceptible to secondary stresses including pests and pathogens. The impacts of these factors may lead to acute or chronic responses and hosts may respond in different ways in terms of time and space depending on the timing and strength of the stress. There are complex processes involved in tree performance and mortality, and often it can be difficult to identify the leading cause of growth decline and death (Whyte et al. 2016). Plants are less able to tolerate and recover from pest infestations and disease attacks because their defensive systems have been impaired, as well as their physiological processes.

10.4 Plant Response to Drought Stress

Plants in their natural environments respond to environmental drought stress in several ways, from temporary reactions to low soil moisture to significant survival strategies, such as early blooming in the absence of seasonal rainfall. The chart given below provides a brief about the responses involved in drought stress and the factors present in the plants which show response to the stress.

Plants exhibit a range of physiological, biochemical, morphological, and molecular level responses to drought stress are observed in plants. These responses collectively enable plants to survive and adapt to drought stress. By conserving water, adjusting their metabolism, and protecting cellular components, plants increase their

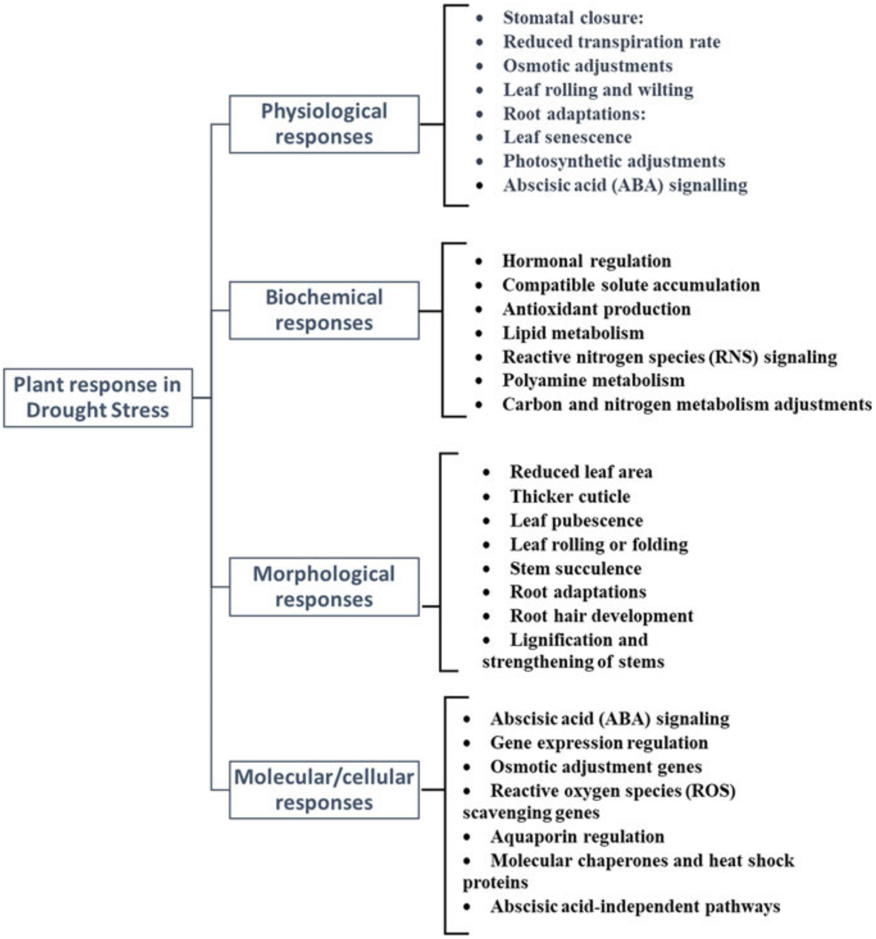

Fig. 10.2 Plant response to drought stress

chances of enduring water-limited conditions and resuming growth and development when water availability improves (Fig. 10.2).

10.4.1 Stomatal Regulation

The closing of stomata is one of the main reactions of plants to drought stress. In addition to allowing for the exchange of gases such as carbon dioxide and oxygen, stomata on the surface of leaves also permit the release of water vapor through transpiration. Plants have a complex signaling system to regulate stomatal opening mediated by the uptake and intracellular synthesis of solutes that reduces the water potential in guard cells and creates a driving force for water uptake (Zhao et al. 2018). To reduce the effects of the drought and prevent excessive transpiration water loss, the stomatal aperture must be dynamically regulated. Stomatal behavior plays a critical role during drought sensing and signaling, yet its modus operandi and crosstalk with other plant phenomena are complex and debatable (Golldack et al. 2014; Lawson and Matthews 2020). During drought, plants close their stomata to reduce water loss. This closure is mediated by hormonal signals, such as abscisic acid (ABA), which is produced in response to water stress.

10.4.2 Leaf Modifications

Plants experiencing drought stress often reduce their leaf area to minimize water loss through transpiration. This can occur through leaf abscission, where older leaves are shed, or through a decrease in leaf expansion and growth. By reducing the overall leaf surface area, plants can conserve water and maintain water balance more effectively. Plants may exhibit various leaf modifications to cope with drought stress. Some plants respond to drought stress by developing leaf pubescence, which is the presence of fine hairs or trichomes on the leaf surface. Trichomes create a layer of boundary air that reduces air movement and thus decreases transpiration rates. They also reflect sunlight, reducing leaf temperature and water loss through evaporation. To reduce water loss through transpiration, plants may exhibit leaf rolling or folding. This morphological response reduces the exposed leaf surface area and creates a protective microenvironment that reduces water loss. Leaf rolling can be observed in grasses, while leaf folding is seen in plants like legumes. Some plants have thick cuticles, which are waxy layers on the leaf surface that reduce water loss through transpiration. Others have smaller or fewer leaves, which helps to decrease the overall surface area for transpiration. In extreme cases, plants may shed their leaves entirely (deciduous plants) to conserve water.

10.4.3 Root Adaptations

The root system detects drought stress first. Even though under these circumstances shoot development is impeded, it continues to grow beneath the earth. Although the growth of the primary root is not affected by drought stress, the growth of lateral roots is significantly reduced, mainly by suppression of the activation of the lateral root meristems (Hasanuzzaman et al. 2013). Plants respond to drought stress by altering their root growth and architecture. They might extend their current roots or create deeper, taproot-like structures to delve deeper into the earth in quest of water. This makes it possible for plants to utilize water supplies that are not present close to the soil surface. Additionally, plants may increase the density of root hairs, which are small outgrowths on the root surface that enhance water absorption.

10.4.4 Antioxidant Production

Drought stress often leads to the generation of reactive oxygen species (ROS), which can cause oxidative damage to plant cells. The well-known antioxidant enzymes in plants include glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione peroxidase (GPX), guaiacol peroxidase (GOPX), glutathione-S-transferase (GST), superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione peroxidase (GPX), guaiacol peroxidase (GOPX), glutathione-*S*-transferase (GST), and so on (Gill and Tuteja 2010). These are divided into enzymatic and non-enzymatic defense systems that function together to control the flow of uncontrolled oxidation under various stress conditions and protect plant cells from oxidative damage by scavenging ROS (Hasanuzzaman et al. 2013). Production of these antioxidants in plants, scavenge ROS and protect cells from oxidative stress.

10.4.5 Osmotic Adjustments (OA)

Osmotic adjustment is a mechanism to maintain water relations under osmotic stress. Drought stress can cause cellular dehydration due to water loss. OA has been linked to sustaining stomatal conductance, photosynthesis, leaf water volume, and growth during drought stress. In response, plants may accumulate osmolytes, such as sugars, amino acids, and proline, which help maintain cellular hydration and protect proteins and membranes (Farooq et al. 2009). These osmolytes increase the osmotic potential of cells, allowing them to retain water and prevent damage.

10.4.6 Hormonal Regulations

Plant hormones play a crucial role in regulating plant responses to drought stress. Major phytohormones, such as abscisic acid (ABA), cytokinin (CK), gibberellic acid (GA), auxin, and ethylene, regulate diverse processes which enable plant adaptation to drought stress (Wilkinson et al. 2012). These hormones regulate a range of physiological and biochemical changes in plants, including stomatal closure, root development, and the activation of genes that respond to stress. The net outcome of the drought stress response is regulated by a balance between hormones that promote and those that inhibit the trait, rather than the individual action of the hormones (Basu et al. 2016).

10.5 Molecular Methods to Mitigate the Adverse Effect of Drought Stress

Drought stress is an inescapable factor that crosses boundaries and has a negative impact on plant growth, quality, and energy production. It is a substantial environmental stress induced by temperature fluctuations, light intensity, and a lack of rainfall. It is a complicated process that drastically modifies many aspects of plants, including their physical structure, functioning, chemical composition, and molecular features, resulting in a reduction in their ability to perform photosynthesis. Vegetation has developed complicated strategies to withstand and adjust to water deprivation, requiring species-specific anatomical and biochemical reactions (Seleiman et al. 2021).

Researchers are particularly interested in using microbes, hydrogels, nanoparticles, and metabolic engineering techniques to improve plants' drought tolerance. These measures include techniques such as controlling antioxidant enzyme activity, maintaining cellular homeostasis, and minimizing the negative effects of water stress. The goal is to increase plant resilience to drought conditions and lessen the negative effects of water scarcity (Seleiman et al. 2021).

By implementing optimal management practices for planting timing, plant density, plant types, and soil and nutrient management, yield losses in field crops exposed to drought stress can be effectively reduced (Parry et al. 2005; Adeyemi et al. 2020). However, as a notable technique for relieving drought stress, the use of genetically engineered plants possessing drought-tolerant characteristics has attracted substantial attention. Drought-tolerant plants are being developed using a variety of methodologies, including classic breeding techniques, and molecular and genomic approaches (Oliveira et al. 2020), where efforts are primarily focused on boosting water extraction efficiency, water consumption efficiency, stomatal conductance, osmotic adjustments, and other features with the objective of improving the plant's ability to endure drought conditions (Naeem et al. 2020). Other techniques include the use of contemporary and more efficient irrigation technologies, proper planting practices, mulching, contouring, the use of osmoprotectants, and the inoculation of plants with specific microbes proven to improve drought tolerance (Solis et al. 2018*)*.

10.5.1 Selection and Breeding Strategies

Until now, traditional breeding procedures have depended on empirical selection based on yield (Galaitsi et al. 2016). The quantitative trait of yield in key staple crops is predominantly impacted by low heritability and considerable genotype-environment interaction (Scopel et al. 2013). As a result, conventional breeding practices are currently being used to increase production (Aslam et al. 2015). Understanding plant physiological processes is required for identifying quantitative trait loci, locating gene sequences, and breeding in quantitative trait loci (Medici et al. 2014). Due to the irregular, unstable, and unpredictable character of drought response, screening for resistant cultivars under open conditions is not practical. However, such screening can be carried out in shielded and/or regulated situations (Ali et al. 2017).

Classical breeding, on the other hand, refers to the effective method of evaluating randomly selected progenies for better drought resistance across varied habitats (Araujo et al. 2015). Under normal conditions, cultivars with low transpiration rates and unchanged water use efficiency (WUE) have little effect on the final yield (Tejero et al. 2018). As part of their examination, researchers are currently conducting genetic analyses of root architecture, relative water content, and osmotic potential (Bertolino et al. 2019). It is critical to prioritize yield-contributing traits with high heredity that affect grain output under drought conditions, even if they do not have the same effect under ideal conditions. This prioritization is based on the ease with which these attributes may be measured (Shavrukov et al. 2017). However, in agricultural systems with restricted water supply, these variables exhibit broad-sense heritability for yield and frequently do not interact with grain production (Curin et al. 2020). In cases of drought stress, the first and most important element that emerges is a decrease in water use efficiency (WUE), which might vary between types and cultivars (Vishwakarma et al. 2017). In such cases, plants respond by reducing the number of stomata and the size of their leaves, which aids in minimizing water loss and maintaining internal water balance (Ding et al. 2021). As a result, certain genotypes and cultivars are susceptible to drought and are unable to adjust to environmental conditions, resulting in low Water Use Efficiency (WUE) (Tardieu et al. 2018). As a result, using a breeding strategy can help to improve WUE, ultimately boosting sustainable agricultural productivity by itemizing biomass produced per unit of water used (Fang and Xiong 2015).

Drought resistance in crop species can be accomplished directly or indirectly through trait genetic diversity, which allows for improvement through selective breeding. Marker-assisted selection (MAS) and genomic selection (GS) are the two basic methodologies used in genomic-assisted breeding. The initial stage in MAS is to find molecular markers linked to the target trait, which is required for selection in breeding programs. GS, on the other hand, is based on the building of selection models based on genetic markers found throughout the genome, as well as the selection of genome-estimated breeding values (GEBVs) in breeding populations via phenotyping the training population. For several decades, MAS has been an important component of many crop breeding programs, whereas GS is a relatively new technology that has just recently been applied to crops (Seleiman et al. 2021).

Molecular markers contribute to marker-assisted selection (MAS) by being situated near quantitative trait loci (QTL) or specific genes linked to a certain target trait. These indicators can be used to identify people who have favorable alleles (Varshney et al. 2014). Using accurate and reliable trait evaluations and a dense set of molecular markers, QTL mapping or genome-wide association techniques are used to choose markers that are related to traits. These approaches have been used to find QTLs linked to drought resilience in a variety of crops, including wheat (Kollers et al. 2013), maize (Brown et al. 2011), sorghum (Huang et al. 2010), rice (Morris et al.

2012), soybean (Hwang et al. 2014), pearl millet (Bidinger et al. 2007) and many other crops.

Genomic Selection (GS) uses all available markers to pick elite lines from a population of genome-estimated breeding values (GEBVs), and GS models are used to select elite lines without the necessity for phenotyping. Unlike MAS, knowledge of QTLs is not required for GS (Nakaya and Isobe 2012). Nonetheless, genomic selection (GS) requires more marker data than marker-aided selection (MAS). This increased density is made possible by using low-cost genotyping technologies that cover markers across the entire genome (Hayes and Goddard 2001). The international maize and wheat improvement center (CIMMYT) is currently using GS in the development of drought-resistant maize (Crossa et al. 2014). Similar research efforts are underway in other crops such as sugarcane, legumes, and wheat, with the goal of implementing this strategy to improve drought tolerance (Gouy et al. 2013; Varshney et al. 2013; Rutkoski et al. 2010).

10.5.2 Molecular and Genomic Strategies

Biochemical and molecular components contribute to the initiation of mechanisms that mitigate the harmful consequences of water stress. Transcription, stress-responsive genes (as indicated in Table 10.1), and the hormone abscisic acid are among these variables (Osakabe et al. 2020). In addition to improving drought resistance, breeding programs aim to improve stress management by introducing transgenic expression of several stress-responsive genes (Rai and Rai 2020; Liu et al. 2020). However, overexpression of these genes frequently leads to a decrease in plant growth rate, limiting their practical application. To effectively address these difficulties, it is critical to continue to focus on the molecular and genetic basis of drought resilience (Hussain et al. 2018).

Genomic and related technology methods can aid in the identification of genes that ameliorate the effects of stress, allowing efforts to preserve and incorporate these genes into future breeding programs (Medina et al. 2016). Stress-tolerant genes work at the molecular level and interact with quantitative loci traits, emphasizing the need of studying their interactions and cloning stress-related genes (Nakashima et al. 2014). In the field of genetic engineering, it is commonly agreed that a combined approach including marker-based selection, molecular approaches, and traditional breeding is the most effective option for increasing plant tolerance to abiotic stress (Bhatnagar-Mathura et al. 2008; Cho and Hong 2006).

The clustered regularly interspaced short palindromic repeats and CRISPR-associated protein 9 (CRISPR–Cas) system of genome editing is a recently developed molecular technique which has been appreciated for its adaptability and ease of operation. CRISPR–Cas-based genome editing is applied in several economically important crops, including cotton, rice, wheat, maize, soybean, potato, and in biofuel crops (Sami et al. 2021; Tiwari et al. 2021)). CRISPR–Cas system has been proved useful in developing resistance to multiple abiotic environmental stresses, including

Table 10.1 Gene associated with plants' ability to tolerate drought stress

S. no	Crop plant	Target gene	Function	References
1.	Rice (*Oryza sativa*)	*OsDREB*	Specifically induced under cold stress conditions	Aharoni et al. (2004)
2.	Rice (*Oryza sativa*)	*OsERF7*	Predominantly expressed in the root meristem, pericycle, and endodermis	Shou et al. (2004)
3.	Maize (*Zea mays*)	*Maize glossy6 (gl6)*	The protein is involved in trafficking of intracellular cuticular waxes and drought tolerance	Li et al. (2019)
4.	Wheat (*Triticum aestivum*)	*TaLEA3*	Rapid stomatal closure in transgenic plants to tolerate drought	Yang et al. (2018)
5.	Apple (*Malus domestica*)	*MdSHINE*	Confers drought tolerance by regulating wax biosynthesis	Zhang et al. (2019)
6.	Potato (*Solanum tuberosum*)	*StDREB2*	Promotes drought tolerance	El-Esawi and Alayafi (2019)
7	Wheat (*Triticum aestivum*)	*TaNAC69*	Increased tolerance to drought	Seleiman et al. (2021)
8	Maize (*Zea mays*)	*NF-YB2*	It increases yield and photosynthetic rate under drought	Seleiman et al. (2021)
9	Rice (*Oryza sativa*)	*AP37*, *OSNAC10*	Drought tolerance and grain yield increased	Seleiman et al. (2021)
10	Sugarcane (*Saccharum officinarum*)	*SodEFF3*	Increase in resistance to drought	Seleiman et al. (2021)
11	Soybean (*Glycine max*)	*P5C5*	Increased in drought tolerance	Seleiman et al. (2021)
12	Tobacco (*Nicotiana tabacum*)	*HSP70-1*	Drought stress tolerance	Seleiman et al. (2021)

salinity, drought, heavy metals etc. Different types of CRISPR/Cas technology have been successfully used to develop drought tolerance by altering genetic features in diverse plant species. By targeting certain agronomically relevant gene regulators, CRISPR–Cas could significantly improve plant tolerance to drought stress and is able to increase average crop production. For example, it was shown that the maize variants modified using CRISPR method were found to be more tolerant towards drought (Shi et al. 2017). Other such experiments also showed that CRISPR–Cas9 method can be effectively implemented to induce novel allelic modifications for developing drought-tolerant crop varieties. However, relatively few studies have explored the application of CRISPR–Cas-methods to improve crop tolerance of drought stress, compared to other abiotic stresses. The research gaps in development of genome-edited crops are the discovery of target genes, effective delivery of CRISPR machinery to the appropriate cells and regeneration of various crops. Particular attention should be given on drought stress response genes and drought stress-induced transcriptional networks to address the issue of target discovery (Joshi et al. 2020). Additionally, a thorough comparative genome-wide analysis can develop a solid baseline for further identification of the potential target genes in crops (Table 10.1).

10.6 Conclusion

Climate change has led to increased biotic and abiotic stresses, posing serious threats to global food security and plant production sustainability. Drought, an abiotic stress, is particularly concerning due to its adverse impact on plant growth, development, and yield, leading to food insecurity worldwide. Drought stress affects plants throughout their life cycle, from germination to maturity, and disrupts various physiological, metabolic, and biochemical processes, hampering plant productivity. However, plants have developed mechanisms to enhance drought tolerance and mitigate its adverse effects.

To address the challenges posed by drought stress, it is essential to explore untapped adaptive traits in different plant species and incorporate them into genotypes that can tolerate water scarcity without compromising productivity. Breeding technologies offer great potential for improving plant performance under water deficit conditions, and various approaches are being explored for drought adaptation in arid and semi-arid environments. Several strategies can be employed by plants to enhance drought tolerance, including modifying growth patterns, reducing transpiration loss through stomatal conductance alteration and distribution, leaf rolling, adjusting root-to-shoot ratio dynamics, increasing root length increment, accumulating compatible solutes, improving transpiration efficiency, regulating osmotic and hormonal responses, and delaying senescence. To overcome the adverse effects of drought stress, researchers need to work further on developing some innovative methods like changes in breeding strategies, alterations in omics technology or novel approaches related to CRISPR/Cas through which a better understanding can be developed about plant responses to drought stress. This can further potentially increase plant productivity in dry environments, and thus can reduce the threats to global food security.

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Chapter 11
The Rhizosphere–A Hub of Emerging Importance for Plant Biotic Interactions

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Abstract The rhizosphere is a microhabitat around plant roots that is actively created and regulated by plants, while having a major impact on plant life itself. Plants constantly enrich the rhizosphere with organic matter from their rhizodepositions and root exudates, shaping the chemical and microbiological composition of the space surrounding their roots. In this chapter, we discuss the interactions between plants and other organisms through the processes in the rhizosphere. Plant-associated microorganisms, such as plant growth-promoting bacteria and mycorrhizal fungi, play important roles in enhancing the survival of plants, through increasing the availability of nutrients from the soil to plants, degrading and immobilizing toxic compounds, alleviating the effects of abiotic stress, acting as biocontrol agents, protecting the plants from pathogens, and bolstering the efficiency of plant responses to biotic and abiotic stress. Moreover, plants use the rhizosphere as a battlefield for mutual competition by releasing allelochemicals that are detrimental to other plant species, and to harmful soil nematodes and insects. Similarly to land plants, aquatic plants also create a rhizosphere around their roots, with important implications for rice cultivation, methane emissions from wetlands, denitrification of aquatic habitats, and wastewater treatment through constructed wetlands. We emphasize how the existing and potential rhizosphere engineering approaches take advantage of the plant-associated microorganisms and allelopathic interactions between plants to improve the health and yield of agricultural crops, and help preserve the natural environment.

Keywords Allelopathy · Mycorrhiza · Nutrient cycling · Phytomicrobiome · Plant growth-promoting bacteria · Rhizodeposition · Rhizosphere engineering · Root exudates · Soil microbiome · Wetland soils

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_11

11.1 Introduction

The rhizosphere, briefly described as the space around plant roots, is an interface through which the plants enter into biotic interactions with other organisms (Hiltner 1904; Rudrappa et al. 2008). These interactions are bidirectional or multidirectional and are mediated primarily by chemical communication. Hence, plants and other organisms release their metabolites into the rhizosphere, which are then taken up and/or metabolized by recipient organisms, affecting their physiological processes and adaptive responses.

By releasing a set of their own metabolites into the rhizosphere, the plants create a microenvironment in the immediate proximity of their root system—a phenomenon known as the rhizosphere effect (Nuccio et al. 2020; Lv et al. 2023). The rhizosphere effect manifests itself most of all on the chemical and microbiological level. By releasing the organic matter into the rhizosphere, the plants modify the chemical composition in the vicinity of their roots, causing alterations in the soil microbiome. The soil microorganisms further alter the organic, as well as inorganic composition of the soil through their own metabolic activity. In this way, the chemical and the microbiological component of the rhizosphere effect complement and cannot be considered separately from each other (Rudrappa et al. 2008; Nuccio et al. 2020; Kaleri et al. 2021).

The organic matter released by the plants into the rhizosphere is comprised of two components: rhizodeposition (a mixture of mucilage, sloughed-off root cells and tissues, lysates and other plant-derived detritus), and root exudates (Dennis et al. 2010). These two components fundamentally differ in several aspects (Fig. 11.1). Rhizodeposition occurs at a far broader scale. It is spontaneous, constitutive, and does not have a regulatory function. Conversely, root exudation is much lesser in scale, tightly regulated (presumably dependent on specific transport mechanisms regulated at the cellular level), and affects the immediate environment around plant roots (Dennis et al. 2010; Pausch and Kuzyakov 2018). There is still considerable confusion around the terms "rhizodeposition" and "root exudation" in literature since "root exudation" is often used to refer to the entirety of organic matter released through rhizodeposition. Moreover, it is unclear how sharp the distinction between the two processes really is, especially regarding their physiological regulation.

Although broader in scale than root exudation, rhizodeposition did not attract much scientific attention until recently. Due to the amount of organic matter involved and its importance for the structuring of soil microbial communities that feed on plant-derived detritus, rhizodeposition has lately become a topic of emerging importance in soil ecology, including the possibility for the selection and engineering of plants with superior rhizodeposition properties, that would be more effective in fostering healthy soil microbial communities (Hallett et al. 2022). This is especially important from the perspective of climate change, whereby crops selected for more efficient rhizodeposition would also be more efficient at soil carbon sequestration, and hence, more beneficial to achieving a negative atmospheric carbon balance (Pausch and Kuzyakov 2018; Hallett et al. 2022; Panchal et al. 2022).

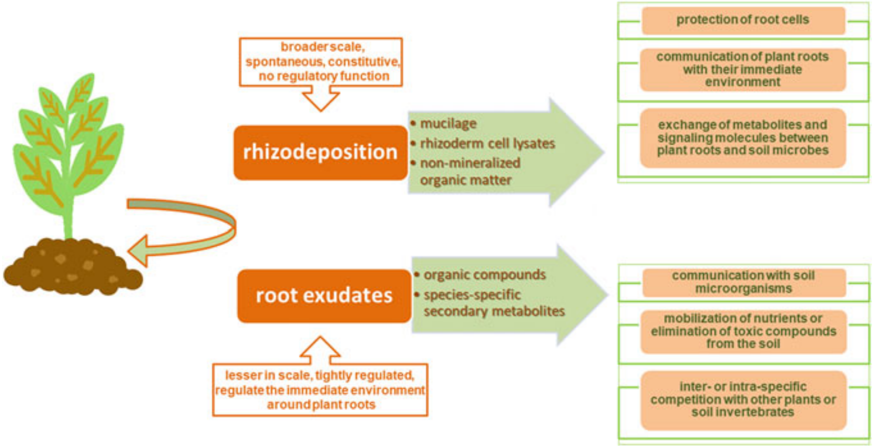

Fig. 11.1 The major characteristics of organic matter released by plant roots into the soil: rhizodeposition and root exudates

Rhizodeposits are made up of three components: (1) the mucilage secreted into the gaps between root cells; (2) rhizoderm cell lysates; and (3) non-mineralized organic matter comprised of cells and tissues sloughed off the root apices (Dennis et al. 2010). These organic substrates make up nutrients for soil microbes, which are engaged in their decomposition and mineralization (Pausch and Kuzyakov 2018; Jacoby and Kopriva 2019). Mucilage makes up the most abundant component of rhizodeposition and consists of a gelatinous polysaccharide matrix in which small organic molecules, as well as proteins, lipids, and minerals, are dissolved (Nazari et al. 2022). This extracellular matrix plays multiple ecophysiological roles and serves as a molecular interface through which the plant roots communicate with their immediate environment. The mucilage protects the root cells from friction and mechanical wounding, from drying, contact with drought-induced air gaps in soil, facilitates the exchange of metabolites and signaling molecules between plant roots and soil microbes, and provides a biofilm-like microhabitat that is generally supposed to be beneficial to plant-growth promoting microorganisms and unfavorable to plant pathogens (Jacoby and Kopriva 2019; Nazari et al. 2022). Moreover, the rhizosphere mucilage is likely co-operatively produced by both plant roots and the soil microorganisms, although the relative contribution of the two to the production of the rhizosheath matrix is a matter of debate (Rudrappa et al. 2008; Chai and Schachtman 2022; Nazari et al. 2022).

Unlike rhizodeposition, root exudation attracts the interest of researchers primarily for its physiological regulation and specificity of the process. Importantly, the release of specific organic compounds, that play specific roles in the regulation of biotic (and also abiotic) factors in the soil environment inspires various rhizosphere engineering approaches, e.g., through promoting the positive interactions between plants and beneficial soil microbes, or through enhancing plant defense mechanisms for resistance to soil-borne pathogens (Backer et al. 2018; Tan et al. 2022).

Through root exudation, plants release secondary metabolites into the rhizosphere. These secondary metabolites are species-specific—every plant species releases a specific set of metabolites into the soil, which is also influenced by environmental conditions. These root exudates have various functions—e.g., they may act in the mobilization of nutrients or elimination of toxic compounds from the soil (Chai and Schachtman 2022). They may also mediate the communication with soil microorganisms (Bakker et al. 2018), inter- or intra-specific competition with other plants (Weston and Duke 2003), or even soil invertebrates such as nematodes and arthropods. In this chapter, we focus primarily on the biotic interactions between plants and other living inhabitants of the rhizosphere.

11.2 The Phytomicrobiome: Plants and Their Associated Microorganisms Form an Inseparable Community

Given a long evolutionary history, bacteria had ample time to colonize all available ecological niches, and plants colonized much later the ecosystems in which bacteria had already become native. Coexistence led to numerous interactions between bacteria and plants that were both beneficial and harmful. In recent decades, we have learned that many microorganisms from the soil in the rhizosphere of plants have a closer relationship with plant tissues and colonize them, forming the so-called phytomicrobiome. The plant and its phytomicrobiome form a holobiont, a term coined by Adolf Meyer-Abich (Baedke et al. 2020). However, plants are not passive in these relationships but rather active protagonists that can dynamically shape their microbiome. Plants influence the soil microbiota by affecting its composition and diversity through root exudates, plant debris, and symbiotic associations or by directly altering soil carbon inputs, nutrient availability, and soil structure (Ai et al. 2015; Nazari et al. 2022). Up to 20% of photosynthetically fixed carbon is converted into small organic molecules deposited through roots, affecting the rhizosphere microbiome (Haichar et al. 2014). This high expenditure shows how vital the phytomicrobiome is to plants. Thus, by depositing organic matter into the rhizosphere, plants provide the nutrients to soil microbes, facilitating their survival and reproduction.

On the other hand, the composition of the soil microbial community that interacts with plants is determined both by historical conditions and current environmental factors (Ge et al. 2008). In crop species for which more data are available, fertilization regimes and crop rotation have been shown to influence microbial diversity. In a long-term study, Ai et al. (2018) found that soil bacteria were more sensitive than fungi to changes in soil nutrient status caused by fertilization. However, fungi responded more dynamically to the changes in crop type. The authors also showed that the increased activities of soil enzymes involved in C, N, and P cycles were directly and positively related to bacterial community structure and fertilizer type (manure or inorganic fertilizer). Kaleri et al. (2021) found differences in soil bacterial diversity when the soil was fertilized with cow manure, or cow manure digested by dung beetles. Dung beetle-digested manure was superior in increasing bacterial diversity, microbial C and N content, and promoting plant growth. Phytomicrobiome diversity is the most important trait that can prevent the development of pathogenic bacteria to both humans and plants (van Elsas et al. 2012; Wei et al. 2019). For instance, Marković et al. (2022) showed that the healthy potatoes and their geocaulosphere had greater bacterial diversity than the potatoes with symptoms of soft root rot grown in the same field, including their respective geocaulosphere. In addition, bacterial genera with detected biocontrol strains were enriched in healthy potato samples.

11.2.1 Plant Growth-Promoting Bacteria: An Invaluable Asset for Future Agriculture

In a world increasingly challenged by overpopulation, climate change, land degradation, and the spread of agricultural pathogens and pests, the phytomicrobiome of agricultural crops is being given increasing importance (Tan et al. 2022). Plant growth-promoting bacteria (PGPBs) affect plant yield and growth rate, their tolerance to abiotic stress, and their resistance to pathogens and pests. The rhizosphere is the most prolific source of PGPBs, with numerous strains isolated and some marketed as biofertilizers and/or biocontrol agents (Bejarano and Puopolo 2020). A special category of PGPBs are endophytic bacteria that thrive in plant tissues, with rhizobia, bacteria that form root nodules and fix nitrogen, being the best studied (Gopalakrishnan et al. 2015). The promotive effects of beneficial bacteria affect plant growth through direct and indirect mechanisms (Glick 1995; Santoyo et al. 2016) (Fig. 11.2). Direct mechanisms encompass all effects of PGPBs whose consequences lead to the direct promotion of plant growth. These include the production of plant hormones, ACC deaminase, nitrogen fixation, and mineral solubilization. Indirect effects of PGPBs on plant growth occur through mechanisms of pathogen control: the production of antimicrobial substances, competition for space and nutrients, quorum quenching, and induction of systemic resistance. However, some of the ecological functions of PGPBs may have both direct and indirect beneficial effects on plant growth. For example, bacterial siderophores, small peptide molecules that bind iron, work both ways, directly on plant growth by increasing iron uptake, and indirectly by taking up iron and preventing pathogen growth (Saha et al. 2016). Recently, the siderophore from *Bacillus amyloliquefaciens* MBI600 was also found to have direct antibiotic activity against *Pseudomonas syringae* pv. *tomato* (Dimopoulou et al. 2021). In addition, many PGPBs can act through more than one mechanism, and environmental conditions may limit or enhance their activity.

Bacteria affect plant growth by producing plant hormones such as auxin and cytokinin. Although auxins form a group of numerous naturally occurring

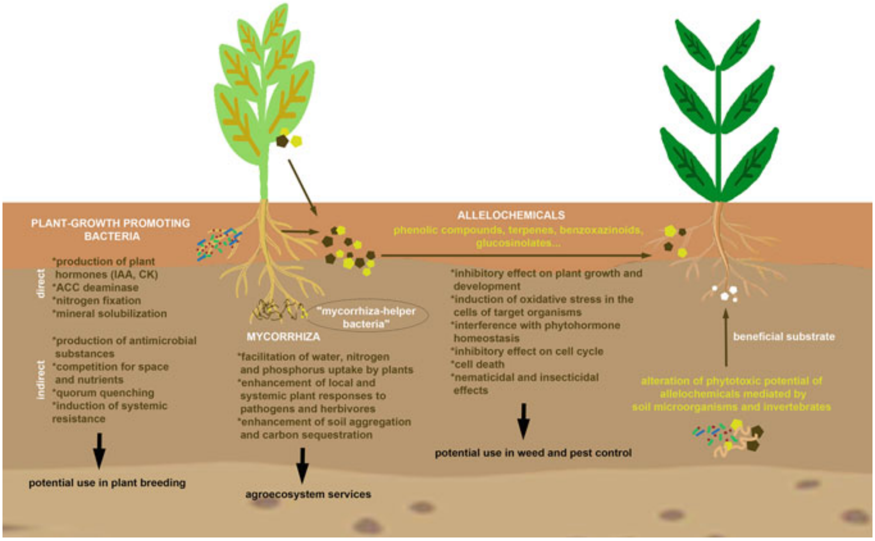

Fig. 11.2 Summary of the most important types of biotic interactions between plants and other inhabitants of the rhizosphere. Plant growth-promoting bacteria exert direct and indirect beneficial effects on plants. Beneficial soil fungi enter into mycorrhizal association with plant roots, which is facilitated by the mycorrhiza-helper bacteria. Allelochemical compounds serve as a mechanism of competition between plants, but can be converted to beneficial substrates by soil microorganisms and invertebrates. The existing and potential benefits from these processes for humans are showcased in black letters at the bottom of the picture

compounds produced by plants, the most important auxin is indole-3-acetic acid (IAA), which acts in geotropism and phototropism, root initiation, cell division, stem and root elongation, vascular tissue differentiation, and apical dominance (Grobelak et al. 2015). However, in addition to plants, up to 80% of all bacteria in the rhizosphere can produce IAA (Glick 1995). The observation that multiple IAA biosynthetic pathways exist in IAA-producing bacteria suggests additional or different roles for this metabolite in bacteria. IAA is used as a signal for gene regulation in some bacteria, suggesting that it makes part of the genetic regulatory networks of microorganisms (Spaepen and Vanderleyden 2011). When these microorganisms interact with plants as part of their ecological habitat, a reciprocal IAA-mediated signaling process is likely to occur in microbe-plant interactions, acting both in pathogenesis and in growth stimulation (Lambrecht et al. 2000; Spaepen and Vanderleyden 2011).

Like auxin, other organisms can produce cytokinins, including bacteria, fungi, microalgae, and insects. In plants, cytokinins affect seed germination, apical dominance, flower and fruit development, and leaf senescence (Werner et al. 2001). In addition, cytokinins induce plant immunity when interacting with pathogens (Grosskinsky et al. 2011; Naseem et al. 2014). Cytokinin-producing PGPBs can be used as a biostimulant for plant growth under abiotic stresses, such as drought

(Mekureyaw et al. 2022), but also for biocontrol of various pathogens, for example, when *Arabidopsis* is primed with cytokinin-producing *Pseudomonas fluorescens* G20-18. G20-18 efficiently controls the pathogen *P. syringae*, whereas cytokinin-deficient mutant strains of G20-18 showed impaired biocontrol against pathogenic bacteria (Grosskinsky et al. 2016). Microorganism-derived cytokinins interact with other plant hormone signaling pathways in a manner similar to plant-derived cytokinins. For example, cytokinins produced by PGP bacteria and microalgae protect the target plants against pathogens, similarly to the exogenous application of cytokinins, or overexpression of their biosynthetic genes (Akhtar et al. 2020). On the other hand, cytokinins from pathogenic sources increase host susceptibility to disease, increase disease severity, and enhance pathogen infection in plants (Spallek et al. 2018).

Alleviating plant stress induced by drought, high salinity, waterlogging, heavy metals, and pathogenicity by increasing 1-aminocyclopropane-1-carboxylate (ACC) deaminase also falls within the scope of PGPB activity (Saleem et al. 2007). Ethylene, a plant growth regulator and stress hormone, is produced under these stress conditions, negatively affecting root growth and, thus, plant growth. PGPBs regulate ethylene production by converting ACC (a precursor of ethylene biosynthesis in plants) to α-ketobutyrate and ammonia. Lozo et al. (2022) showed that the drought-tolerant strains *Bacillus safensis* SS-2.7 and *Bacillus thuringiensis* SS-29.2 produce ACC deaminase and IAA, improving the response of some sweet pepper cultivars to drought by increasing the activity of antioxidant enzymes, although the response was genotype-dependent.

Unlike plant hormones, which may exert both beneficial and harmful effects on plants, nitrogen fixation is a clearly beneficial property of plant growth-promoting bacteria, that appears to act directly. The ability to reduce atmospheric nitrogen to ammonia is an exclusive property of prokaryotic organisms. Many different genera of bacteria possess this ability, and the best known are diazotrophic bacteria that fix N_2 in symbiotic relationships with the roots of certain plants, particularly legumes. The *Rhizobium*-legume interaction is the best-known and agronomically most important (Lindström and Mousavi 2010). *Sinorhizobium* (Saranraj et al. 2021), *Mesorhizobium* (Knežević et al. 2022), *Azotobacter* (Stajković-Srbinović et al. 2016), etc. are also studied and are components of fertilizers that have been used in agriculture for decades. In addition, nodules formed by rhizobia in plant roots can be colonized by nonrhizobial endophytic PGP bacteria belonging to the genera *Bacillus*, *Pseudomonas*, *Streptomyces*, *Actinomyces*, and *Serratia* (Lodewyckx et al. 2002). *Bacillus megaterium* DZK1BH, alone and in association with *Mesorhizobium* sp. 631, stimulated the growth of birdsfoot trefoil and orchardgrass in acidic soil (Knežević et al. 2021).

Minerals such as phosphorus and potassium are present in relatively high concentrations in the soil but are fixed in a mineral form that is unavailable to plants. Microorganisms solubilize inorganic P bound to soil colloids by releasing chelating low molecular weight organic acids (Castagno et al. 2021). Bacteria that solubilize K are common rhizosphere inhabitants and are considered important factors in soil K dissolution (Ahmad et al. 2016). The mechanism by which K is made available to plants is the same as for P–chelation by organic acids produced by microorganisms (Meena et al. 2014).

The production of antibiotics is the most prominent feature of PGP bacteria, which acts indirectly on plant growth and has a direct biocontrol effect. Their role in interaction with plants is antagonism to pathogens. The genus *Bacillus*, along with *Pseudomonas*, is represented by more than a dozen species that use up to 12% of their genome to produce numerous compounds with antimicrobial activity and biocontrol potential (Fira et al. 2018). Ten percent of the genome (13 gene clusters) of the biocontrol strain *B. velezensis* FZB42 is subordinated to the synthesis of antimicrobial compounds (Fan et al. 2018). Recently, the entire genome of the commercial biocontrol strain *B. velezensis* KST 713 was decoded, in which 15 biosynthetic clusters were identified, suggesting that 12% of the genome of this strain is involved in biosynthesis, biosynthetic regulation, and transport of antimicrobial compounds (Pandin et al. 2018). Some are synthesized ribosomally, others non-ribosomally by peptide and/or polyketide synthetases (NRPSs/PKS). Non-ribosomally synthesized cyclic lipopeptides showed great potential as antimicrobial agents (Ongena and Jacques 2008; Zhao et al. 2017). The collection of *Bacillus* spp. isolated from soils in Serbia proved to be a rich source of strains with the potential to synthesize lipopeptides from the iturin, surfactin, and fengycin families (Berić et al. 2012; Stanković et al. 2012). For some of them, the actual production of lipopeptides and their role in biocontrol against bacterial and fungal plant pathogens have been demonstrated in vitro and in planta (Dimkić et al. 2013, 2017; Nikolić et al. 2019).

Competition for limited resources such as space and nutrients is a natural phenomenon that may also play an indirect role in phytopathogen control. Competition for nutrients occurs when a biological control agent reduces their availability in the environment and indirectly limits pathogen growth by absorbing and utilizing nutrients more efficiently. Biological control agents capable of forming biofilms and rapidly colonizing plant roots prevent pathogen-host contact and thus protect against infection (Morris and Monier 2003). Biofilm formation by *B. subtilis* and *B. amyloliquefaciens* strains protects plants from fungal pathogens such as *Rhizoctonia solani* (Mousivand et al. 2012) and *Botrytis cinerea* (Salvatierra-Martinez et al. 2018).

The disease can be reduced when a stimulus triggers defense mechanisms prior to infection by a plant pathogen. Induced resistance is a state of increased defense capacity that a plant develops when appropriately stimulated. Induced systemic resistance (ISR) represents the enhancement of whole plant resistance to various (multiple) pathogens induced by beneficial microorganisms (Choudhary et al. 2007). *Bacillus* spp. has shown the ability to protect numerous plant species by induction of systemic resistance (Kloepper et al. 2004). ISR is mediated by a salicylic acid-independent pathway whose central participants are jasmonic acid and ethylene, and which generally functions without activating pathogen-related genes (Pieterse et al. 2003).

This light overview of possible mechanisms involved in microbe-plant interaction points to vast possibilities of potential use in plant breeding. Recent research aims to use a consortium of bacteria with different and complementary mechanisms to promote plant growth on the one hand, and microbiome engineering on the other, as the ultimate method that should yield great results. To achieve this, we need to understand in detail the interactions of the phytomicrobiome with the plant.

11.2.2 Mycorrhiza: The Underrated Player in the Functioning of Agroecosystems

Mycorrhizal association, or mycorrhiza, is a morphophysiological association between soil fungi and plant roots, which is widely distributed and occurs in more than 80% of species of land plants. Thus, mycorrhiza is believed to have evolved in the early stages of land colonization by plants (Brundrett 2002; Wang and Qiu 2006).

Mycorrhiza can be classified as endo- and ectomycorrhiza, depending on whether or not the hyphae penetrate the root cell walls. Furthermore, the dominant form of endomycorrhiza is arbuscular mycorrhiza, in which the mycorrhizal hyphae form arbuscules, tree-shaped structures which form close connections with invaginations in the plant root cells (Parniske 2008). Arbuscular mycorrhiza is the most widespread, and likely ancestral form of mycorrhiza, from which the other types of plant-fungal symbiosis have evolved, including several independent occurrences of ectomycorrhiza that are all considered to derive from arbuscular mycorrhiza (Wang and Qiu 2006). Arbuscular mycorrhiza is also the most economically important, since it is ubiquitous in major crops, such as maize and wheat (Rillig 2004a). Besides arbuscular mycorrhiza, minor types of endomycorrhiza include the economically important orchid mycorrhiza (Rasmussen 2002; Hossain 2022), and ericoid mycorrhiza, which has developed in plant species that had to adapt to survival in nutrient-poor, heavy-metal-contaminated, or otherwise hostile soils (Cairney and Meharg 2003).

In contrast to endomycorrhiza, ectomycorrhizal symbiosis occurs almost exclusively in trees. It is characterized by the formation of hyphal sheaths coated around tree roots, which enhance the provision of water and phosphates to the roots, while at the same time facilitating the transport of carbohydrates from the tree roots to the fungal mycelia and fruitbodies (Wiemken and Boller 2002; Agerer 2006).

On the developmental level, both ecto- and endomycorrhiza rely on sophisticated cellular and developmental mechanisms, the complex genetic and signaling regulation of which has evolved through millions of years of symbiosis (Wiemken and Boller 2002; Gutjahr and Parniske 2013). The nature of mycorrhiza is essentially mutualistic, although depending on circumstances, one of the symbionts may benefit greater advantage than the other (Hossain 2022). The fungi contribute to the association by providing water, phosphorus, nitrogen, and other nutrients in the acquisition of which they are more efficient compared to plant roots; in return, plants contribute with photosynthetically derived carbohydrates that serve as the energy source for the fungus (Bago et al. 2000; Parniske 2008). Due to their more flexible structure and faster growth rates, fungal hyphae can penetrate deeper and farther into the soil than plant roots, and hence, they are more efficient in the acquisition of water. The water is transferred to plant root cells through mycorrhiza, whereby specialized aquaporins were found to be specifically expressed on plant root cell membranes near mycorrhizal arbuscules. Besides water, some of these mycorrhizally-induced aquaporins are likely also involved in importing ammonium from mycorrhiza to the plant (Uehlein et al. 2007). Compared to plant roots, fungal hyphae are also more efficient in the uptake of inorganic nitrogen from the soil; the nitrogen is then transferred to the plant root cells through mycorrhiza either in the inorganic form, or in the form of amino acids upon assimilation by fungal cells (Müller et al. 2007). Similarly, mycorrhizal associations were shown to increase the availability of soil phosphorus to plants, thanks to superior uptake rates, as well as to the ability of fungi to degrade organic phosphorus from the soil and then import it in the form of Pi (Bucher 2007). In the opposite direction, assimilated carbon is transported from plant roots to the fungal hyphae through the mycorrhiza in the form of carbohydrates. It is estimated that mycorrhizal plants deliver up to 20% of their total assimilated carbon to their mycorrhizal symbionts (Bago et al. 2000; Parniske 2008). Such extensive investment of energy indicates the scale of adaptive importance that the mycorrhizal association holds for the plant host; on the other hand, it also highlights the important role that the mycorrhiza plays in soil carbon sequestration and the reduction of carbon emissions.

Besides facilitating the uptake of water, nitrogen and phosphorus, mycorrhizal fungi have been shown to enhance the survival of their host plants through alleviation of a wide range of biotic and abiotic stresses (Nadeem et al. 2014) (Fig. 11.2). Mycorrhizal associations have been shown to enhance both the local and the systemic responses to pathogens and herbivores; additionally, the biosynthesis of jasmonic acid, which is the primary regulator of response to pathogens and pests, is enhanced in mycorrhizal plants (Pozo and Azcón-Aguilar 2007). Regarding abiotic stress, the mycorrhizal association was shown to confer superior tolerance to drought to host plants not only through increasing water supply, but also through enhancing the systemic response of plants to water stress (Augé 2001). Similarly, arbuscular mycorrhiza enhanced the plant response and survival under salinity stress (Ruiz-Lozano et al. 2012). Among abiotic stresses, a particularly frequently reported beneficial effect of arbuscular mycorrhiza concerns the alleviation of toxicity caused by heavy metals (Hildebrandt et al. 2007; Han et al. 2021).

The mycorrhizal community is not limited exclusively to the plant-fungus relationship. A diverse spectrum of “mycorrhiza-helper bacteria” (MHBs) have been identified, some of which promote the establishment of the mycorrhizal association, whereas others contribute to its maintenance (Frey-Klett et al. 2007). These bacteria promote mycelial extension, the establishment of contact between the fungus and the root, and exert a protective effect on the mycelium of the mycorrhizal fungi (Garbaye 1994). Current evidence indicates that MHBs benefit mostly from the proximity of mycorrhizal fungi, whereas their benefit from the plant’s contribution to the mycorrhizal association might be more indirect (Frey-Klett et al. 2007). In any case, besides the mycorrhizal fungi themselves, these helper bacteria represent another potentially interesting target for the future enhancements of sustainable agriculture.

Overall, it can be concluded that mycorrhizal fungi play an array of important ecological roles (Rillig 2004b) and deliver important ecosystem services, including in agroecosystems (Gianinazzi et al. 2010). On the geological level, mycorrhizal fungi play important roles in soil aggregation and structure (Rillig 2004a; Rillig and Mummey 2006) and nutrient cycling (Read and Perez-Moreno 2003). Unfortunately, the currently existing agricultural practices negatively affect the ecological roles of mycorrhizal fungi, for which a more thorough understanding of the physiological and ecological functions of mycorrhizal fungi is needed (Rillig 2004a).

11.3 Allelopathy: How Plants Engage in Mutual Underground Chemical Warfare

The secondary metabolites released through root exudation may play a role in the inter- and intra-specific competition between the plants themselves. The Greek word “allelopathy” can be interpreted ambiguously, either as “mutual suffering” or “mutual feeling”—but it should not be interpreted strictly as a mechanism of competition, since many allelopathic substances have shown stimulatory effects on plant growth and development when applied in minute amounts (Willis 2007). Nevertheless, the allelopathic interactions between plants are currently of the greatest practical significance when interpreted in the context of competition between plants.

The allelopathic substances are products of plant secondary metabolism and comprise a broad spectrum of chemically diverse compounds (phenolic compounds, terpenes, benzoxazinoids, glucosinolates and others) (Scavo and Mauromicale 2021) (Fig. 11.2). They exert an inhibitory effect on plant growth and development processes of direct practical significance (germination, seedling and root growth). However, this effect is mediated by more subtle physiological mechanisms such as the induction of oxidative stress in the cells of target organisms, interference with phytohormone homeostasis (especially auxin biosynthesis and transport, which reflects negatively on root growth) and the cell cycle, ultimately leading to growth inhibition and cell death (Scavo et al. 2019; Šoln and Dolenc Koce 2021).

Allelopathy is a phenomenon of growing environmental importance, as it often underlies the competitive success of invasive plant species, which release into the rhizosphere their phytotoxic metabolites to which the native plants are unadapted (Hierro and Callaway 2003; Medina-Villar et al. 2017). Allelopathy is also a phenomenon of economic importance, since crop species and noxious weeds engage extensively in mutual allelopathic interactions, in one direction or the other. On the one hand, weeds cause great economic losses to crop growers, through the reduction of yields. Conversely, the allelopathic substances themselves hold a promise for the development of efficient weed control strategies without or with reduced use of synthetic herbicides. Rotational cropping, intercropping, cover cropping, as well as the development of bioherbicides, are diverse strategies through which allelopathic substances, derived from either cash crops or cover crops, can be engaged in weed control (Radhakrishnan et al. 2018; Scavo and Mauromicale 2021). These strategies rely on temporal (rotational cropping) or spatial (intercropping) diversification of crops, covering the empty land with temporary plantations (cover cropping) or with plant-derived waste (dead mulching and green manuring). In these ways, the soil is naturally amended with the allelopathic substances directly through the root exudation of the cover crops, or through leaching of organic matter from their foliage, while at the same time maintaining the soil microbial community composition that is beneficial to the cultivated crops (Scavo and Mauromicale 2021; Quintarelli et al. 2022). For instance, it was shown that garlic intercropping affected soil bacterial composition and enhanced the performance of heavy-metal accumulating plants *Pteris vittata*, *Conyza canadensis*, and *Lolium perenne* (Hussain et al. 2021).

Although allelopathic interactions are primarily considered as the interactions between plants, soil microorganisms contribute to these interactions through metabolizing the molecules derived from root exudates, enhancing, decreasing, or altering their phytotoxic potential (Inderjit 2005). Soil invertebrates can also contribute to the metabolism of allelopathic substances. Thus, it was shown that the vermicomposting of plant waste derived from the noxious weed *Lantana camara* results in the production of a beneficial substrate that can enhance plant growth, thanks to the decomposition of the phytotoxic compounds from lantana by the Californian redworm, *Eisenia fetida* (Hussain et al. 2015).

In the next subsections, we will briefly review the research on allelopathic mechanisms of three important model species studied for their allelopathic potential: the tree of heaven (*Ailanthus altissima* (Mill.) Swingle), apple (*Malus domestica* Borkh), and goosefoot (*Chenopodium murale* (L.) S. Fuentes, Uotila & Borsch).

11.3.1 Tree of Heaven (Ailanthus Altissima): The "Poisonous Tree from Hell"

The tree of heaven (*Ailanthus altissima*) is a deciduous tree species indigenous to North and Central China, which was introduced to Europe and North America in the eighteenth century, and has spread since to most of the rest of the world (Ding et al. 2006). Besides its formidable viability, fecundity, and tolerance to virtually all types of biotic and abiotic stress, the tree of heaven has become a successful invasive species also for its remarkable allelopathic properties (Demeter et al. 2021). Reports of the phytotoxic properties of *A. altissima* date to as back as 1959 (Mergen 1959). In the 1990s, Rod Heisey showed that the phytotoxic substance from *A. altissima* was most concentrated in the roots (Heisey 1990) and identified it as a quassinoid compound, ailanthone (Heisey 1996). In a subsequent field trial, Heisey and Heisey (2003) showed that a dilution series of *A. altissima* root bark methanol extract had a herbicidal effect on 17 different weed and crop species, corresponding to a proportionate dilution series of pure ailanthone. A recent transcriptomic study showed that application of ailanthone induced physiological and transcriptomic responses in three accessions of *Arabidopsis thaliana*, resembling herbicide application. Namely, the application of ailanthone strongly impaired seed germination, shoot and root growth, and induced oxidative stress responses and cellular abnormalities in *Arabidopsis*, affecting most of all the expression of genes involved in oxidative stress, developmental processes, and protein- or DNA- and RNA-binding (Hopson et al. 2022).

Besides ailanthone, a lower level of allelopathic activity was also demonstrated for three other quassinoids from *A. altissima* roots: ailanthinone, chaparrine, and ailanthinol B (De Feo et al. 2003). A comparison between the leaf and root extracts of *A. altissima* showed that the leaf extracts could exhibit plant growth-stimulating effects when applied at low dosage. In contrast, the root extracts were always phytotoxic, confirming that the allelopathic effect of *A. altissima* primarily relies on root exudates (Rehorska et al. 2014, 2016). Interestingly, the root exudates of *A. altissima* were shown to enhance nodulation and nitrogen fixation in the roots of the leguminous species *Trifolium pratense*. This suggests that additional adaptive mechanisms might be engaged besides allelopathic effects, supposedly to facilitate an increase in soil nitrogen levels which would benefit the growth of the tree of heaven (Greer et al. 2016).

11.3.2 Apple (Malus Domestica): A Case of Autoallelopathy?

Among the commercially important fruit crops, the apple tree (*Malus domestica*) is particularly interesting for allelopathic studies. Besides synthesizing unique allelopathic compounds—the dihydrochalcone phloretin and its glucoside phloridzin, the apple is an attractive model system also for its supposed autoallelopathic effect known as the apple replant disease (ARD) (Smailagić et al. 2022). ARD is a widespread phenomenon known to apple growers, manifested as recalcitration in the establishment of new apple plantations on lands on which apple trees had previously grown. However, although the autoallelopathic nature of ARD cannot be ruled out, it is currently considered to have a minor role in ARD, mainly because allelopathic substances are likely too unstable to persist in the soil for longer periods. Thus, a more important role in ARD is attributed to the alterations in soil microbial community composition (Winkelmann et al. 2019). Split-root experiments have confirmed the microbiological nature of ARD, and suggested that ARD occurs locally around the apple roots, without spreading through the soil on a larger scale (Balbín-Suárez et al. 2020, 2021). Additional explanations for ARD have been suggested lately, such as apple root-associated endophytes (Mahnkopp-Dirks et al. 2021), a decreased potential of soil microorganisms for the decomposition of (auto)allelopathic phenolic compounds originating from apple root exudates (Radl et al. 2019), and local associations of soil microorganisms and nematodes (Kanfra et al. 2018, 2022). Solutions have been proposed, such as the use of biochar for the adsorption of the allelopathic agent phloridzin from the soil (Ma et al. 2021; Liu et al. 2022) or the introduction of crop rotation systems (Kanfra et al. 2021).

Autoallelopathy is a known mechanism of intraspecific competition, based on greater sensitivity of early-life processes, such as seed germination and radicle elongation, to the phytotoxic compounds exuded by adult plants which are, themselves, resistant. The autoallelopathic effect of apple root exudates was demonstrated by Zhang et al. (2007), who reported that it was similar in magnitude to the allelopathic effect of peach root exudates, whereas the root exudates of jujuba (*Ziziphus jujuba*) did not show an important allelopathic effect on apple seedlings. Apart from apple, autoallelopathic activity has been shown in other species such as *Solanum carolinense* (Solomon 1983), cucumber (Zhang et al. 2010), buffelgrass (Jernigan et al. 2016), and *Cistus ladanifer* (Chaves Lobón et al. 2019).

The physiological mechanisms underlying the allelopathic effect of apple root exudates were investigated in the hairy root cultures of the apple cultivar Golden Delicious. The liquid medium in which the hairy roots were grown contained four potentially allelopathic substances—two phenolic acids (caffeic and chlorogenic), and two dihydrochalcones (phloridzin and phloretin), while several other phenolic compounds were detected within the root tissue, but not in the culture media, suggesting that these additional compounds are not released into the rhizosphere (Stanišić et al. 2019). Conversely, phloretin was detected in the culture medium, but not within the root tissue, indicating either its extracellular synthesis, or its extremely efficient metabolism and/or export out of the root tissue. The apple hairy roots culture media exerted a pronounced allelopathic effect on *Arabidopsis* seedlings, inhibiting their shoot and root growth and downregulating the expression of cell cycle genes in their shoots (Stanišić et al. 2019). Further research revealed that the phytotoxic effects of phloretin (as likely the most important allelopathically active compound from apple root exudates) include deregulation of the expression of polar auxin transport genes in the roots of *Arabidopsis* and a disturbance in the distribution and composition of the auxin metabolome in the roots, resulting in impaired root growth and development and loss of the gravitropic response and root architecture, reflecting negatively on the growth and viability of whole plants (Smailagić et al. 2022).

11.3.3 Goosefoot (Chenopodium Spp.): A "Pain-In-The-Grass" for Agricultural Crops

Chenopodium (goosefoot) comprises commercially important species of noxious weeds of the family Amaranthaceae, the most important of which are *C. murale* and *C. album*, that inflict economically important yield losses on major cereal crops and horticultural species (Bajwa et al. 2019). Seedlings of wheat, tomato and cucumber showed decreased germination, total leaf area, leaf dry matter, total pigment, carbohydrate, and soluble protein content, when grown in soil that had previously harbored *C. murale* plants (El-Khatib et al. 2004). A similar allelopathic effect on rice seedlings was obtained through enriching the soil with *C. murale* leaf leachate (Inderjit 2006). Additionally, the agar nutrient media on which *C. murale* had grown, showed an allelopathic effect on wheat seedlings (Batish et al. 2007). Intense in vitro production of allelopathic compounds was obtained through culturing *Agrobacterium rhizogenes*-transformed hairy roots of *C. murale* (Mitić et al. 2012). The *C. murale* hairy roots culture media showed a pronounced inhibitory effect on wheat and lettuce seed germination and seedling growth. The allelopathically active compounds within the culture media were identified as caffeic, ferulic and *p*-coumaric acid. However, the concentration of each of these compounds in the culture media was 1,000 times lower than the concentration of the respective pure compounds needed to cause a corresponding physiological effect. This suggests that either extremely strong synergistic interaction, or the presence of other, more potent allelochemicals underlay the observed phytotoxic effects (Mitić et al. 2012). The mechanisms of the allelopathic effect of the *C. murale* hairy root exudates on wheat and *Arabidopsis* seedlings included the causation of oxidative stress and downregulation of core cell cycle genes, indicating that cell cycle arrest, and possibly apoptotic mechanisms, underlay the inhibition of seedling growth (Dmitrović et al. 2015). This was later confirmed by cytological analyses, which revealed extensive cellular damage indicative of oxidative stress, membrane peroxidation, and likely damage to the photosynthetic apparatus (Mitić et al. 2018). The other species of the genus *Chenopodium* notorious for its allelopathic effect on crop species—fat hen (*C. album*), was shown to exert a similar set of allelopathic effects on wheat seedlings (Ghosh et al. 2020).

11.3.4 Allelopathic Root Exudates as Nematicidal and Insecticidal Agents

As inhabitants of the rhizosphere, soil nematodes also interact with plants. Free-living soil nematodes may exert promotive effects on plant growth through beneficial shifts in the composition of the soil microbiome; however, plant-parasitic nematodes are considered major plant pests, and are detrimental to plant growth and viability (Topalović and Geisen 2023). For this reason, plants have evolved resistance mechanisms, including the root exudation of nematicidal compounds. A long-known example is *cis*-dehydromatricaria ester from *Solidago altissima*, which showed nematicidal effects on *Bursaphelenchus xylophilus*, *Diplogaster* sp., and the root-knot nematode *Meloidogyne incognita* (Saiki and Yoneda 1982). Allelopathic substances isolated from the roots of several plant species native to Okinawa also showed a nematicidal effect on *M. incognita* (Taba et al. 2008). Saponins from the root exudates of alfalfa (*Medicago sativa*) showed significant in vitro nematicidal activity on *M. incognita*, on the potato cyst parasite *Globodera rostochiensis*, and on *Xiphinema index*, which is an economically important vector of plant viruses (D’Addabbo et al. 2011). Aboveground plant parts may also contain nematicidal compounds; these compounds penetrate into the soil through littering, mulching, or leaching from the foliage of living plants (Shaukat et al. 2002).

When it comes to insecticidal activity, most accounts of allelopathic substances refer to secondary metabolites present in aboveground plant parts. Contrary to nematodes, the majority of economically important insect pests feed on aboveground parts of crop plants. Thus, the aboveground parts are a more relevant source of insecticidal compounds. These compounds may penetrate into the soil through littering and mulching (Lebedev et al. 2019; Ninkuu et al. 2021). However, evidence has accumulated lately on the insecticidal activity of compounds released through root exudates. An important example are maize roots, which release benzoxazinoid compounds to combat root insect pests (Wouters et al. 2016; Malook et al. 2021; Pan et al. 2022). Interestingly, the effect of benzoxazinoids on the larvae of fall armyworm (*Spodoptera frugiperda*) was found to depend on soil iron content. In iron-poor soils, or when most of the soil iron is chelated, benzoxazinoids exert an inhibitory effect on the larval development of *S. frugiperda*; conversely, in the presence of sufficent quantities of free iron, this interaction becomes stimulatory (Hu et al. 2021).

11.4 The Rhizosphere of Aquatic Plants: A Case of Special Importance

While the concept of the rhizosphere is commonly associated with the idea of land plants, that have their root system anchored within the soil and acquire water mostly from rainfall and irrigation, some plant species are adapted to, or even dependent on an aquatic environment. Even among vascular plants, many species are adapted to life in wetlands, where the soil is flooded for a significant part of the year. Many species within the order Poales are adapted to an emerging lifestyle, with the aerial part of their shoots sticking above the water surface. On the other hand, certain lineages of vascular plants have fully “returned to the water”—they evolved adaptations to a floating, or even submerged lifestyle. Nevertheless, regardless of whether they are anchored in land soil, in flooded soil, in a submerged waterbed, or they are simply floating on the water surface, the roots of all plants always influence the chemical and microbial composition of their immediate environment, creating a rhizosphere.

The rhizosphere of aquatic plants is a specific microenvironment that differs from the rhizosphere of land plants in certain important aspects (Coler and Gunner 1969). Flooded soils are constantly saturated with water, but also poorly aerated, resulting in anoxic or even anaerobic conditions which favor anaerobic metabolism (Laanbroek 2010). Plants that inhabit flooded soils can adapt to anoxic conditions in the soil by forming aerenchyma—specialized gas-filled tubes made up of dead cells, to facilitate oxygen transport from aboveground tissues to roots (Drew 1997). Methanogenic prokaryotes often inhabit the poorly aerated rhizosphere of emerging wetland plants and produce large quantities of methane that is released into the atmosphere, making wetland soils one of the major natural producers of methane, and contributing importantly to carbon emissions (Le Mer and Roger 2001; Conrad 2009) (Fig. 11.3).

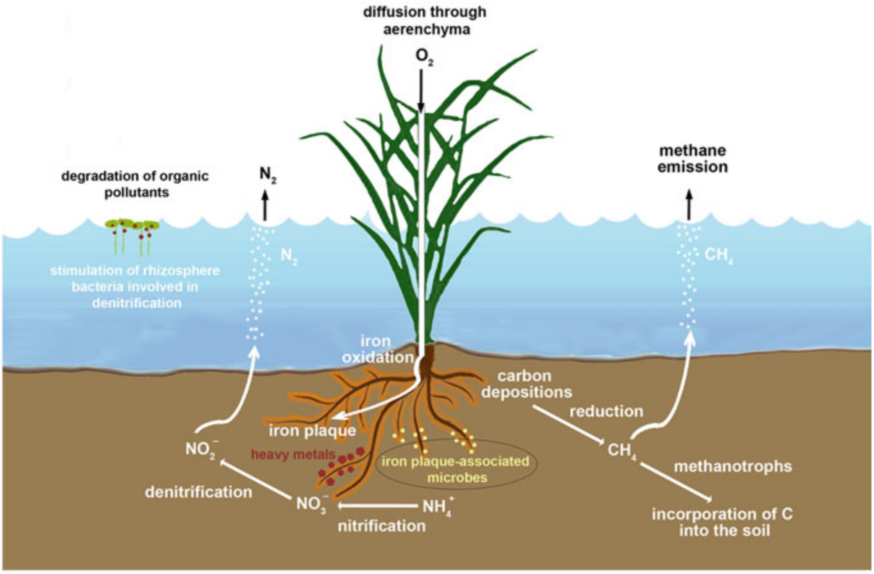

Fig. 11.3 Rhizosphere-related processes in the rhizosphere of aquatic plants. Emerging wetland plants of the order Poales, such as rice or reeds, use aerenchyma for the provision of oxygen to their roots, which are anchored in anoxic soil. Iron plaque is formed on the surface of the roots when Fe(II) is oxidized into Fe(III) in the vicinity of the roots. Iron plaque adsorbs heavy metals and toxic metalloids, but also serves as a microhabitat for iron plaque-associated microbes. Some of these microbes are methanogens, that perform the metabolic reduction of carbon depositions into methane, which is released into the atmosphere. A portion of methane is consumed within the soil by methanotrophic microbes, and incorporated into the soil as organic carbon. Other iron plaque-associated microbes are responsible for nitrification/denitrification of ammonium of organic or fertilizer origin, resulting in nitrogen volatilization. Free-floating wetland plants such as *Lemna* can accumulate heavy metals, and degrade organic pollutants with the help of the bacteria from their rhizosphere. They can also stimulate denitrification by bacteria inhabiting their own rhizosphere

Being one of the three economically most important food crops and a staple crop for half of the world's human population, rice (*Oryza sativa* L.) is the world's most economically important wetland plant (Muthayya et al. 2014). Rice cultivation in wetland soils is sensitive to the formation of iron plaque (Tripathi et al. 2014), to accumulation of arsenic and other toxic metalloids (Mitra et al. 2017), and is challenged by low nitrogen and phosphorus use efficiency (Yang et al. 2021), for which the understanding of the nutrient and microbiome dynamics in the rice rhizosphere is considered an important priority in rice cultivation (Ding et al. 2019).

On the other hand, most aquatic plants have shown great potential for the detoxication of organic pollutants and accumulation of heavy metals, for which they are considered suitable for bioremediation (Brix 1997; Rai 2008; Bhatia and Goyal 2014). For the last 60 years, aquatic plants have been used for the engineering of constructed wetlands—human-made ecosystems designed for wastewater treatment (Vymazal 2011). Emerging plants such as common reed (*Phragmites australis*), cattail (*Typha* spp.), giant cane (*Arundo donax*), or Amur silvergrass (*Miscanthus sacchariflorus*) are considered to be the most useful plants for constructed wetlands; however, free-floating plants such as duckweeds (*Lemna* spp.), water hyacinth (*Pontederia crassipes*) or water lettuce (*Pistia stratiotes*), and even submerged plants such as water milfoil (*Myriophyllum spicatum*) can be used (Vymazal 2022). The plants used in constructed wetlands account for rhizofiltration, phytoextraction and phytostabilization to some extent; however, the most important role in the detoxication of organic pollutants is played by the microorganisms associated with their rhizosphere (Bhatia and Goyal 2014; Gavrilescu 2022). For this reason, the rhizosphere of aquatic plants and their associated microorganisms are an important research topic for environmental microbiology.

11.4.1 Rice Rhizosphere: A Prospective Target for Future Agronomy

The cultivated genotypes of rice (*Oryza sativa* L.) are classified into five clades, roughly grouped into subspecies *indica* and *japonica*, which differ in geographic distribution, irrigation requirements, and tolerance to low or excessive precipitation, including both drought, and submerged lifestyle (Garris et al. 2005; Yang et al. 2014). Although upland rice genotypes, especially within the *japonica* group, can be cultivated on properly irrigated dry land, varieties of both subspecies are mostly cultivated as emerging plants, in temporarily flooded (paddy) fields (Zhang et al. 2020). An extreme example of adaptation to flood is provided by deepwater *indica* cultivars, which are able to survive floods for one month or more, growing in water up to 4 m deep (Kende et al. 1998).

Besides being more abundant in water, flooded soil is primarily characterized by extremely low oxygen levels (Laanbroek 2010; Pezeshki and DeLaune 2012). Oxygen penetration into the soil is restricted to a relatively thin layer of topsoil near the soil–water interface, beneath which the oxygen levels quickly drop to near zero (Le Mer and Roger 2001; Fageria et al. 2011). The lack of oxygen in waterlogged soil shifts the redox balance and creates a strongly reducing environment, leading to the accumulation of toxic reducing metabolites (Pezeshki and DeLaune 2012). Although oxygen is supplied to the roots through aerenchyma, aerobic microorganisms and the roots themselves quickly consume most of it within the topsoil layer (Laanbroek 2010). Rhizodepositions from rice roots supply copious amounts of organic carbon to the soil (Wassmann and Aulakh 2000). Extensive carbon supply in a reducing environment enhances methanogenesis within the rice rhizosphere, whereby methane is produced by highly specialized groups of methanogenic archaea, the Rice Cluster 1 (RC1) archaea (Conrad 2009). Compared to Methanomicrobiales, a group of methanogenic soil archaea provided from temporarily flooded soil but not specifically associated with rice roots, the RC1 archaea from the rice rhizosphere soil were considerably more efficient both at colonizing rice roots, and at causing methane emissions in rice microcosm experiments, suggesting specific adaptations to the environmental conditions typical of the rice rhizosphere (Conrad et al. 2008). Aerobic methanotrophs in the topsoil oxidize a portion of methane produced within the rice rhizosphere, whereas the rest of it is released into the atmosphere through diffusion, ebullition, or through the rice aerenchyma (Wassmann and Aulakh 2000; Le Mer and Roger 2001) (Fig. 11.3). Methane emissions are considered a major environmental concern associated with rice plantations, since they contribute to 15–20% of global methane emissions (Zhang et al. 2020). Hence, shifting the balance between methanogenic and methanotrophic microbes within the rice rhizosphere might become a future target for decreasing methane emissions from rice plantations (Ding et al. 2019).

Besides methane emissions, another soil chemical phenomenon associated with rice cultivation is the formation of root iron plaque (Tripathi et al. 2014). Due to the intense local supply of atmospheric oxygen, which is continuously quickly depleted, the space around the rice roots is subject to a steep redox gradient, favoring the oxidation of Fe(II) to Fe(III) in the immediate proximity of the roots, and creating a stable layer of trivalent iron oxide in the form of a coating—the iron plaque (Alidoust and Isoda 2014) (Fig. 11.3). Iron plaque facilitates the adsorption and precipitation of an array of metalloids and heavy metals, acting differentially as a reservoir or as a barrier to the uptake of both nutrients and toxic metal(loid)s, by plant roots. Thus, iron plaque acts as a barrier to the uptake of common contaminants associated with rice cultivation, such as arsenic and cadmium, while at the same time enhancing the uptake of zinc, phosphorus and sulfur by the root system (Tripathi et al. 2014). Iron plaque formation is affected by the rice rhizosphere microbiome. Thus, functional metagenomic analyses of iron plaque-associated microbial communities, sampled from arsenic-contaminated locations, showed the presence of genes associated with arsenic detoxication within the iron plaque metagenome (Hu et al. 2015, 2019). Another study of the rice rhizosphere microbiome revealed the presence of iron-oxidizing bacteria *Burkholderia* sp. D416 and *Pseudomonas* sp. YGL, which could decrease the cadmium uptake by rice plants by enhancing the formation of iron plaque (Wei et al. 2021). A comparative analysis between the rhizosphere microbiota of two rice cultivars differing in cadmium accumulation revealed the presence of iron-oxidizing *Massilia* and *Bacillus* in the low-Cd-accumulating cultivar, and the presence of iron-reducing *Geobacter* in the high-Cd-accumulating cultivar (Zhang et al. 2022). Experiments with a microbial organic fertilizer containing iron-oxidizing *Thiobacillus* resulted in enhanced iron plaque formation and decreased cadmium uptake, suggesting that iron plaque formation may be utilized in future rhizosphere engineering approaches to enhance the biosafety of rice grown in Cd-contaminated paddy fields (Kong and Lu 2022).

Rice cultivation is also challenged by low nitrogen use efficiency. In a flooded soil, nitrogen fertilizer is subject to quick and efficient nitrification–denitrification sequences within the rice rhizosphere, in which ammonium is first oxidized into nitrite and nitrate, and then reduced into N_2O and molecular nitrogen, which are then released into the atmosphere (Verhoeven et al. 2018) (Fig. 11.3). Application of nitrification inhibitors decreased the denitrification output and improved nitrogen use efficiency in rice paddy fields, confirming that poor nitrogen use efficiency results from losses to nitrification–denitrification (Datta and Adhya 2014; Wang et al. 2017; Meng et al. 2020). Functional soil genetic analyses revealed that nitrification and denitrification rates in paddy soils could be associated with the transcriptional activity of bacterial genes encoding ammonia monooxygenase (*amoA*) and nitrite reductase (*nirK*), respectively (Yoshida et al. 2010; Jin et al. 2014; Zhang and Ji 2018). A recent study revealed that the denitrification step is enhanced by the rice root-associated iron plaque, whereby the root-associated Fe(II) acts as the electron donor for the reduction of nitrite into N_2O and molecular nitrogen (Liu et al. 2019). These insights reveal that while root iron plaque-associated microbiome might be useful in protecting rice plants from heavy metals and toxic metalloids, it may, at the same time, contribute to lowering rice nitrogen use efficiency.

11.4.2 Reeds, Cattails, and Sedges: The Lead Characters of Constructed Wetlands

Reeds, cattails, sedges and other similar fast-growing emerging wetland plants of the order Poales are the most commonly used plant species for wastewater treatment worldwide, most importantly in the form of constructed wetlands (Vymazal 2022). It was suggested that plant biomass, but most of all root biomass, as well as photosynthetic characteristics such as chlorophyll fluorescence, determine the efficiency of wetland plants in wastewater detoxication (Li et al. 2013). In addition, organic matter released from the plant roots serves as a carbon source for denitrifying bacteria that facilitate the removal of nutrients from eutrophic wastewaters (Wu et al. 2017).

Common reed (*Phragmites australis*) is a fast-growing perennial grass species with cosmopolitan distribution, which can be found on all continents except Antarctica, and is invasive in North America (Kowalski et al. 2015). Its fast growth and high tolerance to pollutants, which is partly due to the versatility of the microbial community that inhabits its rhizosphere, make it an excellent choice for phytoremediation of mine dumps and polluted wetlands (Kalu et al. 2021; Wang et al. 2022). The microbial abundance in the rhizosphere of *Phragmites* was reported to be substantially higher compared to other similar wetland species, which was attributed to a superior efficiency of oxygen delivery to the roots, and more intense root exudation (Fang et al. 2021). Culture-dependent analyses and functional metagenomics revealed the roles of the *Phragmites* rhizosphere microbiome in hydrocarbon degradation (Abed et al. 2018), and iron and manganese oxidation leading to the formation of Fe/Mn plaque around the reed roots, which further acts as a sequestration site for heavy metals and toxic metalloids, some of which are further oxidized into less toxic atomic forms by the rhizosphere bacteria (Wang et al. 2021). It has been proposed that the future rhizosphere engineering approaches for bolstering the bioremediation performance of common reed in constructed wetlands should encompass the use of synthetic microbial communities, the enhancement of Fe/Mn plaque formation, and co-plantation of *Phragmites* with other wetland species of plants to enhance the exudation of allelopathic metabolites from the roots of common reed (Wang et al. 2022).

Another species with similar ecophysiological characteristics, which is more drought-tolerant than common reed (Corno et al. 2014) and especially efficient in the phytosequestration of heavy metals, is giant reed (*Arundo donax*) (Nsanganwimana et al. 2014). High efficiency in the extraction and sequestration of heavy metals by *A. donax* is due to its large biomass and fast growth (Nsanganwimana et al. 2014), but also its association with rhizosphere microbes, including arbuscular mycorrhizal fungi that facilitate the uptake and tolerance to cadmium and other heavy metals (Sarathambal et al. 2017; Ondreičková et al. 2019). Besides cadmium, *Arundo* was shown as highly efficient in removing selenium (El-Ramady et al. 2015), arsenic (Salas-Luévano et al. 2017), and copper (Oustriere et al. 2017), but also in enhancing denitrification in eutrophic wastewaters (Tsiknia et al. 2013; Meng et al. 2014; Xu et al. 2019).

Cattails (*Typha* spp.) is a genus of highly resilient wetland plants with widespread distribution, which are efficient in the rhizofiltration of organic pollutants such as azodyes (Kumar et al. 2018), but also in the hyperaccumulation of heavy metals such as Cu, Zn, Ni, and Cd (Salem et al. 2014; Nguyen et al. 2021). In a recent comparative analysis of ten wetland plant species, broadleaf cattail (*Typha latifolia*) was reported to be the best performer in shoot growth, biomass accumulation, and efficiency of hydrocarbon degradation. In a culture-dependent analysis of the *Typha*-associated microbiome, 12 hydrocarbon-degrading bacterial strains were identified: 8 in the rhizosphere, and three and one in the root and shoot endosphere, respectively (Hashmat et al. 2019). Other advantageous traits of cattails are high oxygen release rates (Wiessner et al. 2002), and high nitrogen removal efficiency (da Costa et al. 2015), which might be attributable to a high richness and diversity of ammonium-oxidizing prokaryotes in the rhizosphere of *Typha* (Wang and Gu 2013).

Sedges (*Cyperus* spp.) are efficient in rhizofiltration and phytosequestration thanks to the texture of their roots which facilitates microbial attachment, pollutant adsorption and high oxidation efficiency in the rhizosphere (Kyambadde et al. 2004). Similarly to *Typha*, *Cyperus laevigatus* was reported to be highly efficient at hydrocarbon degradation, and 21 hydrocarbon-degrading bacterial strains were identified within its associated microbiome: 9 within the rhizosphere, and 5 and 7 within the root and shoot endosphere, respectively (Hashmat et al. 2019). In a comparative analysis of six wetland species, *Cyperus flabelliformis* was reported as the best performer in terms of nitrogen and phosphate removal and tolerance to wastewater toxicity–which was attributed to the higher efficiency of oxygen delivery to the roots, and of root iron plaque formation (Mei et al. 2014).

The use of constructed wetlands for wastewater detoxication has been evolving for several decades, and today's wastewater treatment systems are substantially more sophisticated than 50 years ago (Vymazal 2011, 2022). However, continuous improvements will be needed to mitigate the challenges imposed by the constant growth of the human population, the occurrence of novel polluting materials, and the significant carbon footprint generated by wastewater treatment. Similarly to rice plantations and natural wetlands, the constructed wetlands have become an important source of methane emissions due to the intensity of carbon depositions in a poorly oxygenated waterlogged soil (Zhu et al. 2007). Reducing these methane emissions should become one of the important priorities in the future of constructed wetlands technology. One of the approaches to reducing methane emissions from constructed wetlands could be the use of microbial fuel cells (Zhang et al. 2021). Microbial fuel cells (MFCs) were first constructed with the idea that the redox reactions within the soil of constructed wetlands could be used to generate renewable electricity simultaneously with wastewater treatment (Yadav et al. 2012). Operating the MFCs was reported to alter the composition of rhizosphere bacteria located at both the anode and cathode of the fuel cell (Rathour et al. 2019). This was beneficial for achieving a decrease in methane emissions from the treatment system, presumably because the operation of the MFC enhanced the competitiveness of electrogenic Proteobacteria over methanogenic archaea (Zhang et al. 2021). Other rhizosphere-inspired or rhizosphere-oriented engineering approaches can be expected to appear in the near future for an enhancement of the efficiency of wastewater treatments.

11.4.3 Duckweeds (Lemnoideae): An Alternative Approach to High Efficiency-Wastewater Bioremediation

Duckweeds are tiny monocotyledonous plants, the evolution of which has proceeded through progressive simplification and reduction of their body plan, as an adaptation to a free-floating lifestyle in freshwater lakes and ponds. The duckweed subfamily, Lemnoideae, consists of 37 species categorized into 5 genera, out of which *Spirodela* represents the most ancestral form, *Landoltia* and *Lemna* are intermediate, while *Wolffia* and *Wolffiella* are the most derived and simplified forms, which have even lost their root system (Lemon and Posluszny 2000). Due to extremely fast multiplication, high bioaccumulation rates and tolerance to a wide spectrum of organic and inorganic pollutants, duckweeds are being extensively studied for the application of their bioremediation potential (Luhana 2022). For instance, Japanese duckweed (*Lemna japonica*) was shown to be superior to water hyacinth in terms of nitrogen and phosphorus recovery efficiency despite having a lower biomass multiplication rate, making it an overall better candidate species for wastewater remediation (Zhao et al. 2014). High starch and protein content within the duckweed fronds make them a promising raw material for bioethanol production, or even for use as animal feed or future human food (Liu et al. 2021). However, differential efficiency in relative growth rate, nitrogen removal rate and protein content was found between duckweed genotypes, suggesting that decisions on genotype selection must be made to meet the specific cultivation goals on a case-to-case basis (Walsh et al. 2022).

Although the existence of rhizosphere symbionts of duckweeds and the responses of their community composition to environmental influences have been studied for more than 50 years (Coler and Gunner 1969, 1971), research interest for their capability of pollutant degradation has considerably grown over the last decade. In 2010, *Acinetobacter calcoaceticus*, a bacterium from the rhizosphere of *Lemna aoukikusa*, was proven able to biodegrade phenol (Yamaga et al. 2010). In 2011, the efficient colonization of the roots of *Lemna minor* by *Bacillus amyloliquefaciens* was visualized through the expression of the green fluorescent protein (GFP) (Fan et al. 2011). A culture-dependent analysis revealed the presence of 23 cultivable bacterial strains (mostly *Aeromonas* and *Exiguobacterium*) and one protozoan (*Euglena acus*) in the rhizosphere of *Lemna gibba* (Quisehuatl-Tepexicuapan et al. 2016), while in the rhizosphere of the giant duckweed, *Spirodela polyrrhiza*, 80 cultivable bacterial strains were identified (Matsuzawa et al. 2010). In the rhizosphere of *Lemna minor*, 60 cultivable bacterial strains were identified, most of which were tolerant to high concentrations of phenol (Radulović et al. 2019a). When incubated together with their original microbial rhizosphere community, *L. minor* plants were able to multiply in vitro; the original *Lemna* plant-bacterial communities were also more efficient at removing the exogenously added phenol from the culture media than either the bacterial cultures, or the axenic cultures of *Lemna* (Radulović et al. 2019b). Six phenol-tolerant bacterial strains belonging to *Hafnia alvei*, *H. paralvei*, *Serratia marcescens*, *S. nematodiphila*, *Klebsiella oxytoca* and *Lelliottia* sp., were shown able to colonize the roots of *L. minor* in co-culture, and were able to form biofilms (Radulović et al. 2020). A subsequent study showed that co-culture of *L. minor* with *Hafnia paralvei* C32-106/3, the bacterial strain found most prospective for a combined plant-bacterial bioremediation approach, improved the plant responses to oxidative stress caused by phenol, in terms of high peroxidase activity, hydrogen peroxide and ascorbate production, and low malondialdehyde accumulation (Radulović et al. 2021). Besides phenol, the *Lemna* rhizosphere bacteria were suggested to play a role in the bioremediation of the herbicide isoproturon (Böttcher and Schroll 2007), and in the plant tolerance to and accumulation of heavy metals such as cadmium (Stout et al. 2010; Zheng et al. 2023), chromium (Tang et al. 2015), copper and zinc (Ishizawa et al. 2019) (Fig. 11.3).

In the bioremediation of wastewaters heavily polluted with nitrogen, denitrification poses an important challenge (Vymazal 2022). Being highly efficient denitrifiers, duckweeds are considered a convenient remediation option to this end (Zhao et al. 2014; Walsh et al. 2022). Lu and co-authors (2014) showed that both *L. minor* and *S. polyrrhiza* were able to stimulate nitrogen removal by their rhizosphere bacterium *Pseudomonas fluorescens*, through root exudation of fatty acid methyl esters and fatty acid amides. The excretion of fatty acid amides by the roots of *S. polyrrhiza* was correlated to excess nitrogen and a consequent slowdown in duckweed growth (Sun et al. 2016). The mechanism of enhancement of nitrogen removal included a stimulation of the bacterial nitrate and nitrite reductases by the excreted erucamide, up to threefold (Sun et al. 2016). The excretion of another compound, stigmasterol, by the roots of *S. polyrrhiza*, was later found to be specifically induced by *Pseudomonas*. Similarly to erucamide, stigmasterol enhanced nitrogen removal through the stimulation of the bacterial nitrite reductase; it also enhanced the capability of *Pseudomonas* to form biofilms (Lu et al. 2021). These examples show the compelling ability of aquatic plants and their rhizosphere bacteria to effectively communicate for a co-operative nutrient use and bioremediation. Increasing the efficiency and the amplitude of such communication through novel rhizosphere engineering approaches, such as the synthesis of artificial proteins that could bind the molecular components of both root cell walls and bacterial cells, bringing them together more efficiently (Feng et al. 2022), might pave the way for next-generation wastewater treatment systems with increased bioremediation efficiency.

11.5 Conclusions and Future Perspectives

In the recent decades, the progress in systems biology has led to increasing scientific awareness of the holistic nature of living systems. The biotic interactions that drive the coevolution of organisms which belong to different kingdoms but share common habitats, can now be interpreted as homeostatic mechanisms within "metaorganisms" or "superorganisms" (Corning 2008; van Baalen and Huneman 2014; Hassani et al. 2019). Thus, botanical research has progressed from the research on individual plants, to incorporate ecophysiology, plant ecology, microbiology, and even environmental science, entomology, and other areas of life sciences. Plants cannot be researched and explained without considering the complex biotic interactions with all other organisms that take part in shaping plant life.

From the human perspective, plant research is important above all in the context of agriculture, agroecology, and nature conservation. In all these contexts, organisms from other kingdoms, as well as plants of lesser interest that share the living space with the target plants, must be considered important factors due to the biotic interactions, which take part most of all within the rhizosphere. In this review, we showed how plants shape the chemical and microbiological composition of their rhizosphere; how they interact with plant growth-promoting bacteria and mycorrhizal fungi; how they use their root exudates for nutrient acquisition, communication with beneficial microbes, and interspecific competition with other plants, as well as soil invertebrates; finally, we showed how the rhizosphere of aquatic plants plays similar ecological roles as the rhizosphere of land plants, while also performing functions that are specific to the aquatic environment.

The increasing awareness of the biotic interactions within the rhizosphere has yielded new approaches to solving common agricultural and ecological problems. The "rhizosphere engineering" approaches take into account the complex composition of the rhizosphere habitat, and its versatile ecological functions.

In agricultural and environmental microbiology, rhizosphere engineering has blossomed with the recent advancements in soil microbiology and metagenomics. Firstly, the growing pool of sequenced microbial genomes has enabled the identification of bacterial and fungal species through the sequencing of 16S rRNA and internal transcribed spacers (ITS), respectively (Schoch et al. 2012; Sinclair et al. 2015). Furthermore, the evolution of bioinformatics has enabled the use of functional pathway databases such as KEGG, COG, and others, for complex functional profiling of entire microbiomes through versatile computational tools such as, for instance, PICRUSt and FAPROTAX (Langille et al. 2013; Louca et al. 2016; Douglas et al. 2020). In the future, further growth of genomic and metagenomic databases, followed by the evolution of bioinformatic tools for their interpretation, is expected to contribute to the targeted use of selected microbial communities as biofertilizers and biocontrol agents for the enhancement of agricultural and environmental outputs.

As we have further shown in this chapter, rhizosphere engineering is also expected to enable advancements in combating allelopathic weeds, either through the "use of their own weapons" by developing new, allelopathy-based bioherbicides, or through engineering the soil microbiome to suppress the noxious weeds, or at least to enhance the rhizospheric degradation of their phytotoxic allelochemicals. In the case of aquatic plants, rhizosphere engineering can be employed to reduce methane emissions from natural, agricultural, and constructed wetlands; to enhance iron plaque formation in cadmium- and arsenic-polluted rice paddy fields; to suppress nitrification–denitrification sequences in rice paddy fields, and conversely, to enhance denitrification and the degradation of other organic pollutants in constructed wetlands; and to perform a multitude of other ecosystem services, going as far as producing renewable energy. A full understanding of the rhizosphere and its complex ecological functions will thus enable humankind to utilize its benefits, bringing advancements in agricultural outputs and environmental protection.

Acknowledgements The work of the authors is funded through the contracts 451-03-47/2023-01/200007 and 451-03-47/2023-01/200178 of the Ministry of Science, Technological Development and Innovation of Republic of Serbia.

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Chapter 12
Genomic and Proteomic Approaches to Enhance Stress Tolerance in Plants for Creating Stress-Resilient Species

Santanu Samanta and Aryadeep Roychoudhury

Abstract Plants are sessile beings and therefore, they inevitably encounter several biotic and abiotic stress factors during their entire life cycle. Environmental and climate changes can alter the physiological state of a plant and trigger several modulations for acclimation and adaptation to unfavorable conditions. To meet the challenges of climate change, understanding the mechanisms that crop plants employ to resist and combat environmental stress factors is of considerable interest to ensure sustainable agricultural production and food security. Growing global demand for food for expanding populations in the era of climate change demands the development of stress-tolerant crop cultivars. For several decades, researchers are working toward improving crop plants for developing climate-resilient elite genotypes. Within the last two decades, the combination of two major "omics" tools has advanced our knowledge of stress regulatory networks, thereby benefitting crop improvement programs. This chapter is intended to be a synopsis of updated and comprehensive knowledge concerning all possible combinations of advanced genomic and proteomic approaches in this regard. It includes information on the most significant achievements of the genomic and proteomic approaches, which will assist sustainable crop production under various suboptimal conditions, including biotic and abiotic, and the future directions for harnessing these sophisticated, high-throughput methodologies to enhance yield stability in terms of agricultural production. In this chapter, attention is paid to highlighting the currently available tools in the genomic and proteomic research areas and the synergistic knowledge of these two major omics strategies for designing our future crops with new tactics to withstand hostile environment.

Keywords Functional genomics · Microarray · Next generation sequencing · Proteomics · iTRAQ · Mass spectrometry · Stress tolerance

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_12

12.1 Introduction

Being a sessile organism, plants live in constantly challenging environment from vegetative to the post-reproductive phase. These adverse environmental conditions have several detrimental effects on agricultural productivity and threaten food security (Robertson and Swinton 2005; Wang and Frei 2011). Environmental stressors can be divided into two major categories, biotic and abiotic. Biotic stressors include insects, fungal pathogens, bacteria, nematodes, rodents, plant herbivores, etc. The term abiotic stress encompasses mainly salinity, drought, heat, chilling, ozone, flooding and heavy metals, which are poised to be the major causes of plant productivity and yield losses worldwide. It is expected that these stress factors will become even more prevalent in the near future due to the effects of global climate change (Feng and Kobayashi 2009; Haile et al. 2017). Moreover, chronic exposure to these stress factors might affect the chemical composition of crops, and thus the quality of agricultural products (Guzmán et al. 2021). In the present scenario, inducing plant resistance is critical for improvement in crop yield and also for environmental sustainability. Stress tolerance in plants is a convoluted network involving biochemical, molecular and physiological processes that are difficult to untangle. Therefore, detailed understanding and developing strategies to improve plant tolerance and resilience are one of the most important targets in the field of plant-environment interaction.

Understanding the molecular mechanism to enhance stress resistance using conventional methods is less effective because of the complexity of stress tolerance traits. The prevailing low yield and quality loss of cereal crops and vegetables have made researchers redirect their focus to enhance stress tolerance for generating stress-resilient species. This stands out to be rather one of the most sustainable solutions owing to the increasing nutritional demands in the context of changing climate. In the past two decades, “omics” approaches have progressed in the agricultural research field, viz., genomics and proteomics which are important for better understanding and uncovering the underlying biological pathways and mechanisms during stress exposure (Cushman and Bohnert 2000; Kosová et al. 2018). The integrative approaches give a snapshot of the genome- and proteome-wide analysis of plant stress tolerance which provide an insight into the stress-responsive network(s) leading to improvement in crop cultivation. The present chapter aimed to offer comprehensive knowledge on the advancement of high-throughput genomics and proteomics approaches that can help future researchers in understanding the basis of such environmental stress tolerance for the enhancement of agricultural productivity (Fig. 12.1). The overview of such studies seeks to provide novel insights into the integrated mechanisms and regulations involved in plant environmental stress response and to translate this knowledge for better utilization for creating stress-resilient species.

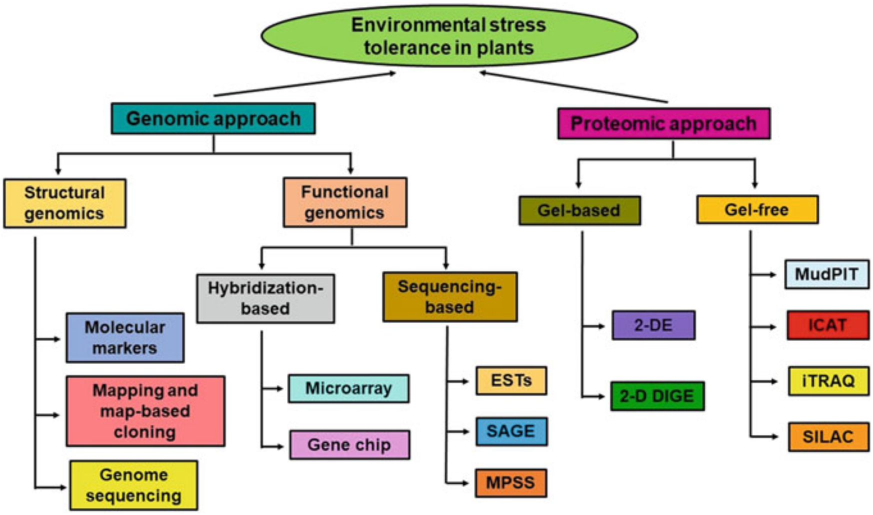

Fig. 12.1 Various techniques of genomic and proteomic approaches contributing to stress tolerance in plants for crop improvement programs

12.2 Genomic Approaches

Genomics is an interdisciplinary branch of "omics" which deals with the structure, function, evolution, mapping and editing of a given genome. The researchers identify the collective characterization and quantification of an organism and provide annotation. The rapid advancement of genomics has been exponentially boosted by the development of sequencing in the 1970s (first generation), continued into the mid-1990s (next-generation sequencing), and currently utilizes third-generation sequencing technologies. Currently, genomics-based approaches through advanced high-throughput tools have revolutionized discovery-based research to facilitate the understanding of even the most complex biological systems. These advanced technologies directly affect the applicability of the production of crop-resilient species by translating the entire genomic regions and decoding the molecular responses of plants (Gilliham et al. 2017).

12.2.1 Structural Genomics

Structural genomics seeks to describe the three-dimensional structural knowledge of the genome by experimental structure determination and aims to delineate the identification and determination of the order of genomic entities. Structural genomics emphasize the high-throughput determination of protein structures. Enormous progress has been made on high-throughput technologies and methodologies that will speed up the macromolecular structure determination. Some of these techniques are discussed in brief below.

12.2.1.1 Genome Sequencing

In the previous two decades, tremendous progress has been made in genome sequencing technologies that act as engines of the genome era including whole genome sequences. Next-generation sequencing (NGS), which has revolutionized genome research, has mostly superseded the conventional Sanger sequencing due to the efficiency of higher throughput data with lower cost, as well as enhanced rate (Roychoudhury 2020). These advancements allow scientists to process sequencing of entire genomes that have become feasible in a short period of time. The fundamental goal of NGS is the parallelization of DNA sequencing so that millions of molecules of genetic material can be sequenced in a single machine run (Patel and Jain 2012). The first NGS instrument developed was the Roche 454 pyrosequencing. This sequencer is based on the detection of pyrophosphates released during nucleotide incorporation, rather than dideoxynucleotides to terminate the chain elongation. Later on, Solexa released a genome analyzer, which was purchased by Illumina. This method utilizes the technology of sequencing by synthesis. The third technology SOLiD (Sequencing by Oligo Ligation Detection) was commercialized by Applied Biosystems (Now Life Technologies) (Valouev et al. 2008). The Illumina and SOLiD sequences generated a much larger number of reads than Roche 454 (30 and 100 million reads, respectively) (Liu et al. 2012; Goodwin et al. 2016). Emerging developments for more sophisticated NGS technologies, like the Intelligent Biosystems CRT platform by Qiagen (Srinivasan and Batra 2014), Polony sequencing (Shendure 2005), and a single molecule detection system (Helicos Biosciences) (Pushkarev et al. 2009) hold promise for the next wave of sequencing evolution. The application of NGS in agricultural research facilitates successful identification of molecular markers, correlated with both quantitative trait loci (QTLs) and specific genes, thus enabling the optimization of results obtained from traditional breeding techniques (Mateo-Bonmatí et al. 2014).

12.2.1.2 Mapping and Map-Based Cloning

Traditional breeding methods in commercial cash crops like rice, wheat, barley, and maize from the past several decades expanded in the field of mapping traits of interest related to diverse biotic and abiotic stress modulation. In the past twenty years, several progresses in genomic approaches have escalated the precision and efficiency of conventional breeding methods (Varshney et al. 2005). The availability of increased genome sequencing data and high-density single nucleotide polymorphism (SNP) platforms facilitates the development of new powerful approaches to the mapping of complex traits (Holland 2007). DNA markers are now extensively used for mapping/tagging (Singh et al. 2007; Li et al. 2009; Tsilo et al. 2009). Thus, these approaches are useful for marker-assisted breeding for gene introgression, mapping QTLs, or finding new or rare alleles linked with a trait of interest. By mapping markers associated with desirable traits, it is possible to identify areas of the genome and identify genes associated with specific stress-tolerance mechanisms (Teulat et al. 2003; Kalladan et al. 2013). Therefore, using mapping approaches, it is easier to detect the linkages between stress tolerance and different physiological traits for molecular breeders or environmental researchers.

Map-based cloning (positional cloning) is a traditional strategy, which involves the detection of a mutant phenotype for preparing a high-density genetic map around the region harboring specific agronomic traits, to point out the gene of interest. Map-based cloning is also referred to as ‘reverse genetics’ because the strategy does not demand prior knowledge about the gene or its product, instead, it requires knowledge about the chromosomal location of the gene of interest (Jander et al. 2002; Peters et al. 2003). The advantage of map-based cloning is that it easily identifies the underlying genetic cause of a variation, which can be used for cloning various disease-resistance genes (Singh et al. 2016). However, map-based cloning includes several drawbacks, including its labor-intensive, time-consuming process and requires several technical steps. With the rapid advancement in sequencing technologies and chromosome sorting methods, map-based cloning became more accessible, and some important achievements were made in a large number of cereal crops, such as rice (Vij and Tyagi 2007) as well as in some legumes including soybean (Watanabe et al. 2009).

12.2.1.3 Molecular Markers

Genomics applications including molecular markers provide an immensely popular tool for raising stress-resilient crops. Day-by-day, development of molecular markers has laid the groundwork for different aspects of crop improvement programs (Telem et al. 2016). The molecular markers are used for the detection and exploitation of DNA polymorphisms and these are often associated with specific genes. Their association with genes/QTLs regulating the traits of interest has also been exploited in some cases for indirect marker-assisted selection (MAS). In any case, molecular markers should meet some basic criteria, such as (i) frequent occurrence in the genome, (ii) selective neutral behavior, (iii) high reliability or reproducibility, i.e., should be close to the investigated locus, (iv) must have easy access, (v) easy and fast assay, (vi) being highly polymorphic in nature. Owing to advances in sophisticated genomics tools and automation, dense molecular maps are developed in recent times (Mackill et al. 1999; Landjeva et al. 2007; Ortiz 2010; Illa-Berenguer et al. 2015).

Among the different types of molecular markers, SSR (simple sequence repeat or microsatellites) and SNP markers are particularly important for breeding purposes (Kesawat and Das 2009). SNPs are increasingly becoming the marker of choice in breeding programs due to large abundance in the genome. SNPs are invaluable for genome mapping and more amenable to automation for high-throughput genotyping

(Rafalski 2002). These are widely prevalent types of molecular markers, which make them most suitable for genomic studies (Flint-Garcia et al. 2003; Varshney et al. 2006). In addition, SNPs are less mutable with respect to other markers, particularly microsatellites. SNPs show high heritability, making them extremely suitable for ideal molecular markers (Gupta et al. 2001). The recent introduction of sophisticated tools that have emerged in the genomics field, like microarrays and NGS platforms have allowed the detection of vast numbers of SNP markers in crop plants via comparative sequencing methods. However, for complex plant genomes like polyploid species, the loci that are polymorphic within a single genotype must be taken into consideration for SNP-typing (Mammadov et al. 2012). For such genomes, constructing a reference sequence has been regarded as unattainable to date.

12.2.2 Functional Genomics

Functional genomics involves the development and application of genome-wide experimental approaches to assess gene function by utilizing information provided by structural genomics. In the present genomic era, large-scale exploitation of high-throughput tools has enlightened the complex area of plant stress tolerance and adaptation to develop improved varieties/cultivars. Basically, functional genomics deal with the function of a gene in regulating or contributing to the trait of interest (Roychoudhury et al. 2011). The techniques involving functional genomics mostly utilize sequence or hybridization-based approaches which are discussed briefly. This approach allows a deeper understanding of cellular complexity under several physiological processes.

12.2.2.1 Hybridization-Based Techniques

Microarray and Gene Chip

During exposure to environmental stress factors, plants modulate various biochemical and metabolic alterations, which results in the alteration of thousands of genes. Massive parallel analysis of biological data using microarray provides an excellent tool for the analysis of thousands of genes at the same time in the same reaction (Slonim and Yanai 2009). Microarray technology is rapidly becoming a central platform for functional genomics. Generally, the hybridization-based approach is based upon cross-linking of the target DNA with cDNA or oligonucleotide probes to determine expression. The assays have been developed on a solid surface to which numerous different genomic sequences called probes are typically immobilized in arrays of spots that have been fluorescently labeled. Typical microarrays contain thousands of millions of probes on a single chip or microscope slide used for the analysis of genomes or transcriptomes. Thereafter, each fluorescence signal will be individually detected (Kerr et al. 2000; Heller 2002). Furthermore, this technique also offers an effective way to assign putative functions of genes that depend upon their transcript pattern. Gene chip technology is especially effective to determine the functional specificity of genes within a gene family, which is usually common in plant genomes.

Microarray and gene chips are being increasingly utilized in the field of plant science for efficiency towards global coverage of a complex genome in a single microarray to find out the candidate genes responsible for phenotypic alterations. Under stress exposure, the complete quantitative information regarding relative transcript profiling of genes corresponds to their response towards stress modulation with the fold change. In addition, these techniques also aid to predict tentative gene functions responsible for providing stress tolerance at genome-wide and transcriptome-wide levels. However, these methods also possess some drawbacks, like cross-hybridization and background noise, etc. that may limit their usefulness. Despite having some drawbacks, the global gene expression analysis tools have been widely employed in model plants [*Arabidopsis* (Richards et al. 2012) and rice (Jung et al. 2013)] as well as some economically important crop plants like tomato (Martínez-Andújar et al. 2021), wheat (Quijano et al. 2015), soybean (Le et al. 2012), barley (Close et al. 2004) and maize (Allardyce et al. 2013) to unravel stress responses.

12.2.2.2 Sequencing-Based Techniques

Expressed Sequence Tags (ESTs)

Among the plant genome, ESTs are currently the most widely sequenced nucleotides in terms of the number of sequences and the total nucleotide count. Many ESTs have been sequenced as a substrate for cDNA array-based expression analyses. ESTs provide a robust sequence resource that can be exploited to unravel the environmental stress-exposed gene catalog (Parkinson and Blaxter 2009). ESTs are derived from the cDNA libraries from gene expression analyses during diverse developmental stages. The major aim of developing these EST libraries for the functional analysis of genomes is that they have easy accessibility to genome annotation (Varshney et al. 2006). In functional studies of stress-responsive genes, ESTs have been used to decipher corresponding genes unambiguously due to their rapid and cost-effective benefits. Profiling of stress-responsive transcripts exploiting EST-sequencing databases have already been undertaken in various crop species including rice, wheat, maize, cotton, tomato, soybean, sorghum, etc. (Goff 1999; Walbot 1999). Presently, over a million ESTs are deposited in the National Center for Biotechnology Information (NCBI) generated from a number of crops and other different plant species. To decipher differentially expressed genes, the cDNA library from different stress-exposed plants, and their developmental stages provide valuable information to perform EST sequencing. Another gene-indexing database SwissProt also furnishes information regarding stress-responsive genes among different plants which helps to reveal putative functions under various stress responses (Sreenivasulu et al. 2007).

EST sequencing is widely employed in case where whole genome sequences are absent, more importantly in crop plants with large and repetitive genomes.

Serial Analysis of Gene Expression (SAGE)

Another quantitative approach where the abundance of thousands of transcripts is simultaneously measured is the SAGE, which is a powerful genome-wide expression profiling approach (Hu and Polyak 2006). In SAGE, mRNA sequences are trapped to oligo-dT and subsequently reverse-transcribed to form cDNA. After that, small sequence tags are extracted and ligated to form a long concatemeric chain and sequenced, which leads to complete quantification of gene expression. Despite being one of the advanced techniques, SAGE remains under-utilized in the plant research field; however, some modified SAGE, such as SuperSAGE and DeepSAGE have been used in some plants like rice, *Pinus taeda* and *Arabidopsis thaliana* (Matsumura et al. 1999, 2003, 2010; Lorenz and Dean 2002; Gibbings et al. 2003; Jung et al. 2003; Nielsen et al. 2006). The expanded tag size of modified SAGE provides greater efficiency to annotation, which makes these methods suitable for sequence analysis (Nielsen et al. 2006; Matsumura et al. 2010). In recent times, SAGE has been extensively utilized in crop improvement programs to investigate stress-responsive genes, with the availability of extensive EST databases from different species (Matsumura et al. 1999; Jung et al. 2003). Previously, Wei et al. (2004) demonstrated that combining 5’-rapid amplification of cDNA ends with SAGE analysis allowed the localization of the transcription initiation site. Several researchers employed this technique for the characterization of global gene expression analysis to reveal low-temperature stress in *Arabidopsis* leaves (Jung et al. 2003; Robinson and Parkin 2008).

Massively Parallel Signature Sequencing (MPSS)

A quite similar approach to SAGE, namely massively parallel signature sequencing, is one of the newest tools enabling the in-depth analysis of transcripts on a genome-wide scale. MPSS is a similar tag-based method, where comparatively larger sequence tags are ligated to microbeads facilitating the analysis of millions of transcripts simultaneously (Brenner et al. 2000). The advantage of this method over SAGE is greater specificity and sensitivity. Previously, Sunkar and Zhu (2007) reported that MPSS can also be utilized for small RNA (miRNA, siRNA, tasiRNA) expression analysis in plants which are crucial players under various environmental stress regulatory networks. There are many publicly available plant MPSS databases available, that contain expression data from different genotypes of commercially available crop species, like rice, maize and soybean (Nakano et al. 2006). These recorded data can be used for the purpose of extraction, compilation and comparison of newly generated data for functional analysis of gene expression.

12.3 Proteomic Approaches

Proteome analysis is a very powerful tool since the proteins are directly involved in a majority of cellular events (Komatsu et al. 2003). In the last decade, proteomic studies have been extensively used to investigate their molecular responses under several stress conditions in plant research. Advancements in high-throughput proteomic techniques made it possible to evaluate and identify many more proteins involved in stress response relevant to crop improvement programs (Vanderschuren et al. 2013). Proteomics is advantageous over other omics tools in terms of capacity to detect functional aspects, quantification, protein–protein interactions, protein localization as well as post-translational modifications (Hirano et al. 2004; Zhao and Jensen 2009; Roy et al. 2011). Both biotic and abiotic stresses trigger profound changes in plant proteomes aimed at the adjustment of metabolism to an altered environment as well as strengthening plant stress tolerance. Generally, quantitative proteomic approaches can be classified as either gel-based or gel-free methods. A brief overview of these methods is discussed below.

12.3.1 Gel-Based Proteomics

Gel-based (top-down) proteomic techniques are widely exploited to quantify the abundance of proteins in different biological samples. Traditionally gel-based techniques, especially two-dimensional gel electrophoresis are popular approaches in plant proteomic research.

12.3.1.1 Two-Dimensional Gel Electrophoresis (2-DE)

Initially, plant proteomics research was largely a qualitative approach describing protein profiles using two-dimensional gel electrophoresis (2-DE). This is the most classical and one of the widely utilized tools for profiling the alteration of plant proteome in various plant species, capable of resolving thousands of proteins in a single run (Rabilloud et al. 2010). For this method, proteins are first separated in the first dimension based on their intrinsic isoelectric point (pI) referred to as isoelectric focusing (IEF), and then, in the second dimension according to their molecular weight. These separated proteins are then stained for protein visualization using one of the several staining methods, such as anionic dye (Coomassie brilliant blue), silver staining (silver nitrate), autoradiography, radioactive isotopes, fluorescent staining or labeling, fluorography or phosphor-imaging (Berth et al. 2007; Goez et al. 2018). The next steps are image analysis with computer-assisted image evaluation systems in order to quantify each protein and allow qualitative comparison of samples.

Nowadays, this method is widely utilized in whole proteome research, due to its parallelism, robustness, and reproducibility of 2-D gels, easy and efficient interfacing with other biochemical techniques, and unique ability to analyze complete proteins at high resolution (Dowsey et al. 2003; Bandow et al. 2008; Ruiz-Romero et al. 2010). More importantly, it is compatible with MS and other downstream analyses. Despite having numerous advantages, this method possesses drawbacks also. Some of the issues include poor detection of low abundant proteins [proteins those recruited to signal transduction and regulatory proteins (transcription factors)], highly acidic/basic proteins, or proteins with extreme size or hydrophobicity (Santoni et al. 2000; Gygi et al. 2000; Ong and Pandey 2001; Tonge et al. 2001; Bae et al. 2003). In addition, the method is error-prone, takes longer time, and frequently requires repeated manual editing, which may unintentionally introduce bias into the results. Still, 2-DE provides a visual representation of the proteome, thus, 2-DE is expected to work as a complementary tool to novel gel-free-based approaches for quantitative proteomics.

12.3.1.2 Two-Dimensional Difference in Gel Electrophoresis (2-D DIGE)

Using classical 2-DE to compare different proteomes is difficult to perform due to extensive gel-to-gel variation. The introduction of fluorescent reagents for protein labeling has overcome the difficulties of simple protein staining methods in this field. A promising alternative to the 2-DE approach is two dimensional-fluorescence difference in-gel electrophoresis (2-D DIGE), which is a more sophisticated technique that uses three different florescent tags (Cy2, Cy3, and Cy5) to label up to three samples to be run together on the same 2D gel (Unlü et al. 1997; Lilley and Friedman 2004; Marouga et al. 2005). In this technique, different dyes emit different fluorescence signals for identification. 2-D DIGE allows the comparison and normalization of complex protein mixtures in parallel, which are resolved on the same gel (gel-to-gel comparison). Additionally, it enhances the reproducibility of protein profiling and differences in protein expression between two different protein samples easier to compare and more accurately imaged (Lilley and Friedman 2004).

Since proteins are pre-labeled in this method, no gel manipulation after electrophoresis is necessary (Arruda et al. 2011). Additionally, it requires only a small fraction of proteins (0.025–0.050 mg) with respect to 2-DE, therefore, 2-D DIGE avoids the limitation of the existence of highly abundant proteins in the samples (Dunkley et al. 2006). As compared to 2-DE, 2-D DIGE requires 50% fewer gels, making this method more economical. This method is successfully applied to analyze subtle alterations of protein expression levels to uncover biotic stress in *Medicago truncatula* (van Noorden et al. 2007; Schenkluhn et al. 2010) and abiotic stress responses like freezing in *Arabidopsis thaliana* (Li et al. 2011), drought in young pedunculate oak (*Quercus robur*) (Sergeant et al. 2011), ozone (Bohler et al. 2011), and cadmium in poplar (Kieffer et al. 2008; Durand et al. 2010).

12.3.2 Non-gel (Gel-Free) Proteomics

In gel-free (bottom-up) shotgun proteomics, the appearance of mass spectrometry (MS) has become a feasible approach for global protein expression profiling, which may be further divided into either label-based or label-free. Gel-free separation techniques utilize multi-dimensional capillary liquid chromatography coupled to tandem MS/MS, which offers a deep exploration of complex proteomes and provide a more detailed snapshot of protein composition (Roe and Griffin 2006; Tang et al. 2008). Gel-free techniques are much faster and cheaper as compared to conventional complete gel-based methods.

12.3.2.1 Multidimensional Protein Identification Technology (MudPIT)

MudPIT is an optimized analytical expression profiling strategy, allowing comprehensive analysis of proteins from highly complex mixtures. MudPIT first revolutionized the field of proteomics by changing the procedure of sample preparation of traditional 2-DE to direct digestion in solution form. Furthermore, it transformed the operation of proteomics from a low-throughput, offline process to a high-throughput, online mode (Florens and Washburn 2006). In this method, protein samples are separated stepwise through a biphasic microcapillary column comprising a combination of reverse-phase materials and a strong cation exchanger (SCX), followed by tryptic digestion. The series of the two columns are lined up on an ESI–MS/MS instrument. The data generated from the MS/MS help to measure the protein content of the sample (Eng et al. 1994). Due to possessing enhanced separation ability, it can be a good example of induced proteome coverage for the bottom-up proteomic approaches (Mathy and Sluse 2008).

MudPIT requires less time to analyze a highly complex system, such as whole proteomes. Moreover, it is capable to detect low-abundance proteins, which is an advantage of this technique (Washburn et al. 2001). However, the drawback of this method is the lack of quantitative data (Bayer et al. 2006). This so-called “second generation” proteomic technique was first employed in yeast and mammals, later on, successfully applied in plant proteomic research (post-transcriptional modifications, interactomics) in different crop plants like rice (Koller et al. 2002), *Arabidopsis* (Bayer et al. 2006), lettuce (Cho et al. 2009) and pumpkin (Cho et al. 2010). Recently, molecular breeders used this technique to unveil the mechanisms liable for controlling tiller numbers in cereal crops (Lee et al. 2011).

12.3.2.2 Isotope-Coded Affinity Tag (ICAT)

ICAT is another gel-free quantitative proteomic strategy, which is based on isotope (chemical) labeling. This strategy distinguishes between two populations of proteins using reactive probes that differ in isotope composition. The methodology comprised three elements: an affinity tag (biotin), for isolation of ICAT-labeled peptides; an isotopically-coded linker for incorporation of stable isotopes; and a specific reactive group with specificity toward sulfhydryl groups of cysteinyl residues. The approach is based on the stable isotopes incorporated by selective alkylation of cysteines with either a heavy-isotope or a light-isotope. Later, two labeled proteins are pooled and allowed to trypsin digestion (Gygi and Aebersold 2000). The labeled peptides are fractionated by passing through a microcapillary reverse-phase liquid chromatography, followed by a monomeric avidin-agarose column. In addition, MS/MS spectrum further identifies the sequence information based on the relative abundances of the eluted light and heavy peptides (Patton et al. 2002; Shiio and Aebersold 2006).

Because ICAT does not involve 2-DE technique and relies on MS for protein assessment, this method can be used to compare membrane proteomes (Dunkley et al. 2004a, b). Using this strategy, it is now possible to measure the redox regulatory systems of proteins which allows quantitative analysis of the redox proteome and ozone stress in plants (Hägglund et al. 2008, 2010; Miles et al. 2009; Dietz 2011). Precise and confident localization of a specific protein to an organelle is problematic, due to similar densities as well as continuous mobility of these proteins between the cellular compartments. Taking advantage of ICAT labelling, Dunkley et al. (2004a, b) studied the localization of organelle proteins to the endoplasmic reticulum and Golgi apparatus, which can be implemented in plant-environmental stress-related studies. ICAT can be useful in crop breeding programs in which breeders search for desired proteins regulating a crucial biological role in a particular variety.

12.3.2.3 Isobaric Tags for Relative and Absolute Quantification (iTRAQ)

Another chemical labeling strategy that allows simultaneous quantification of proteins across multiple samples, iTRAQ has quickly gained popularity in proteomics research (Nogueira et al. 2012). It is an easy-to-use tool to examine proteomic changes under complex biological systems. Additionally, iTRAQ-based proteomic analysis renders the relationship between proteins, and protein–protein interactions in multiprotein complexes (Ross et al. 2004; Martínez-Esteso et al. 2014). Unlabeled protein samples were first digested with trypsin and labeled with different isobaric tags independently. These labeled peptides from different samples are then mixed together and separated by liquid chromatography. Identical peptides with different samples labeled with different isotopes are chromatographically indistinguishable and appear as a single precursor. The isolated peptides are finally run through tandem mass spectrometry (MS/MS) for further fragmentation and subsequently generate a collection of mass spectra.

Compared to earlier methods, iTRAQ is robust due to stable N-hydroxysuccinimide ester chemistry. In addition, it offers better quantitative reproducibility, high throughput methodologies, improved sensitivity, and allows simultaneous quantification of up to eight samples in a single run (Schmidt and Urlaub 2009; Noirel et al. 2011; Evans et al. 2012). Moreover, this technique is free from the restriction of sample property. For its wide flexibility in the experimental protocol and powerful efficient quantification, this approach is widely utilized for the differential expression study of plant proteomes (Zieske 2006; Jorrín et al. 2007; Jorrín-Novo et al. 2009; Oeljeklaus et al. 2009). Several investigations have been carried out using this sophisticated tool to reveal plant responses to pathogens: α-proteobacterium *Candidatus* Liberibacter *asiaticus* in Mandarin *Citrus reticulata* (Xu et al. 2015), *Pseudomonas syringae* in *Arabidopsis* (Kaffamik et al. 2009) and *Fusarium graminearum* in *Zea mays* (Mohammadi et al. 2011). This approach has also been used to gain a comprehensive understanding of the mechanisms underlying abiotic stress tolerance during cadmium exposure in barley (Schneider et al. 2009) and Indian mustard (Alvarez et al. 2009) and boron stress in barley (Patterson et al. 2007).

12.3.2.4 Stable Isotope Labeling by Amino Acids in Cell Culture (SILAC)

Based on metabolic labeling approach, SILAC is a potent technique to address alteration in proteomics and post-translational modifications, that control cellular decisions under stress exposure. The simplicity and robustness of the SILAC have led to quantifying protein turnover in the proteome-wide scale reliably and more precisely, over chemical labeling and label-free quantitative strategies (Cox et al. 2009). This technique enables amino acid-containing stable isotopes in a growth medium to encode cellular proteomes that chromatographically coelute for quantitative analysis (Ong et al. 2002, 2003). Compared to previously discussed methods, SILAC allows combining the light and heavy labeled protein samples early in the experimental protocol which considerably reduces sample handling errors. The advantages including ease of implementation, excellent data generation ability, and compatibility with experimental workflows made this technique highly popular among proteomic researchers (Mann 2006).

Although probably the most widely used labeling strategy in animal systems, SILAC has generally been regarded as unsuitable for plant systems. Being autotrophic organisms, plants are capable to produce all amino acids from inorganic nitrogen and therefore have inefficient incorporation of exogenously supplied labeled amino acids. SILAC in plants was first described in *Arabidopsis* suspension cells used to find out the regulation of expression of glutathione-S-transferase under salicylate-induced abiotic stress and to analyze the signal-dependent phosphorylation events during that treatment (Gruhler et al. 2005).

12.3.2.5 Protein Microarray

Protein microarray is another gel-free approach where hundreds or thousands of proteins can be simultaneously screened in a single experiment. To quantify protein abundance for screening biomarker studies during several biotic and abiotic stresses in plants, this technique is extremely useful. In addition, stress-induced alteration in plant proteome changes involves a myriad of intermolecular interactions in a real-time manner (Chandra et al. 2011; Lourido et al. 2014). Presently, protein microarrays comprise of three major classes: analytical, functional and reverse-phase protein microarrays. Analytical microarray generally allows differential expression profiling, while functional microarray enables the study of numerous biochemical properties of proteins, including protein–protein, protein-DNA, protein-lipid, and protein-peptide interaction. Reverse-phase protein microarray is specifically utilized to identify the existence of altered protein in the sample, which may be the result of disease (LaBaer and Ramachandran 2005).

12.3.3 Mass Spectrometry

To perform large-scale analysis of amino acids and peptides generated from modern proteomic techniques, mass spectrometry (MS) can be used (Schulze and Usadel 2010). It plays a central role in protein research and the field of proteomics. Typically, proteomics based on mass spectrometric techniques has been put forward in the direction of breeding new cultivars of crop and vegetable plants tolerant to the affecting stresses as well as possessing finer qualities of agronomic traits (Jorge et al. 2015). Initially, liquid chromatography (LC) coupled to MS/MS was used for the detection of trace-level analytes at high throughput, where peptide masses may overlap due to the presence of a complex background, using spectral information from mass spectrometry.

The major breakthrough came in this field with the appearance of two new techniques, such as electrospray ionization (ESI) and matrix-assisted laser desorption/ionization (MALDI) (Domon and Aebersold 2006). These methods enable gentle ionization of analytes and subsequent transfer of ionized molecules from the condensed phase into the gaseous phase with minimal fragmentation, which made polypeptides accessible to mass spectrometric analyses. ESI–MS system is generally used for complex peptide mixtures, while MALDI is used to analyze relatively simple peptide mixtures. MALDI instrumentation is often used in conjunction with complex multistage analyzer [simple time-of-flight (ToF), tandem time-of-flight (ToF/ToF) or hybrid quadrupole time-of-flight (Q-Q-ToF)] depending on the complexity of the molecule. The function of the ToF mass analyzer is to measure the mass-to-charge (m/z) ratio of peptide mixture from its time of flight within a vacuum tube of a defined length (Aebersold and Goodlett 2001; Aebersold and Mann 2003).

The quantitative information obtained in MS/MS mode is used to detect the molecular mass of specific proteins, as well as detection and characterization of post-translational modification or further covalent modification of specific or desired proteins which is reflected from the alteration of mass of proteins. Tandem mass spectrum (MS/MS) involves multi-stages of mass analysis of the resulting fragments which provide more detailed structural characteristics of the analyte (Aebersold and Goodlett 2001). The MS-based spectra provide useful information for plant researchers and molecular breeders to determine the fate of individual proteins that might help in understanding specific roles played under adverse environmental conditions.

12.4 Application of Genomic and Proteomic Approaches to Study Environmental Stress Tolerance

12.4.1 Salinity Stress

Salinity stress is a global problem particularly for modern agriculture causing inhibition and impairment of crop cultivation. Plant growth and productivity are adversely affected during exposure to salt stress, except halophytes (Yokoi et al. 2002). Several researchers have focused their attention to develop salt-tolerant crops to maintain annual productivity. Understanding the mechanisms that enable plant growth under saline environment is pretty much essential during ever-changing climatic conditions. Over the last decade, a number of attempts using genomic and proteomic attempts have been carried out to gain knowledge under salinity stress in different plants. Recently, a group of researchers screened a panel of 179 Vietnamese landraces of rice and identified 26 new QTLs using genome-wide association mapping (GWAS), of which ten act pleiotropically to regulate different levels of plant responses under salt stress. They also revealed that different genes under these QTLs play a crucial role in order to tolerate salt stress-induced injuries (Le et al. 2021). Another GWAS study identified 293 significantly associated quantitative trait nucleotides (QTNs) responsible for salt tolerance, which could be utilized for further exploration and validation for marker-assisted selection to develop salt-tolerant wheat cultivars (Chaurasia et al. 2021).

In recent times, proteomic approaches provide molecular insight into different branches of agricultural research. There are several proteomic studies illustrated mainly based on 2-DE, although MS-based approaches have also become common. For example, a proteomic study using 2-DE identified 31 differentially regulated salt stress regulatory proteins, of which 8 identified salt-responsive proteins under salt-stressed rice roots (Chitteti and Peng 2007). Similarly, Fatehi et al. (2012) made a systemic proteomic analysis in contrasting barley genotypes [salt-susceptible (Line 527) and salt-tolerant (Afzal)] and detected 18 different salt-responsive proteins by MALDI-ToF/ToF–MS responsible for various cellular functions, including photosynthesis, protein translation and processing, energy metabolism, signal transduction, and reactive oxygen species scavenging and defense.

12.4.2 Drought Stress

Scarcity of water is another major environmental limiting factor due to global climate change. Drought-induced loss in crop yield exceeds losses from all other causes, thus affecting productivity around the world. Crop loss, due to drought stress, has a devastating impact on the agriculture industry as well as the economy (Shanker et al. 2014). A better understanding of drought tolerance mechanism is the first step in the crop breeding strategy to develop towards developing tolerant varieties. A group of researchers performed univariate and multitrait multivariate GWAS mapping in coast redwood (*Sequoia sempervirens*) and giant sequoia (*Sequoiadendron giganteum*) to identify several candidate genes associated with drought-related traits, which contributed towards a better understanding of drought tolerance from the genomic point of view (De La Torre et al. 2021). In another study, utilizing multi-locus random-SNP-effect mixed linear model data unveiled that 20 QTNs were found to be significantly associated with drought tolerance-related traits in upland cotton (*Gossypium hirsutum*) plants. Further, GWAS mapping, RNA-seq analysis, and qRT-PCR verification identified 4 candidate genes, *RD2*, *HAT22*, *PIP2*, and *PP2C*, which play an important role in drought tolerance (Hou et al. 2018).

Enormous progress has been made in drought-stressed plants by employing proteomic approaches. Drought-induced alteration in leaf proteome was investigated by 2-DE and quantitative analysis showed statistically significant changes in 79 leaf proteins in *Beta vulgaris.* Among them, 45 proteins were down regulated and 27 proteins were up regulated in response to drought. By using LC–MS/MS, twenty protein spots were detected that were engaged to play some role in plant stress regulation. Some of these proteins were able to play important breeding targets for generating drought-tolerant cultivars (Hajheidari et al. 2005). Drought-induced differential proteomic analysis in leaves of common bean (*Phaseolus vulgaris*) using 2-D DIGE technique showed that abundance of 58 proteins was changed in Tiber (drought-tolerant), while the number was 64 in case of Starozagorskičern (drought-susceptible). These proteins were involved in counteracting drought-induced modulation in the respective varieties, which could be used as biomarkers in the selection process for drought tolerance in plants (Zadražnik et al. 2013). Comparative proteomic analysis harnessing iTRAQ, LC–MS/MS study spotted 1,976 proteins expressed in canola (*Brassica napus*) under drought stress. Functional analysis showed 417 proteins associated with photosynthesis, metabolism, stress and defense to enhance stress tolerance. The temporal pattern of proteome changes and functional characterization of the identified proteins provided a deeper insight into the molecular mechanisms underlying drought tolerance (Koh et al. 2015).

12.4.3 High-Temperature Stress

The constant rise in ambient temperature is the inevitable part, driven largely by an increasing amount of greenhouse gases in the atmosphere. Sustaining high yields of crop plants under high-temperature stress is an important agricultural goal for food security. The catastrophic loss of cereal crop productivity under thermal stress results in widespread famine (Qu et al. 2013). The studies using genomic and proteomic tools provide a clear insight regarding in plant responses to high-temperature stress so as to develop thermal stress-tolerant crops via molecular breeding. Genome-wide expression analysis illustrated 607 heat-responsive genes and 39 heat-tolerance genes in European maize inbred lines. Of these, 28 genes were strongly up regulated with increasing heat levels in thermal-susceptible inbred lines, as compared to the tolerant inbreds, while the remaining genes exhibited the reverse regulation pattern (Frey et al. 2015). Recently, Rahaman et al. (2017) conducted a GWAS study integrating 37,539 SNPs able to decipher 115 significant markers and 20 QTLs associated with heat stress-affected traits during the flowering stage in spring-type *Brassica napus*. The identified markers and QTLs can be utilized for thermotolerance screening, which might be useful for the development of tolerant cultivars for governing yield stability in increasing temperature.

To counteract stress-induced injury, plants have to modulate significant proteome composition. Since proteins are closely interrelated to plant stress response, proteomic study significantly contributes to our understanding of molecular mechanisms underlying plant stress acclimation (Kosová et al. 2011). A proteomic analysis based on 2-DE coupled with MALDI-ToF/MS in thermo-susceptible rice genotype, IET-21405 revealed a total of 73 protein spots in rice leaves. Further functional analysis of 73 differentially expressed heat-shock proteins (HSPs) were mainly linked with thermal stress-induced defense, followed by signal transduction, metabolism, trafficking and protein synthesis. Their findings suggest that heat shock proteins (HSPs) play an indispensable role in preventing cellular damage upon elevated temperature (Kumar et al. 2017). In another study, a comparative proteomic study by 2-DE demonstrated that 46 protein spots changed in abundance, of which, 13 proteins were differentially expressed in response to high temperature with a distinct difference in three studied rice genotypes (Moroberekan, IR-64, and N22) during anthesis (Jagadish et al. 2010). Interestingly, cold-shock and heat-shock proteins were up regulated significantly in N22 (most tolerant), which probably contributed to thermotolerance during elevated temperature.

12.4.4 Cold Stress

Cold or low temperature is a strong limiting factor, and restricts productivity, especially in subtropical and temperate grain crops. Thus, the collection of genomic and proteomic data is of great importance which can assist plant breeders to develop cold-tolerant crops and retrieval mechanisms against chilling stress. To understand the molecular mechanism of cold tolerance in rice, GWAS analysis was performed. A total of 235 significantly associated SNPs were confirmed. Among them, 120 and 88 SNPs were responsible for cold stress and chilling adaptation, respectively. Moreover, by integrating colocalized SNPs, 11 and 12 QTLs were found to be associated with cold stress and chilling acclimation, respectively. This study provides a platform for the identification of new candidate genes in the genetic improvement of chilling acclimation in rice (Li et al. 2022). Another investigation in rice by Yang et al. (2020) identified a total of 159 genetic loci by using phenotypic and GWAS analysis from a set of 200 indica rice populations. Furthermore, by integrating GWAS with RNA sequencing, they obtained 179 overlapping candidate genes. These findings provide valuable information for developing molecular markers for the purpose of rice breeding programs to develop tolerant indica rice varieties for better plant growth and annual production under cold stress.

Cold stress, which includes chilling and/or freezing temperature, greatly affects the plasma membrane proteins, which are the first site of primary injury (Takahashi et al. 2013). Proteomic research provides a platform for the identification and quantification of plant proteins that play a key role in stress perception and cold acclimation (Jozefowicz et al. 2020). Previously, Hashimoto et al. (2009) reported that rice roots grown under cold stress showed enhanced expression patterns of plasma membrane proteins recruited to membrane permeability and signal transduction. Proteomic study of cold-affected *Arabidopsis thaliana* rosette leaves displayed that 22 and 18 protein spots with about 2.0-fold changes in protein abundance were separated and appeared in 2-D gels, when exposed to 6 °C and 10 °C, respectively. Out of 22 proteins, 13 were identified using MALDI-TOF alone or in combination with ESI–MS/MS, while only one spot was identified through ESI–MS/MS. Many of these proteins play important roles in the context of cold-stress responses (Amme et al. 2006). Quantitative proteomic profiling using iTRAQ labeling technique provided a global perspective of petunia seedlings by Zhang et al. (2016). The study quantified a total of 2430 proteins; among them, 117 cold-responsive proteins were differentially expressed with respect to control plants, which are the potential candidates associated with plant responses under low-temperature stress.

12.4.5 Flooding Stress

Excessive rainfall within a short period of time causes flooding conditions, which substantially diminishes crop growth and yield in low-lying rainfed areas. Flooding usually causes submergence or partial submergence stress (oxygen limitation) in plants, due to restricted gas diffusion underwater (Tewari and Mishra 2018). Currently, agricultural scientists have focused upon developing flood-tolerant germplasm so that they can endure for longer time under waterlogged conditions. Although a lot of information is available under other abiotic stresses, very little attention has been paid to flooding stress. Recent phenomenal progress in high-throughput omics approaches could be suitably utilized in this area, which will subdue the deleterious effects of flooding stress on agriculturally important crops. In recent times, a GWAS study identified QTNs involved in seed-flooding resistance-related traits (germination rate, normal seedling rate, and electric conductivity), by analyzing a panel of 347 soybean lines and genotypic data related to 60,109 SNPs. A total of 25 and 21 QTNs were linked with all three traits, of which 3 major QTNs were identified. Furthermore, the gene annotation program revealed 9 candidate genes that imparted flooding tolerance (Yu et al. 2019). To investigate the role of membrane proteins during cold stress, plasma membranes were isolated from the root and hypocotyl of soybean seedlings after exposing the seedlings under submerged conditions for one day. Proteomic studies using 2-DE followed by nano-LC–MS/MS-based analysis detected a total of 150 protein spots, of which, 14 spots were altered by flooding, 12 proteins were up regulated and the remaining two proteins were down regulated. These proteins played crucial roles in response to regulation to cope up flooding injury (Komatsu et al. 2009). The outcome of this experiment can be useful for plant breeders for gene pyramiding to create new germplasm in flood-prone areas.

12.4.6 Biotic Stress

Climate change-induced environmental vagaries have amplified the attacks from plant pathogens, such as viruses, bacteria, fungi and nematodes causing immense damage to agricultural products worldwide. In economic terms, biotic stress factors also routinely constrain crop quality and yield because of plant diseases. To combat the devastating effects of pathogenic organisms in modern-day agriculture, plant breeders are attempting to discover proper ways to better decipher the closer look towards plant-microbe/plant-pathogen interactions. The latest achievements and discoveries in omics tools, especially genomic and proteomic approaches have allowed us to understand pathogenic detriments to make crops disease-resistant to minimize yield losses. For example, the BPH (brown plant hopper, *Nilaparvata lugens* Stål) is one of the most serious pests of all rice herbivores, causing wilting and complete drying of rice plants. The proteins were extracted from susceptible (raised from Taichung Native 1, sensitive to BPH) and tolerant (carrying BPH resistance gene, *Bph15*) rice lines and iTRAQ-labelled peptides were analyzed by nanoLC-MS/MS system. The proteomic analysis detected a total of 693 distinct proteins, of which the expression of 293 and 258 proteins showed a massive change in abundance in the susceptible and resistant lines, respectively, when they were infested by the BPH. Functional characterization identified that these proteins are responsive to jasmonate biosynthesis, oxidative stress, metabolic processes, and carbohydrate and amino acid metabolism in both lines; however, somewhat higher expression levels appeared in the susceptible lines after BPH treatment (Wei et al. 2009).

The inductive role of compatible and incompatible interactions in the accumulation of pathogenesis (PR)-related proteins by pepper mild mottle virus (PMMoV) in *Capsicum chinense* was demonstrated by Elvira et al. (2008). Spanish (PMMoV-S) and Italian strain (PMMoV-I) of pepper mild mottle virus resulted in incompatible and compatible interactions, manifested by the L^3 resistance gene, which was active in PMMoV-S, but not in PMMoV-I. Proteomic analysis using 2-DE displayed differential accumulation patterns of PR proteins in both compatible and incompatible viral strains of PMMoV. Further MALDI-ToF and MS/MS analysis revealed isoforms belonging to peroxidase (PR-9), acidic β-1, 3-glucanase (PR-2), chitinase (PR-3), osmotin-like protein (PR-5), peroxidases (PR-9), germin-like protein (PR-16) and PRp27 (PR-17). In hypersensitive reaction, three of these PR proteins, PR-3, pR-5, and pR-17 were specifically enhanced during PMMoV-S-mediated activation of *Capsicum chinense* L^3 strain. Furthermore, this report has shown that each protein has a characteristic expression pattern, thus pointing toward the complexity of their regulation.

Phytophthora sojae is a causative agent of root and stem rot disease in soybean. Zhang et al. (2011) performed a proteomic study to investigate the effects of soybean hypocotyls during exposure to *P. sojae.* For this purpose, the researchers used two soybean lines [susceptible line (NG6255) and tolerant line (Yudou25)] challenged with the physiological race of *P. sojae* (PNJ1). 2-DE coupled with MALDI-ToF/ToF analysis detected 46 differentially expressed proteins. In NG6255, only 20 proteins were significantly affected (of which 11 were up regulated and 9 were down regulated), while 26 proteins were significantly affected (12 up regulated and 14 down regulated) in case of Yudou25. All of the identified proteins were connected with energy regulation, protein destination and storage, defense machinery, energy metabolism, protein synthesis, as well as secondary metabolism. This experiment provides proteomic insight for studying protein regulation during plant-oomycete interaction.

12.5 Conclusion and Future Perspectives

“Omics-assisted” approaches have given a more holistic view of the molecular response in plants under varying environmental stress conditions. Studying the dynamic plant genome and proteome has become comparatively easy and accurate with the advancements in various techniques and methodologies in the modern era. With these advancements in computational resources and instrumentation, the cost of omics have been lowered many folds for plant physiologists and molecular breeders to thoroughly understand intricate operational cascades in different crop and vegetable plants with economic benefits. The comprehensive nature of multi-omic studies provides an entirely new avenue and future research programs should be planned accordingly. Finally, integration of these genomics and proteomics data with other branches of omics, such as transcriptomics, metabolomics, lipidomics and interactomics, with rapidly evolving bioinformatics tools as well as the interactive databases can better lead us towards a comprehensive understanding of the multiple factors playing roles in plant tolerance under changing climatic conditions. The development of stress-resilient cultivars or high-yielding crop varieties is directly needed to meet the need for food demands and guarantee nutritional security for expanding populations in near future. Further characterization of molecular biomarkers involved in a variety of biotic and abiotic stresses is highly desired by plant breeders to resolve many facts behind precise mechanisms of stress mitigation for developing crops with increased tolerance and better yield in terms of agricultural production.

Acknowledgements Financial assistance from Science and Engineering Research Board, Government of India through the grant [EMR/2016/004799] and Department of Higher Education, Science and Technology and Biotechnology, Government of West Bengal, through the grant [264(Sanc.)/ST/P/S&T/1G-80/2017] to Prof. Aryadeep Roychoudhury is gratefully acknowledged.

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Chapter 13
Biochar-Assisted Phytoremediation for Heavy Metals-Contaminated Soils

Shazma Muzammal, Asma Akram, Muhammad Bilal Shakoor, Sajid Rashid Ahmad, Mujahid Farid, and Muhamamd Hassan Shakoor

Abstract The use of biochar in phytoremediation of heavy metals-contaminated soils is considered a very beneficial approach. The biochar application in phytoremediation method results in the removal, degradation, or stabilization of heavy metals from soil media. Various other chemical, biological and physical techniques are used for the treatment of heavy metals-contaminated soils but biochar application to soils is proved to be a much better option than different conventional methods. Biochar when added to soil can enhance nutrient retention ability, soil structure, water holding capacity and microbial activity thus producing a favorable environment for the growth of plants. Efficient plants are selected for phytoremediation method which is based on their potential to sustain or uptake heavy metals without significant damage to their growth. They show great potential to uptake and sustain high levels of heavy metals in their roots or aerial parts. The biochar application in soil along with phytoremediation can reduce the bioavailability of heavy metals to plants thus restricting their significant uptake. Moreover, it also minimizes the danger of groundwater pollution and dispersion of heavy metals in environment. Overall, biochar-assisted phytoremediation has proved its significance as a capable and ecofriendly method to resolve widespread issue of heavy metals contamination in soils thus presenting a sustainable substitute to conventional treatment methods.

Keywords Accumulation · Biochar · Heavy metals · Phytoremediation · Soils

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_13

13.1 Introduction

The importance of soil for the survival of living organisms is very well understood. The presence of certain soil microbes and crucial nutrients in the soil are very essential for its health and fertility. However, deterioration of soil due to heavy metals is one of the main issues across the world. Multiple sites globally, are facing extreme soil destruction and infertility due to the addition of heavy metals as a result of certain anthropogenic activities. The addition of lethal natured heavy metals into soil particularly through waste management activities, industrial and agricultural processes etc. is not only making the soil inhabitable for certain soil microorganisms but also posing a serious threat to food security on a global level. Many scientists have been focusing and researching on the possible sustainable methods that can help the contaminated soil to regain its natural stability. Moreover, a lot of methodologies proposed by different researchers proved that rehabilitation of soil is not an easy task due to certain technical and financial implications. Several physicochemical and biological methods like ion exchange, precipitation, vitrification, land farming, encapsulation, chemical fixation, solidification, composting, bioventing etc. are not considered good to provide the favorable results with lesser or no negative environmental impact. On the contrary, biochar assisted phytoremediation is the one eco-friendly and cost-effective technique that is able to give better results when applied on heavy metals contaminated soil. The use of hyperaccumulators with the amendment of organic biochar has proved to be one of the best methods developed to treat the unhealthy soil. This method has certain amount of benefits over other conventional techniques e.g., it has the potential to immobilize heavy metals in soil, makes the soil stronger for maximum crop yield, increase carbon sequestration potential of soil etc. A variety of biochars has been used along with effective plant species to extract heavy metals out of the contaminated soil. Some of them are; rice husk biochar assisted phytoremediation, tea waste derived biochar assisted phytoremediation, bamboo biochar assisted phytoremediation, banana peel biochar assisted phytoremediation, coconut and hardwood biochar assisted phytoremediation, corn cob and cotton straw assisted phytoremediation etc. Hence, on the basis of remarkable results given by the above mentioned biochars for the removal of heavy metals like Cd, Pb, Zn, As, Cr, etc. this methodology is mostly preferred over others by scientific community.

13.2 Soil as a Background for Living Things

In particular, the soil, which is the top layer of the crust, stands in for the "living epidermis" of the globe. A specific combination of minerals, organic matter, and a channel of pore spaces filled with water and air create the complex habitat known as soils. Many diverse types of soil organisms living here conduct essential soil processes and functions (Kabata-Pendias 2000; Sintim et al. 2022). In addition to being a source and reservoir of pathogens, beneficial microorganisms, and the total microbial diversity in a broad variety of organisms and ecosystems, soils are a crucial component of one's health.

Because of the ecosystem services that the soil provides to sustain life on the planet, its significance should not be understated (Islam et al. 2022). Human food is primarily produced through farming on grassland and arable lands. Additionally, fruitful and sustainable cultivation on agricultural soils will be the foundation of food production for human society in the future (Gerke 2022). As all plant species absorb the inorganic nutrients and water required for their development, the soil serves as the substrate for their survival (Blum 2013; Dong et al. 2021). It creates a natural water filter and regulates the exclusion of extra water. Soluble organic carbon (SOC) is used to hold large amounts of organic carbon (Amoah-Antwi et al. 2020). With about 80% of the world's terrestrial carbon (C) stored underground, soil is the second-largest C sink after the seas. According to estimates, soil organic matter (SOM) contains 58% of the earth's organic carbon (Joos and Tender 2020).

Consequently, soil helps preserve biodiversity by supporting interactions between numerous soil microhabitats, which are home to a variety of species including upper mammals and microorganisms (Sintim et al. 2022; Dror et al. 2021).

The management of soil organic matter for high soil fertility and high carbon storage in soils, which may mitigate for rising CO_2 concentrations in the atmosphere. The supply and cycling of plant nutrients at a high level, which is highly influenced by soil organic matter. Additionally, both now and in the future, the agricultural soils will have a significant impact on the availability of food for an increasing human population (Gerke 2022).

13.3 Heavy Metals (HMs) Pollution in Soil

Heavy metal contamination of soil has become an environmental issue on a global level in recent years. Environmental pollution requires immediate global outlook because it threatens soil and water resources. Heavy metal contamination of soil is mainly driven by accelerated population growth and increased anthropogenic activities, such as the haphazard disposal of municipal refuse and industrial effluents (Shah and Daverey 2020; Irfan et al. 2021). Metals and metalloids with an atomic mass greater than 20 and a chemical density greater than 5 g/cm^3 are classified as heavy metals (Kabata-Pendias 2000; Alloway 2013). Numerous heavy metals have a much greater density than in liquid, ranging from over 4 g/cm^3 to 5 g/cm^3, and are typically toxic to plants, humans, and other animals without consideration to their fixations (Siddeeg 2020).

While anthropogenic activities like excessive sewage disposal, drainage systems, slime applications, diesel exhaust, mineral extraction and refining processes, urban growth, agricultural activities, and industrial growth contributed to the accumulation of heavy-metal contamination in soil, the geography of the area is specifically in need of minor component concentrations in soil condition (Wadhawan et al. 2020). Cadmium (Cd), mercury (Hg), copper (Cu), arsenic (As), lead (Pb), chromium (Cr), uranium (U), and zinc (Zn) are the most prominent HMs found in the atmosphere (Wuana and Okieimen 2011; Qin et al. 2021). According to Jabeen et al. 2009, lead (Pb) can remain in soil for more than 150–5,000 years and can stay there in high quantities for up to 150 years after being applied to the soil as sludge. Cadmium (Cd) has a biological half-life of roughly 10–30 years (Berglund et al. 2015).

Over 20 million hectares of soil have been contaminated by heavy metals globally (Liu et al. 2018). Many heavy metals are necessary for biological systems, but only in small amounts because they are highly toxic at higher levels and can lead to cancer, hyperkeratosis, skin lesions, and issues with the brain, kidneys, and gut (Ayangbenro and Babalola 2017; Akpomie and Conradie 2020).

13.4 Sources of HMs in Soil

The two main sources of heavy metals entering the earth are anthropogenic and natural sources.

13.4.1 Natural Sources

Heavy metal (loids) in contaminated areas can come organically from the parent soil, or geogenic source. Many heavy metals reside in chemical complexes rather than as single molecules, making them easier for living cells and tissues to directly absorb (Derakhshan Nejad et al. 2018). While typical heavy metals include zinc (Zn), lead (Pb), mercury (Hg), nickel (Ni), copper (Cu), arsenic (As), cadmium (Cd), and chromium, heavy metals can also take on other chemical forms in soil, including silicates, hydroxides, sulphides, oxides, organic, and phosphate compounds (Cr). Even though they are present in very small amounts, they are thought to be a significant contributor to issues with human health and the environment. The pedogenic weathering of parent soil materials also explains the trace metal release (less than 1000 mg/kg) of heavy metals into the soil ecosystem (Kabata-Pendias 2000; Oladoye et al. 2022).

13.4.2 Anthropogenic Sources

Due to the constant production of products and mechanical processes to satisfy the high levels of demand from the enormous human population and the concurrent release of effluents or refuse, the environment has become more polluted. Sources of heavy metals include anthropogenic processes like chemical water discharge, wastewater, industrial and farming operations, as well as smelting and mining operations. Due to chemical effluent wastes, soils near industrial metropolitan regions are typically more polluted and contain higher concentrations of heavy metals like Pb, Cu, Cd, and Zn (Oladoye et al. 2022). Some specific heavy metal issues have been linked to certain industrial activities, such as lead (Pb) in automobiles, arsenic (As) in insecticides, zinc (Zn), copper (Cu), and arsenic (As) in smelting processes, and vanadium (V), nickel (Ni), mercury (Hg), tin (Sn), and selenium (Se) in the combustion of fossil fuels (Vhahangwele and Mugera 2015). Agriculture and industry have a significant impact on heavy metal pollution in agricultural soil and plants, especially in soils near cement and electroplating plants (Alengebawy et al. 2021).

13.5 Effect of HMs Contaminated Soil on Environment

In a nutshell heavy metals disrupt the ecosystem's balance, degrade soil qualities, reduce crop yields, and pose serious hazards to human health by getting into the food chain (Shah and Davarey 2020). These heavy metals are toxic in nature because they can harm both people and animals. When a chemical substance can hinder an organism's ability to develop, survive, or reproduce, it is considered toxic. They affect various systems, organs, and tissues in various organisms through a variety of processes, some of which are still unknown (Ali et al. 2019). The distinct physicochemical characteristics and features of each metal define its specific toxicological mechanisms of action. Heavy metals (As, Cr, Cd, Hg, and Pb) have been classified as a public health issue due to their high toxicity. This pollution has gotten worse due to the quickening pace of urbanization and industrialization and increased dependence on synthetic agrochemicals. The high concentration of heavy metals in the soil has a negative effect on soil quality, structure, function, nutrients, and biological activity (Pan et al. 2016).

According to estimates from the National Research Council (NRC) of 2007, there were approximately 45 billion tonnes of materials discovered in 2010 and that number is expected to rise to 70 billion tonnes by 2030. Surface mining leaves behind abandoned ground barren of vegetation, soil structure, and biodiversity (Venkateswarlu et al. 2016). A substantial amount of debris or excess material, which are typically highly contaminated with possibly toxic elements, are typically produced as a result of the excavation activities. However, because of the pH, inadequate levels of biological matter and nutrients, deteriorated pedological structure, low water accessibility, and high levels of dangerous heavy metals, these remains and debris materials cannot provide a favorable substrate for vegetation cover (Wang et al. 2017).

13.6 Impact of HMs Contaminated Soil on Food Security

The second and third Sustainable Development Goals (SDGs) approved by the United Nations general assembly for the year 2030 highlight the importance of reducing food insecurity. It has been observed that contamination with heavy metals in farming soils has increased over the past ten years. This has been ascribed to complexity and a rise in a number of anthropogenic activities, including mechanization, excessive industrialization, and the usage of chemicals (Ashraf et al. 2019; Suman et al. 2018). Heavy metal contamination of agricultural soils is a serious environmental issue and a danger to agricultural output due to their biological half-lives, non-biodegradable nature, toxicity, persistence, and biological accumulation in the food chain (Lü et al. 2018).

It has been established that the levels of metals in food derived from contaminated soil surpass those permitted by law, potentially posing health risks and carcinogenicity. It can result in severe diseases of the liver, lung, nervous system, and immune system as well as bone fractures and malformations, cardiovascular problems, dysfunctional kidneys, hypertension, and other significant diseases of those systems (El-Kady and Abdel-Wahhab 2018). Additionally, consumption of contaminated water and shellfish has been linked to the presence of some xenobiotic heavy metal-based complex compounds (Anani and Olomukoro 2018). These complexes cause the death of both land and aquatic fauna and vegetation when their level of accumulation exceeds their capacity for absorption.

13.7 Various Techniques for Treatment of HMs Contaminated Soils

Consequently, it is crucial to implement cutting-edge and site-specific remediation technologies that can efficiently and securely clean up heavy metal-polluted soils (Ok et al. 2020). Various soil remediation methods have been used over the past few decades (Khan et al. 2015). These techniques concentrate on lowering soil heavy metal maximum and/or bioavailable concentrations and their potential processes in the food supply chain (Ok et al. 2020).

Different chemical and biological techniques and approaches are generally used to effectively remove HMs from soil (Fig. 13.1). According to a study, there are two categories into which soil remediation methods can be divided: (a) ex situ remediation, which entails excavating contaminated soil and treating pollutants afterwards; and (b) in situ remediation, that entails treating the pollutant-target on-site (Li et al. 2019). Furthermore, specific microorganism species are capable of performing the remediation. In contrast, in situ remediation may provide some technological, financial, and environmental benefits (Gholizadeh and Hu 2021). The most effective method must be chosen based on the characteristics of the soil, but it is also important to consider the HM concentration and the intended use of the contaminated soil (Ali et al. 2019).

For the removal of heavy metals from soils that are contaminated, a number of remediation methods have been used, including leaching, adsorption, absorption, electrokinetic remediation, landfilling, and vitrification (Ren et al. 2023a, b). These traditional techniques for cleaning up the environment have a number of drawbacks, including incomplete removal, high energy requirements, the production of a lot

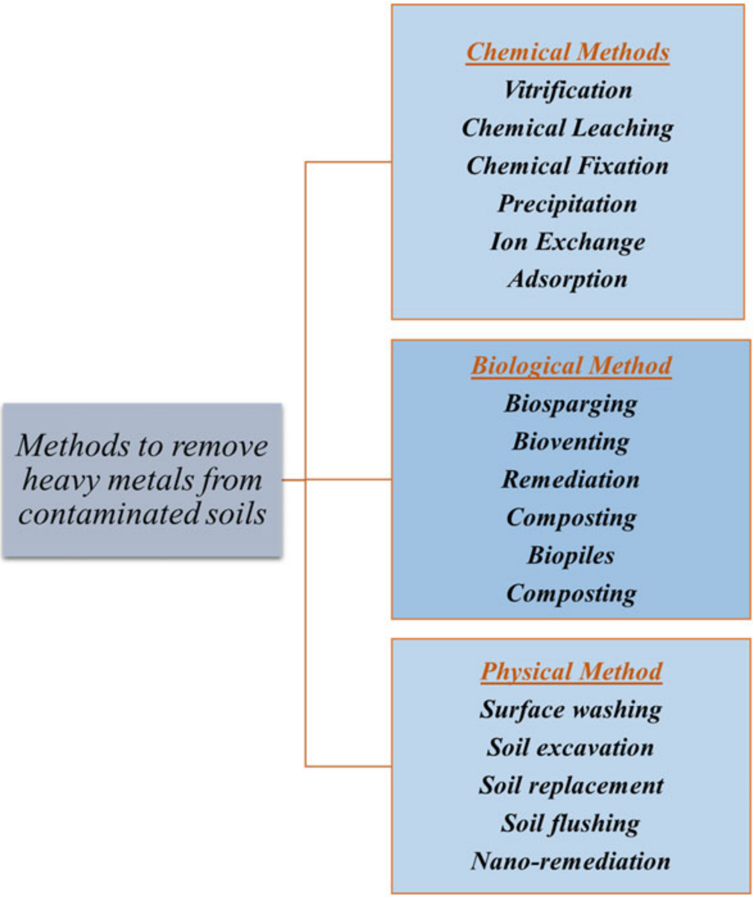

Fig. 13.1 Various techniques to treat heavy metals contaminated soil

of toxic sludge, being restricted to a limited region, and being expensive (Zamora-Ledezma et al. 2021). A traditional physical remediation method can cost between 60 and 90 percent of the total expense of reclamation (Maiti 2012). These techniques are not suitable for use on a broad scale due to their high energy and chemical specifications, as well as their time and cost constraints. These conventional methods, collectively known as "pump and treat" and "dig and dump" techniques, are all confined to limited areas and have drawbacks. By destroying the essential component of soils, these techniques can also disturb the soil's original microflora and result in permanent changes to soil properties. Additionally, the use of chemical technologies can result in secondary pollution issues, which will result in the production of a lot of sludge and raise the expense of sludge management (Awa and Hadibarata 2020).

13.8 Current Trend of HMs Remediation Techniques

Soil remediation is crucial to prevent adverse impacts, lower the probability of toxic metals harming the environment, and assure a healthy environment for future generations (Cristaldi et al. 2017). The heavy metal-contaminated soil is cleaned up using a variety of methods, including soil replacement, thermal desorption, chemical leaching, and electrokinetic remediation (Table 13.1).

Table 13.1 Various techniques to treat heavy metals contaminated soil

Technique	Principles	Pollutant	References
Natural attenuation	Reducing or preventing pollution at contaminated sites by using organic techniques	Zn, Cu	Agnello et al. (2016)
Thermal desorption	Making pollutants more instable with heat or high temperature, and afterwards eliminating them from the soil aggregate	Hg, Cu	Back et al. (2020)
Electrokinetic	Utlising electric potential to remove dirt contamination from straight electric current	Mn, Pb, Cu, Cr	Tang et al. (2017)
Soil flushing	The process of dissolving contaminants in soil with an aqueous solution	Pb, Cu	Lee et al. (2011)
Soil washing	A procedure for scrubbing soil, cleaning it with liquid or a chemical additive, and splitting the clean soil from the contaminants and washwater	Cd	Mu'azu et al. (2018)
Vitrification	A process that involves electrically heating contaminated soil until inert glass forms	Zr, Pb	Dellisanti et al. (2009)
Phytoremediation	An approach that uses living plants to remove hazardous pollutants from water, air and soil	Cu, Ni, Pb, Cr, Zn	Doni et al. (2015)
Incineration	Application of combustion to waste products with contaminants	Cd, Pb	Atanes et al. (2019)
Solidification	When contaminants interact with additives, a process occurs whereby the contaminants become immobile	Cd, Zn	Xia et al. (2019)
Rhizoremediation	A procedure wherein microorganisms in the rhizosphere decompose soil toxins	Cu, Cr	Ontanon et al. (2014)
Oxidation	By means of chemical oxidants to oxidise and degrade organic contaminants in the subsoil of the soil	Cr, Zn, Cd	Guo and Zhou (2020)
Bioaugmentation	Using additional bacterial populations to speed up the bacterial decay of a soil pollutant	Zn, Pb	Sprocati et al. (2012)

13.9 Phytoremediation

The Latin term "remedium," which means to correct or remove, and the Greek word "Phyto," which means plants, were combined to form the word phytoremediation. Using specific plant species referred to as hyperaccumulators, phytoremediation is an in-situ remediation method that removes heavy metals from the soil and thereby reduces their mobility (Chandra et al. 2023).

For the restoration of contaminated soil, different physical and chemical methodologies were rejected by scientific communities due to the several limitations like strict labor work, extremely high prices required for treatment and maintenance and certain physico-chemical properties of soil that can make soil harsh for further plant growth (Sheoran et al. 2011). Due to the severe increase in soil pollution and disturbance in food chain over the past few years, scientists were in search of introducing cleaner and eco-friendly method which can help in the extraction of non- biodegradable heavy metals from the polluted soil (Wuana and Okieimen 2011; Gogoi et al. 2021). One of the best alternatives to chemical and physical methods for the heavy metals' removal from contaminated soil was the development of a technique named bioremediation. It included the immobilization or removal of certain contaminants from soil using natural and organic systems (Lamine and Saunders 2022).

Phytoremediation, an environmental friendly and comparatively cheaper technology was introduced during the last two decades in which plants and associated soil microbial organisms that were genetically modified used to extract contaminants like heavy metals and convert them into less harmful metabolites (Bolan et al. 2014; Mahar et al. 2016). This efficient technology is not only suitable for the extraction of heavy metals but for pollutants like polychlorinated biphenyls, pesticides, radionuclides and organic contaminants as well (Lone et al. 2008; Vithanage et al. 2012). Chaney (1983) was the scientist who brought the idea of phytoremediation and his concept was appreciated and accepted globally because of its certain benefits (Ali et al. 2012).

In-addition, this technique has received special attention due to its feasible nature. During an in-situ phytoremediation, simply plants and sun along with some soil microbes are required to treat heavy metals. Likewise, very less labor force, machinery and cost further makes this method superior and less toxic over other expensive conventional practices (Burges et al. 2017; Yadav et al. 2018). The main objectives of phytoremediation are as follows:

- Utilization of efficient plants (e.g., poplar, willow etc.) in such a way that not only used for metal extraction but also aids in the production of energy (Abhilash et al. 2012).
- Secondly, phytoremediation significantly works to improve the soil quality slowly by making the land sturdier for good crop production (Vangronsveld et al. 2009; Ali et al. 2012).
- Also, this cleaner technology provides the best cost-effective alternative as compared to other physico-chemical methods (Sarma 2011).

13.10 Mechanisms of Phytoremediation

Phytoextraction, Phytostabilization, Phytodegradation, Phytodesalination, Rhizofiltration, Phytodegradation, and Phytoevaporation are some of the processes of phytoremediation (Table 13.2). However, a number of factors, including the plant species, the characteristics of the medium, the bioavailability of the metal, and the incorporation of chelating agents, may impact these mechanisms (Awa and Hadibarata 2020).

13.11 Biochar Assisted Phytoremediation

Since the heavy metals are toxic to plants, the success of phytoremediation relies on the growth of the plant as well as its ability to absorb metal contaminants. A favorable soil additive can be used to promote plant development as well as for soil remediation in order to get around these problems (Rojjanateeranaj et al. 2017). A method that shows potential for cleaning up soil contaminated with heavy metals is biochar-assisted phytoremediation. In the absence of oxygen, organic matter is heated to create biochar, a carbon-rich substance that has been shown to increase soil fertility, structure, and ability to hold water. By lowering the bioavailability of heavy metals and promoting plant development when incorporated into plants, biochar can help with the remediation of soil that has been contaminated by heavy metals (Moore et al. 2018; Pandey et al. 2020).

13.12 Characteristics of Biochar

According to reports, biochar is very efficient at adsorbing a variety of organic compounds, both natural and man-made. Given its exceptionally aromatic nature, a large surface area, micropore volume, and numerous amounts of polar functional groups, biochar has been shown in multiple previous studies to be efficient in the uptake of a variety of organic chemicals, including pesticides, PAHs, and emerging contaminants like steroid hormones (Kookana et al. 2011).

The porous structure, high retention of water, variety of functional groups, excellent cation-exchange capacity, and a broad surface area are some of the distinguishing characteristics of biochar. The sort of feedstock materials and the degree of pyrolysis have the greatest influence on these characteristics (Simiele et al. 2020; Tu et al. 2020).

When using biochar as an amendment to remediate heavy metal-contaminated soils, one should take into account the types of heavy metals present as well as the temperature at which the biochar is produced. This is because the characteristics

Table 13.2 Techniques of phytoremediation

Strategies of phytoremediation	Description	References
Phytovolatilization	It is based on the mechanism in which pollutants are taken up from plants and converted into volatile form so they can be released into the atmosphere	Padmavathiamma and Li (2007)
Phytostabilization	This technique further aids in the prevention of contaminants to make their way in the groundwater and food chain. It is considered as one of the good methods that help in the stabilization of toxic pollutants having great potential to cause damage	Wuana and Okieimen (2011)
Phytoextraction	In this method, removal of certain pollutants takes place from polluted water, soil or sediments. Efficacy of removal depends on multiple factors of plants to be used. For example; they should have an ability to translocate heavy metals, best rate of growth, high tolerance rate against heavy metal accumulation etc. Moreover, utilization of hyperaccumulator plants further helps in the production of very less biomass which is easy to handle	Chaney et al. (1997)
Phytodegradation	In this technique, particularly organic pollutants are degraded by using enzymes instead of microorganisms that are usually present in rhizosphere. This method is however, not suitable for non-biodegradable pollutants	
Phytodesalination	For the better removal of salts from the soils that are heavily affected by salt accumulation, phytodesalination is the most preferred technique. The use of halophytic plants instead of glycophytic plants is noticed to give better results in order to deal with toxic heavy metals present in polluted soil. By the use of this technique, a great decrease in salinity was observed and that ultimately helped in the better growth of plants	Zorrig et al. (2012)
Phytofiltration	Different forms of phytofiltration such as caulofiltrartion (in which shoots of plants are used), rhizofiltration and blastofiltration are involved for the removal of contaminants like heavy metals from polluted water bodies	

of the biochar are dependent on the pyrolysis conditions, such as the highest treatment temperature, moisture content of the feedstock, residence time, and the type of feedstock used (Zhang et al. 2013).

In order to create biochar, a variety of organic wastes and materials have been used, such as raw pine chips, paper-mill waste (Table 13.3), plant tissue, peanut hulls and pecan shells, pine chips and poultry litters, forage plant biomass, citrus wood, bunches of empty fruits, cotton seed hulls, rubber wood sawdust, sewage biosolids, rice husks (Zhang et al. 2013).

Table 13.3 Influence of biochar application on heavy metals bioavailability in soil

Feedstock	Temperature	Contaminant	Effect	References
Eucalyptus	560 °C	Zn, Cu	Reduced As, Cu, Ni levels in maize seedlings	Namgay et al. (2010)
Cotton stalks	400 °C	Cd	Adsorption or co-precipitation can reduce the solubility of Cd and Zn in soil	Zhou et al. (2008)
Orchard prune residue	500 °C	Pb, Ni, Cr, Cd	Cd shows the greatest decrease in bioavailability, with Pb and Zn also significantly reduced; however, pH and Cation exchange capacity(CEC), and water-holding capacity all increased	Fellet et al. (2011)
Green waste & chicken manure	500 °C	Pb, Cu	Cd and Pb deposits are significantly reduced by using Indian mustard plant	Park et al. (2011)
Hardwood	450 °C	As	Considerable As reduction in Miscanthus leaves	Hartley et al. (2009)
Rice Straw	–	Cd, Cu	Significant decrease in Cu, Cd and lead concentrations in polluted soils; detection of biochar functional groups with high Cu adsorption affinity	Jiang et al. (2012)
Oak Wood	450 °C	Pb, Cu	Bioaccessibility is decreased by 12.5%, and bioavailability is decreased by 75.8%	Ahmad et al. (2012)
Sewage sludge	450 °C	Cu, Ni, Zn	Significant decrease in the plant availability of the metals under investigation	Méndez et al. (2012)

13.13 Applications of Biochar Assisted Phytoremediation

According to Ippolito et al. (2012), biochar can enhance the quality of contaminated soil, stabilise heavy metals there, and significantly lower crop exposure to heavy metals. Thus, the use of biochar could possibly offer an innovative approach for the clearing-out of heavy metal-contaminated soils.

1. Reduce heavy metal bioavailability: Biochar has been demonstrated to lessen the solubility of heavy metals by adsorbing the metals to its surface, leaving them less absorbable by plants. As a result, there is less chance of toxicity from heavy metals in vegetation, animals, and people (Ghosh and Maiti 2021).
2. Enhance plant growth: By offering a source of nutrients along with improving soil structure, biochar increases soil fertility and encourages plant development. This is crucial for phytoremediation because strong plants can absorb and metabolise heavy metals more effectively, which allows them to eliminate more of them from the soil (Gholami et al. 2020).
3. Improve soil quality: By raising soil pH, lowering compaction, and enhancing water-holding ability, biochar can enhance soil quality. This encourages plant development and can lessen the likelihood of soil erosion (Gong et al. 2019a, b).
4. Increase carbon sequestration: A carbon-rich substance called biochar can be employed in order to sequester carbon in the earth, thereby reducing climate change. We can remediate heavy metal-contaminated soil using biochar-assisted phytoremediation, and we can also capture carbon in the process (Abbas et al. 2020).

13.14 Rice Husk and Biochar Assisted Phytoremediation

A heavy metal like lead due to its accumulation in plants, particularly when plant roots uptake it, can cause chaos on a large scale. The effect of lead on the health of plants whether directly or indirectly results in the chlorosis of leaf, lesser or no growth, imbalance in the nutrient uptake, improper functionality of enzymes etc. (Hou et al. 2018; Hovmand et al. 2009). Moreover, the toxic level of Pb even triggers the formation of reactive oxygen species (ROS). These reactive species in return reacts with cell organelles, nucleic acids, chloroplast etc. and become a source of damage to plants depending upon their time of exposure (Kumar and Prasad 2018; Ashraf et al. 2015). Despite of various conventional techniques like electrokinetic remediation, ion exchange, vitrification, reverse osmosis etc. metal stabilization is considered as the most useful and environmental friendly technique. This economically stable technique not only helps in dealing with toxic heavy metals but also gives extra stability to soil which ultimately aids in giving better yield (Zama et al. 2018; Ye et al. 2019). Biochar, on the other hand, is gaining much attention due to its unique carbon-rich properties. Particularly, the ability of carbon sequestration makes biochar a rich source for certain benefits like soil stability, less or no greenhouse gas emissions, better nutrient holding capacity etc. (Jefferey et al. 2017; Mohan et al. 2018). Moreover, according to an experiment, leaching loss by lead was reduced to a significant level by using biochar made up of pig manure in organic soils with low carbon rate (Mehmood et al. 2018; Qin et al. 2018). Similarly, another research claimed that a rice plant was used in which mobility of lead was reduced by using wheat straw biochar (Bian et al. 2014). Utilization of biochar along with rice husk ash (RHA), showed great results regarding the soil health and its interaction with metals (Zama et al. 2018). RHA is obtained when rice husk is burned and it is considered as a very valuable by-product from agricultural point of view. It holds the special attention due to its major constituents i.e. upto 50% cellulose, 20% of hydrated silica and lignin that consists of about 25–30% (Kiran and Prasad 2019). Certain properties of rich husk ash like large surface area, light in weight, extremely porous in nature make it an excellent adsorbent to deal with the mobility of deadly metals in the polluted soils (Bhattacharyya and Gupta 2008). In addition, presence of functional groups like phosphate, amino, carboxyl, sulphydryl, phenol and amide assists biosorbents to form complexes with heavy metals and kick them out of the contaminated soils (Singh et al. 2019).

However, during a research, consumption of plant with a metal stabilization technique was tested and for that purpose, a plant species named *Ricinus communis L.,* was used. This plant was selected particularly due to its consumption as a biofuel substrate, exceptional adaptability, good productivity of biomass and above all resistive nature towards different stresses whether biotic or abiotic (Bauddh et al. 2015; Kumar and Prasad 2018). The main purpose of this study was to check the ability of biochar and rice husk that was added as an amendment in *R.communis* to manage the toxicity and mobility of lead in soil (Kiran and Prasad 2019). The experiment was carried out for about 60 days. The results showed that by the addition of rice husk biochar in R.communis, a significant decrease in the lead concentration was observed. Lead was removed by around 80% through shoots, roots and leaves of selected plant (Kiran and Prasad 2019).

13.15 Tea Waste Derived Biochar Assisted Phytoremediation for Cd Removal

Cadmium, another toxic heavy metal became successful in making its way in the river sediments where there is a high risk of its absorption by aquatic plants. The bioaccumulation may result in the destruction of food chain (Huang et al. 2018). Therefore, an immediate economically feasible and environmentally stable technique was required to cope up with this serious issue.

A group of researchers decided to utilize plants along with the biochar in order to check their combined effect to remove cadmium. Biochar, as mentioned earlier has been a great alternative to certain physicochemical techniques for the past few years.

The carbonaceous material helps in improving the microbial activity in soil and also plays an important role in refining phytoremediation (Nie et al. 2018).

However, tea waste derived biochar at different concentrations was used to facilitate the process of phytoremediation in order to get the cadmium out of the river sediments. River sediments on the other hand, serve as a major sink for heavy metal accumulation (Xue et al. 2018). For the experimental purpose, ramie seedlings were selected. Different concentrations of tea waste were added to the sediments contaminated with cadmium and ramie seedlings were cultivated over that area. Results showed that tea waste derived biochar at specific concentrations i.e.100, 500 and 1000 mgkg^{-1}, showed greater results by converting the cadmium into less toxic form. Moreover, this conversion also helped in the access of cadmium in cell wall and other soluble parts of the respective cultivated plant. This in return helped in the translocation and accumulation of cadmium in the ramie seedlings. In- addition, this biochar also aided in the reduction of oxidative stresses in ramie seedlings and enhanced the function of different enzymes like phosphate, urease etc. to lower down the level of cadmium in the contaminated soil. The conclusion showed that tea waste derived biochar was proved to be very beneficial in the cadmium removal even at low concentrations (Gong et al. 2019a, b).

13.16 Biochar and Compost Supported Phytoremediation of *Moringa Oliefera*

Similar to the above mentioned experiments, another biochar assisted phytoremediation was performed by using *Moringa oliefera* in order to check the potential of this plant towards lead toxicity (Ogundiran et al. 2018). Lead noxiousness in plants has produced certain amount of lethal diseases. According to a research, the level of lead upto 900 mg/kg can certainly results in the extreme ecological risk to microbes present in soil (Zeng et al. 2007). Due to its very less negative environmental impact and sustainable nature, phytoremediation is gaining much recognition. The translocation of contaminants like heavy metals from roots to shoots is very useful for the soils that are contaminated with different pollutants (do Nascimento et al. 2006; Doumett et al. 2008). Moreover, specialized plants used for this purpose are termed as hyperaccumulator plants (Wong 2003).

During the experimentation, rice husk biochar and groundnut shell biochar were used along with sunflower-poultry manure compost. All the products were selected based on different physical parameters like particle size, cation exchange capacity, availability of macronutrients etc. Before their utilization in the experiment, the seeds of overnight soaked M. Oliefera were subjected to two weeks incubation period and then transplanted in the soil. Both of the biochars were individually applied in a certain ratio and faced the incubation period of two weeks into the soil. After that, for about two weeks, application of Moringa Oliefera was done in the soil. Certain physical properties of plants like number of leaves, growth of stem, plant height was observed for upto 8 weeks. Moreover, lead concentration after 8 weeks was noticed to be about 2100 mg/kg in the roots and shoots of the respective plant. This resulted concentration showed the ability of M. Oliefera to deal with lead toxicity. Furthermore, addition of compost also improved the metal extraction capability of roots and shoots of M. Oliefera. Hence for soil that is particularly contaminated with lead, the combination of biochar, compost and M. Oliefera was proved to be best to get rid of lead contamination (Ogundiran et al. 2018).

13.17 Bamboo Biochar Assisted Phytoremediation

Willow (Salix spp.), a woody species that grows quickly and is resistant to metals, is an appropriate choice for phytoremediation. Salix also generates a lot of biomass, which can be used for energy generation and easy disposal. Salix also has a number genetic variations, rapid growth, a deep and extensive root system, the ability to sprout again after harvest, high levels of activity of antioxidant enzymes in the leaves, effective transpiration, and a high capacity for nutrient uptake (Cao et al. 2017).

Bamboo biochar (BBC) has a large specific area, abundant microporous and mesoporous structure, as well as high HM adsorption capacity (Ouyang et al. 2014), which suggests its tremendous potential as a soil amendment (Ouyang et al. 2014). Bamboo biochar (BBC) is a carbonaceous substance that contains a lot of organic matter and can significantly improve the soil organic matter (SOM).

The application of bamboo biochar could stimulate the roots to produce organic acids. According to reports, root exudate can accelerate the release of leftover metal and subsequently mobilize HMs in the rhizosphere (Lefevre et al. 2013). To increase the amount of dissolved organic matter (DOM) in soil, applied Bamboo biochar (BBC) can discharge DOM into the soil (Li et al., 2018). By forming soluble organometallic complexes with metals, the organic ligands in soil DOM can trigger HMs (Li et al. 2020). Overall, the BBC amendment can enhance the root environment of plants and encourage the action of soil enzymes (Kolton et al. 2011).

According to Batty and Dolan (2013), adding BBC could hasten the uptake of nutrients and water while improving the roots' capacity to assimilate Cd, Zn, and Cu from the rhizosphere. This would increase the absorption as well as accumulation of HMs in the plant. According to Habiba et al. (2015), adding BBC could improve plants' ability to interchange gases, which would subsequently boost the mobility of Cd, Zn, and Cu from the soil to the plant's above-ground tissues. Previous research (Salam et al. 2019) also indicated that the improvement of SOM, N, P and K by amendment, facilitating the development of plants and the accumulation of HMs (Cu, Zn, Cd and Pb).

13.18 Banana Peel Biochar Assisted Phytoremediation for Cd Removal

Heavy metal Cd is regarded as a non-essential element for vegetation. According to reports, Cd is harmful to plants, causing necrosis and a deficiency in the photosynthetic process. Chlorophyll, plant development, and phytobiomass are all negatively impacted by these unbalanced physiological processes.

The banana fruit is an extensively grown crop and is eaten all over in the globe. It is the second most widely cultivated fruit product worldwide. Peels from bananas are regarded as a refuse item of the banana industry. It is the most significant organic source of potassium, a crucial macronutrient for developing plants and healthy soil. Despite this, there is a lack of use for banana skin biochar, which has industrial uses (Shah et al. 2022). Banana peel waste and its biochar have been extensively used and acknowledged as a potent waste for the remediation of heavy metal-contaminated water in numerous studies as an absorbent to remove heavy metals from an aqueous system (Akpomie and Conradie 2020).

Banana skin biochar has also been linked to improvements in soil's biochemical characteristics and a decrease in greenhouse gas emissions (Sial et al. 2019). Banana peel disposal is also made possible by the use of banana peels as biochar in phytoremediation. To the best of our understanding, there haven't been any studies done yet on the use of banana peel biochar in phytoremediation of heavy metals (Shah et al. 2022).

In new research, the remediation of Cd-contaminated soil using B. Pilosa plant utilizes banana peel biochar as soil amendment. It was discovered that the physiological traits of the B. pilosa are differentially influenced by banana peel biochar (Root, shoot, dry biomass and chlorophyll). The banana skin biochar may have a beneficial impact on the enzymes urease, dehydrogenase, shoot length, and root length (Nigam et al. 2019).

Banana peels were utilized in this research to create biochar. Fresh banana leaves were washed in distilled water and dried at 80 °C until they reached a consistent weight to make biochar. The desiccated banana peels were ground up and pyrolyzed in an oxygen-restricted muffle furnace for two hours at 500 °C (Bashir et al. 2018). A 0.5 mm sieve was used to further grind and sieve the pyrolyzed product. The biochar was dried at 80 °C after being washed multiple times with distilled water, and it was then placed in a glass receptacle for later use. The pH, electrical conductivity, surface morphology, and functional groups on the surface of the produced biochar were used to characterize it.

It had been found that in treatments with both concentrations of Cd (5 mg/kg and 20 mg/kg), biochar applied at a greater application rate resulted in the maximum Cd uptake by a shoot. The highest Cd uptake in shoots was seen in treatments using the lowest Cd concentration (5 mg/kg) and the greatest biochar concentration (200 mg/kg), which were followed by treatments using no biochar and biochar at low concentrations (Shah et al. 2022).

The application of more biochar with Cd contamination, however, demonstrated greater Cd uptake and accumulation in the root and shoot. In order to increase phytoremediation of heavy metal-contaminated soil, it is proposed that the combination of banana peel biochar with heavy metal accumulator plants may be a viable option (Wang and Wang 2019).

13.19 Date Palm Magnetized Biochar Assisted Phytoremediation

The introduction and accumulation of different heavy metals in soil is facilitated by mining activities, which eventually results in serious environmental pollution (Table 13.4). Such contaminated soils might be restored through the use of different immobilising substances. As a result, date palm-derived biochars (BCs) (BCs: produced at 300 °C, 500 °C and 700 °C) and magnetized biochars (MBCs) were used in this research to stabilise heavy metals (Cd, Pb, Cu, and Zn) in mining contaminated soil (Rodriguez-Franco and Page-Dumroese 2021).

The waste from date palms was gathered, dried at 60 °C, cut into pieces measuring about 3–5 cm, ground, and separated using a sieve of 0.5 mm. The sieved components were pyrolyzed at temperatures of 300 °C, 500 °C, and 700 °C for 4 h to create non-magnetic BC. In the meantime, the sieved materials were treated with a solution of ferrous chloride and ferric sulphate and the pH was increased to 11 using NaOH to create magnetic biochar (MBCs). Following filtration separation, the materials were repeatedly rinsed in distilled water before being dried in an oven tuned to 60 °C (Alazzaz et al. 2023).

Non-magnetized BCs and MBCs both had distinctive surface characteristics that varied depending on the decomposition temperature. In general, BCs and MBCs produced at lesser temperatures for pyrolysis (BC-300 and MBC-300) had higher moisture contents and volatiles, whereas BCs and MBCs produced at 700 °C had higher ash and residual crabon contents as well as higher EC and pH. The probability for immobilizing soil-borne metals and reducing their concentration in shoots and plant uptake was increased in all of the synthesized BCs and magnetized BCs. The soil treated with magnetized BCs revealed the greatest reductions in soluble Cu (70%) and Zn (64%) concentrations, whereas Cd and Pb were found to be below detection limits (Alazzaz et al. 2023).

13.20 Conclusion

The major human-caused events that lead to the contamination of soil from heavy metals are mining, industrial processes, and agriculture. When fertilizers are used for agricultural purposes and gardening, heavy metals like Zn, Cd, Cu and Pb are

Table 13.4 Different biochar assisted phytoremediation methods to treat heavy metals

Type of biochar	Type of plant used	Treated heavy metal	Result	References
Rabbit manure waste	*Brassica Napus*	Co, Pb, Zn, As, Cr and Cu	Reduction of Cobalt by 32%, Lead 95% and Arsenic 98%	Gasco et al. (2019)
Pinewood	*Salix alba, S.purpurea* and *S.viminali*	As and lead	No significant decrease in arsenic but reduced the lead concentration by 70%	Lebrun et al. (2017)
Bamboo (*Bambusa vulgaris*)	*Brassica napus*	Cr, Ni, Pb, Zn, Cu, Cd	Reduce the concentration of Pb, Zn and Cu by 71%, 53% and 84% respectively	Munir et al. (2020)
Coconut and Hardwood	*Salix dasyclados*	Pb and As	Upto 78% removal of Lead	Lebrun et al. (2020)
Oak, Hornbeam and Beech	*Phaseolous vulgaris*	As and Pb	Removal of lead by 90% in soil pore water	Nandillon et al. (2019)
Corn con	*Jatropha curcas*	Cu, Pb, Zn and Cd	Decrease Cd by 70%, Pb by 53% and Zn by 41%	González-Chávez et al. (2017)
Sewage sludge and pruning trees	*Sarcocornia fruticosa*	Cd, Zn and Pb	Significant reduction of Pb, Zn in roots of plants	Álvarez et al. (2020)

released. It is possible to turn biochar assisted phytoremediation into a workable technology for cleaning up contaminated soils. Of course, biochar has the potential to lessen the bioavailability and effectiveness of both organic and heavy metal contaminants in soil. The effectiveness of remediating contaminated soils can be impacted by the extremely heterogeneous physicochemical properties of biochars made from various biomass materials and under various pyrolysis circumstances (such as temperatures). Hence biochar in combination with phytoremediation con be a potential option for treatment of heavy metals contaminates soils.

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Chapter 14
Impact of Changing Abiotic Environment on Photosynthetic Adaptation in Plants

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Abstract Plants rely on photosynthesis to convert light energy into chemical energy. However, their photosynthetic performance can be greatly affected by changes in the abiotic environment such as temperature, light intensity, and water availability. This draft summarizes the impact of changing abiotic conditions on photosynthetic adaptation in plants. Plants have developed various adaptive mechanisms to optimize their photosynthetic efficiency under different abiotic stresses. For example, under high light intensity, plants may regulate their photosynthetic apparatus by reducing the size of their light-harvesting antenna or increasing the activity of photorespiration. Similarly, under low water availability, plants can close their stomata to prevent water loss and reduce their photosynthetic activity, or activate molecular pathways to enhance drought tolerance. Understanding the molecular mechanisms underlying these adaptations is essential for developing strategies to improve crop productivity and sustainability under changing environmental conditions. Advances in molecular biology and biotechnology have provided new tools for identifying genes and proteins involved in photosynthetic adaptation in plants. These findings can be applied to develop crop varieties that are better adapted to different environmental conditions, such as drought, high temperatures, or high salinity. Despite the progress made in understanding the impact of changing abiotic environments on photosynthetic adaptation in plants, there are still many challenges to be addressed. The complex interactions between plants and their environment, as well as the potential effects of multiple stresses, require further investigation. In addition, there is a need to develop sustainable agricultural practices that can mitigate the negative impacts of climate change on crop productivity.

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_14

Keywords Abiotic stress · Photosynthesis · Drought · High-temperature · Salinity

14.1 Introduction

Water, carbon, light, and mineral fertilizers are the basic building blocks for plant growth. Abiotic stressors are environmental factors that dampen plant morphogenesis below optimal levels. Abiotic stressors, such as water deficiency, cold temperature, chilling, salt exposure, thermal stress, floods, and nutritional imbalances, as shown in Fig. 14.1, pose one of the most significant risks to the plant morphogenesis (Liu et al. 2022). The impact of abiotic stressors on plants can manifest in various ways. Over time, these stresses can influence the physiological, morphological, and biochemical functions of plants, resulting in alterations in processes such as photosynthesis, transpiration, stomatal conductance, root and shoot development, protein denaturation, and chlorophyll levels (Khalid et al. 2019). Abiotic stressful situations in plants are dynamic, challenging, elastic, and plastic (Skirycz and Inzé 2010; Cramer 2010). The way a plant responds to abiotic stress depends on the damaged organ or tissue. For instance, gene transcription expressions in plants roots vary significantly depending on the type of stress (Dinneny et al. 2008). The differentiation between short and long-term stress, along with its duration and degree of severity, influences the complexity of the reaction (Tattersall et al. 2007).

Besides the other environmental stresses, drought also has a severe impact on crops worldwide. Drought stress primarily affects grain filling and the reproductive stages. Drought-induced stomatal permeability decline has a protracted influence on plant's CO_2 absorption capacity. Yield and the growth of the plants are stunted due to the reduction of the photosynthesis process and the exchange of gases. Water deficits impede plant growth through two mechanisms: reduced H_2O absorption by sustaining cells and enzymatic alteration of the viscoelastic characteristics of the plant cell wall. This alternation can occur through oxidative reactions action on the plant's outer membrane enzymes (Skirycz and Inzé 2010). Water deficits impede plant growth through two mechanisms: reduced water absorption by plant cells and enzymatic alteration of the rheological characteristics of the plant cell wall. This alternation can occur through the action of reactive oxygen species on the plant's cell wall enzymes (Skirycz and Inzé 2010). Furthermore, as observed in the interaction between pectic acid and Ca^{2+}, when there isn't enough water, the structure of cellular membranes changes without the help of enzymes (Boyer 2009). Drought can have an impact on grain yield, depending on the growth stage, duration, and severity (Hummel et al. 2010). Drought-resistant cultivars and agricultural management practices can assist to mitigate the detrimental impacts of drought stress (Wahab et al. 2022).

Salinity is considered as the most prevalent damaging environmental stressor that severely reduces the quality and yield of plants all over the world. About 20% of the global total arable land is suffering from salt stress, and these salty regions are constantly expanding because of both anthropogenic and natural activity (Hasanuzzaman and Fujita 2022). The major morphological consequence of salt is noted to

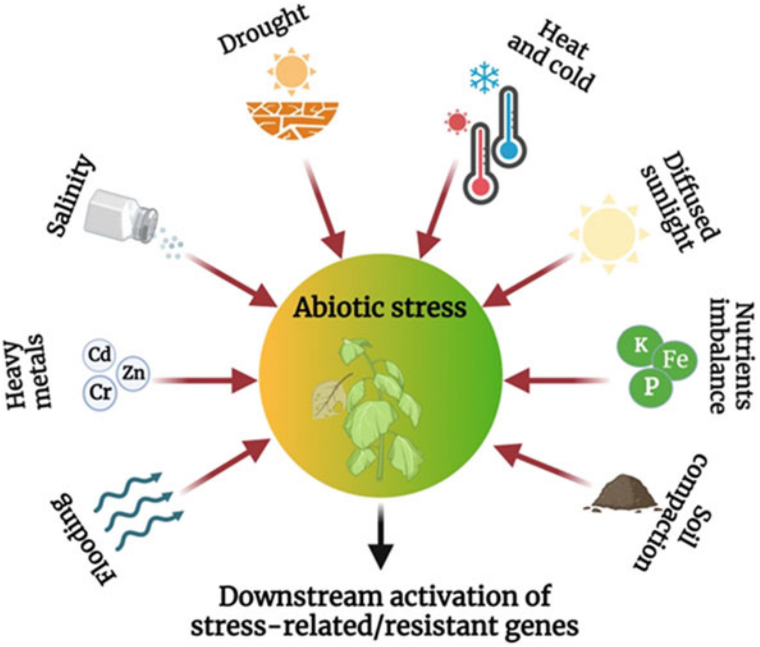

Fig. 14.1 Several kinds of abiotic stresses that can affect plant growth

be a decrease in growth. Numerous biochemical mechanisms within the plant are responsible for this phenomenon. It is believed that an excessive amount of salt slows down the absorption of water and inhibits development due to its osmotic impact. Salts can impede growth through specific ion toxicity, increased in osmotic pressure, or elevated alkalinity, all of which can affect cellular integrity and biochemical pathway processes (Mudgal et al. 2010).

Plants are susceptible to thermal stress when they absorb energy from the heat transfer by the high temperature causing the soil temperature to rise above from the air temperature. In such conditions, and the leaves of the plants struggle to dissipate the heat which comes from the solar radiations. As a result, the transpiration rate is low and frequently vulnerable to heat stress. Plants under heat stress experience various disruptions that alters the stability of membranes and proteins. This stress also disrupts photosynthesis and interferes with protein and nucleic acid metabolism (dos Santos et al. 2022). Nutrient imbalances in plants significantly impact plant behavior, such as plant sensitivity to abiotic stress, patterns of growth, and the mechanism of the antioxidants action. The constraints of the environment and the low availability of mineral nutrients cause a decline in crop productivity (Kumari et al. 2022).

A common route of toxicity for all these abiotic stimuli in plants is the production of ROS due to membrane instability and oxidative damage. Additionally, the activity of RUBISCO restriction causes a further reduction in plants' photosynthetic activity. Degradation of the enzymes affects the accumulation and biosynthesis of the pigments. Environmental factors, such as an increase in temperature (global warming), can disrupt the cellular homeostasis. Consequently, species vary significantly in their ability to adapt to these conditions (Sharma et al. 2020a, b, c). One of the rising ecological consequences associated with climate change is the problem of abiotic stress on plant morphogenesis. The challenges to agricultural production are worsened by the competition between the growing human population and the environment for resources (Pereira 2016). Due to the continued global climate degradation, pesticide use, and industrialization, abiotic pressures are getting more intense everywhere (Naing and Kim 2021).

Photosynthetic processes differ among C3, C4, and CAM plants because of the presence for nitrogen use efficiency, high water retention, and carbon concentration. C4 plants exhibit superior photosynthetic properties compared to both C3 and CAM plants. Under stressful conditions, C4 plants may allocate resources more effectively due to the higher water and nitrogen usage efficiency (Singh and Thakur 2018). Abiotic stressors influence plant mesophyll and stomatal conductance by regulating CO_2 concentrations at carboxylation sites (Li et al. 2022).

Plants frequently close their stomata in reaction to abiotic stressors. Stomatal guard cells can rapidly initiate closure when adverse conditions arise by sensing various environmental stress signals from both the interior as well as the exterior. Additionally, stomata hinder pathogen invasion by limiting their access to leaves. A phytohormone (ABA), well-known for its capacity to cause stomatal closure, is produced and mobilized during stress conditions (Agurla et al. 2018). Protein synthesis is inhibited, and protein folding and processing are increased as one of the initial biochemical feedback to abiotic stressors and the suppression of growth (Vincent et al. 2007; Liu and Howell 2010).

The need to raise crop productivity has increased significantly due to factors like a growing worldwide populace, declining agricultural land due to urban sprawl and soil erosion, and the cultivation of biofuel crops on agricultural land (Foley et al. 2011; Godfray et al. 2010). To fulfil the per capita calorie requirements, agricultural production is predicted to increase by 100–110% between 2005 and 2050. Projections are consistent with the rise in actual per capita revenue (Tilman et al. 2011). Due to the dangers posed by climate change, this trend is envisioned to worsen. Because of these observations, our mission to ensure food supply for all people on the planet without further harming our natural ecosystem faces a significant challenge.

14.2 Plant Response to Abiotic Stresses

14.2.1 Response at Cell Level

Under typical conditions, metabolic processes such as photosynthesis cause cells to create reactive oxygen species (ROS) (Foyer and Shigeoka 2011). For a variety of physiochemical processes, including plant morphogenesis and reactions to biological and environmental issues, ROS serves as a signalling molecule when it is present in minute amounts (Baxter et al. 2014; Tripathy and Oelmüller 2012). Yet stressors like salt, heat, bright light, cold, and heavy metals can cause more ROS to develop (Singh et al. 2015; Pandey et al. 2015). To scavenge overabundance of ROS, plants contain an antioxidant defence mechanism with both non-enzymatic and enzymatic constituents (Abogadallah 2010). The non-enzymatic component consists of ascorbic acid, tocopherol, glutathione, phenolics, carotenoids, flavonoids, and other substances, whereas the enzymatic component contains SOD, peroxidase, catalase, glutathione reductase, and other enzymes (Gill and Tuteja 2010; Kasote et al. 2015; Sharma et al. 2012). Nonetheless, oxidative stress can happen and cause DNA, lipid, and protein damage that results in cell death if the rate of reactive oxygen species formation outpaces the plant's detoxification capacity (Tripathy and Oelmüller 2012).

14.2.1.1 Phytohormones Response

Heavy metal concentrations can inhibit or damage important enzymes and proteins, as well as disrupt the replacement of vital metallic ions in biological molecules. This disruption affects the cellular membranes permeability and can lead to changes in essential plant mechanisms including respiration, photosynthesis, and maintaining internal stability. When plants are exposed to natural stressors such as hazardous heavy metals, they produce reactive oxygen species, which can interfere with the transmission of hormonal signals. Hormones like abscisic acid, auxin, cytokinins, ethylene, and others listed in Table 14.1, are crucial for managing stress and assist in supplying essential enzymes for cellular defense, as well as preserving polypeptides and fatty acids.

Changes in Abscisic acid (ABA) levels serves as the initial indicators of a plant's response to diverse environmental stressors like dry spell, salt, and high temperatures (Leng et al. 2013). According to Bücker-Neto et al. (2017), ABA plays an important part in the plant's response to different situations by activating a variety of signalling pathways. A regulatory sequence in guard cells is activated by elevated abscisic acid levels, and this causes guard cells to outflow K^+ ions, which lowers turgidity and finally causes stomata to close (Lim et al. 2015; Salazar et al. 2015). Researchers hope to improve human health by encouraging the translation of several genes that generate enzymes that aid in the generation of protective peptides such as dehydrins, osmoprotectants, and delayed embryonic widely available polypeptides, ABA aids plant tolerance to abiotic stress (Sah et al. 2016; Dar et al. 2017). Elevated ABA concentration in leaves affects tissue turgor, cell wall elasticity, and the hydrodynamic distribution of roots. Moreover, it reduces the levels of photosynthetic enzymes and leads to carbohydrate buildup, both of which have a negative feedback loop effect on photosynthesis (Vishwakarma et al. 2017).

Ethylene, a second hormone that plants generate, serves as a signalling molecule to aid in their capacity to react to a wide range of difficult circumstances. The precise nature of ethylene's function in controlling environmental stresses is unknown and depends on the circumstance (Tao et al. 2015; Kazan 2015). Research has revealed

Table 14.1 Role of plant hormones in mitigating abiotic stress

Plant/crop	Nature of stress	Hormonal response	Tolerance level	References
Koelreuteria paniculata	Heavy metal (Cd)	Amount of Auxin, Gibberellic Acid, jasmonic Acid and ZT decreases; Abscisic Acid increases	150–250 µM	Yang et al. (2018a, b)
Soybean (*Glycine max* L.)	Heavy metal (Cd)	Upsurge in Abscisic Acid, Abscisic acid glucose ester and Dihydrophaseic acid; reduction in Jasmonic acid observed	40 mM	Pérez Chaca et al. (2014)
Wheat Seedlings (T. aestivum cv. L.)	Heavy metal (Zn, Pb & Cd)	Pb lesser the amount of free proline in seedlings; Increased ABA synthesis when treated with a high concentration of Zn; with Pb concentration, Abscisic acid & Gibberellic acid increase the phenolic soluble compound responsible for decreasing the heavy metal toxicity	100–300 (µM)	Ergun and Oncel (2012)
Rice	Heavy metal (Cd)	Cd-stressed seedlings were treated with 0.3 mM $MnSO_4$ resulting in the recovery of Cd-induced stress response in plants	0.3 mM	Rahman et al. (2016)
Rice	Heavy metal (Cd) contaminated soil	Exogenously applied Auxin precursor L-TRP decreases Cd uptake into grains and increases Cd uptake in rice straws	30 mg/kg	Farooq et al. (2015)
Arabidopsis thaliana	Heavy metal (Cd)	Brassinosteroids (BR) showed similarity to Cd; a biosynthesis inhibitor i.e., Brz display the same results as BR; application of eBL (synthetic brassinosteroid) to Cd-induced plants inhibits root growth	50 µM & 200 µM	Villiers et al. (2012)
Tomato (*S. lycopersicum* L.)	Heavy metal (Cd)	High-level Cd stress was observed in wild-type strain than the ethylene-insensitive non-riped and auxin-insensitive diageotropic	1 mM	Alves et al. (2017)

(continued)

Table 14.1 (continued)

Plant/crop	Nature of stress	Hormonal response	Tolerance level	References
Barley seeds	Heavy metal (Cd)	Inhibition of coleoptile elongation decreased after kinetin and gibberellic acid application on Cd-stressed plants	0.5–10.0 mM	Munzuroglu and Zengin (2006)
Maize (*Zea mays* L.)	Heavy metal (Cd)	Maize treated with Auxin neutralizes the toxicity induced by Cd below the 100 μM	10–1000 μM	Karcz and Kurtyka (2007)
Maize *(Zea mays L.*)	Heavy metal (Cd)	Salicylic acid (500 μM) treated maize overcome the growth inhibition caused by the Cd	25 mM	Krantev et al. (2006)
Maize (*Zea mays* L.)	Heavy metal (Cd)	Cd-treated plants reduced photosynthesis i.e., inhibit CO_2 fixation in plants; reduction in Cd-induced toxicity observed in plants pretreated with Salicylic Acid	10–25 μM	Krantev et al. (2008)
Maize (*Zea mays* L.)	Heavy metal (Cd)	Maize plants treated with Salicylic acid and its salt i.e., Sodium Salicylate; both help in alleviating the Cd-induced toxicity but in different ways; the acidic form reduced Cd accumulation in roots while its salt form lessens the Cd accumulation in leaves as well as in roots by increasing the amount of phytochelatin		Gondor et al. (2016)
Barley	Heavy metal (Cd)	A partial decrease in Cd-induced toxicity was observed in Salicylic acid treated maize at germination level but didn’t affect the Cd concentration in roots	25–100 μM)	Kalai et al. (2016)

(continued)

Table 14.1 (continued)

Plant/crop	Nature of stress	Hormonal response	Tolerance level	References
Barley (*Hordeum vulgare*)	Heavy metal (Cd)	Cd increases the activity of antioxidant enzymes in Barley seedlings which are controlled by Salicylic acid through detoxification; leaves treated with Salicylic acid demonstrate a high level of tolerance towards Cd	25 μm	Metwally et al. (2003)
Fenugreek (*Trigonella foenum-graecum*)	Heavy metal (Cd)	Salicylic acid-treated seeds display enhanced germination and increased shoot and root length by ameliorating the negative effect of Cd	30 mg/L	Espanany et al. (2015)

that for plants to properly adapt to shifting external factors, ethylene production needs to be carefully regulated (Kazan 2015; Tao et al. 2015). In the early stages of adaptation, ethylene is thought to help plants deal with salt stress. However, excessively highlevels of ethylene may impede plant growth and development even after acclimation, which can be detrimental to plant survival (Tao et al. 2015). The presence of ethylene and the way it interacts with other plant hormones may affect how plants respond to stress and how they operate as a whole (Iqbal et al. 2017). Addition, two essential plant hormones, salicylic acid and jasmonates, play important functions in plant resistance to abiotic stressors (Kazan 2015).

14.2.1.2 Responses by Amino Acids

The non-essential proteinogenic amino acid proline is accumulated by plants as part of a defensive strategy against abiotic stresses such as salinity, dry spell, and heavy metals (Krasensky and Jonak 2012; Hossain and Dietz 2016). It's worth noting that thermal stress produces more heat-sensitive cultivars than proline buildup in plants like tobacco and thaliana (Krasensky and Jonak 2012). On the other hand, proline accumulation was seen in peach tree shoots that had previously been exposed to cold circumstances (Shin et al. 2016). In addition to stabilizing proteins and membranes, proline also serves as an osmolyte, a molecular activator, a redox buffer, and a ROS remover to mitigate cell damage caused by stress (Krasensky and Jonak 2012; Hossain and Dietz 2016). During the stress recovery period, proline acts as a nitrogen source (Gupta and Huang 2014). Proline boosts the production of photosynthates and antioxidant defense enzymes, promoting salt tolerance in a wide range of plants, including tobacco and olive (Gupta and Huang 2014). The cell's redox equilibrium is preserved by employing the glutamate pathway to synthesize proline from NADPH, which requires two moles of reduced nicotinamide adenine dinucleotide phosphate to generate one mole of 2-pyrrolidinecarboxylic acid (Hossain and Dietz 2016). During salt stress, proline synthesis in plants promotes limitless carbon fixation and lowers photoinhibition and excessive reactive oxygen species generation (Hossain and Dietz 2016).

Plants rapidly amass the non-protein peptide aminobutyric acid in reaction to numerous external stresses such as cold, heat, dehydration, and salinity (Kinnersley and Turano 2000). The preservation of intracellular pH, electrolyte balance, and carbon–nitrogen equilibrium, and γ-Aminobutyric acid (GABA) metabolism are all closely related processes (Li et al. 2016; Krasensky and Jonak 2012). According to recent studies, GABA may lessen heat stress in plants by boosting photosynthetic process and elevating the actions of radical quenching enzymes (Li et al. 2016). In numerous plant signal transduction pathways, GABA has been discovered to act as a modulator of stress-induced stimuli (Bouche and Fromm 2004; Li et al. 2016; Yu et al. 2014).

14.2.1.3 Responses by Glycine Betaine

Plants produce an osmolyte termed as glycine betaine (GB) as a defence mechanism against challenging growing circumstances such as salt, desiccation, and ultra violet radiation (Ashraf and Foolad 2007). Many plant species, though, do not produce GB; tobacco and arabidopsis lack this substance, whereas barley and spinach create larger levels of GB in their chloroplasts (Fariduddin et al. 2013). By regulating osmotic pressure, stabilizing proteins and membranes, and lowering ROS, GB protects the PS-II system and preserves pigments, thereby contributing to the cell maintenance (Gupta and Huang 2014; Krasensky and Jonak 2012).

14.2.1.4 Responses of Polyamines

Small, positively charged molecules known as polyamines are found in all living organisms, including microbes, vegetation, and mammals (Liu et al. 2015). According to studies, the ability of a plant to withstand stress and polyamine concentration are related. Plants' polyamine levels rise when they are subjected to numerous stressors, such as excessive salt, heat, cold, heavy metals, and desiccation (Tiburcio et al. 2014). Polyamines have been linked to various aspects of plant morphogenesis, in addition to helping plants adapting to abiotic stress. They include fruit ripening, xylem differentiation, biofilm production, embryonic competence, pollen development, apoptosis, and signalling channels (Tiburcio et al. 2014; Tisi et al. 2011; Liu et al. 2015). The plant benefits from polyamines' critical role in preserving cell membrane stability, gene translation regulation that make osmoprotective solutes, decreasing the generation of ROS and achieving ion balance between Na^+ and Cl^- in diverse cell divisions (Gupta and Huang 2014). Spermidine, butane-1,4-diamine, and spermine are three of the most common polyamines identified in photosynthetic organisms (Krasensky and Jonak 2012).

14.2.1.5 Responses of Carbohydrates

Carbohydrates, a byproduct of photosynthesis, provide the main reservoir of energy for a wide range of biological functions. Disaccharides like sucrose and trehalose, oligosaccharides from the raffinose family, and fructans are the three main sugar types involved in how plants respond to stressed conditions (Keunen et al. 2013). To keep the turgor of the cell and stabilize membrane structures, these soluble sugars function as osmoprotectants and osmotic regulators (Gil et al. 2014). Because fructans readily dissolve in water and don't crystallize at very low temperatures, they are particularly helpful to plants under intermittently cold and dry conditions (Krasensky and Jonak 2012). For example, resurrection plants use sugar accumulation as a defense mechanism against circumstances brought on by total dehydration (Djilianov et al. 2011). While under water stress, fructans can also serve as a supply of hexose sugars, helping to keep membrane structure intact and assisting in osmotic adjustment (Krasensky and Jonak 2012). It is well known that fructans integrate into the head groups of the tonoplast to stabilise it under stressful conditions (Keunen et al. 2013) (Fig. 14.2).

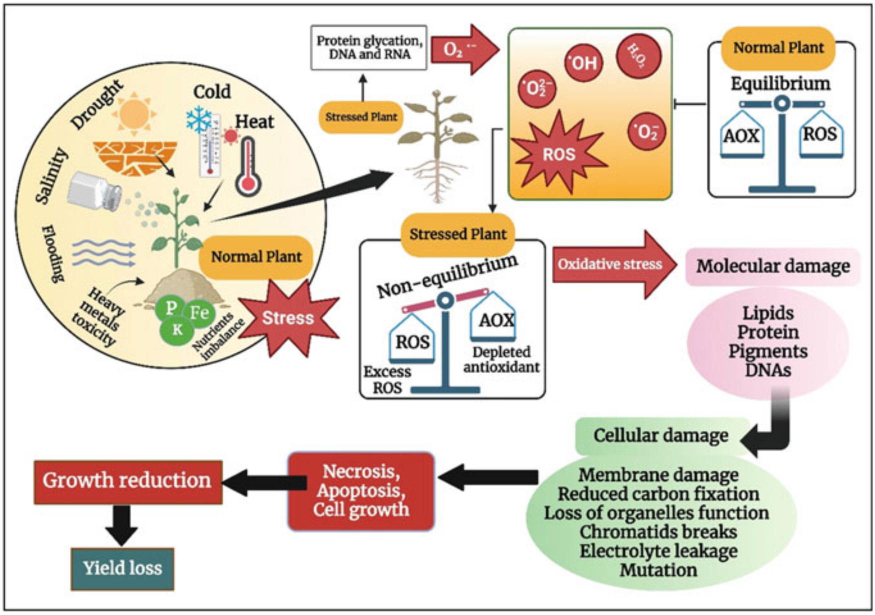

Fig. 14.2 Abiotic stress causes oxidative stress, with ROS, including $^1O_2$, $O_2^{\bullet-}$, H_2O_2, $OH^\bullet$, methylglyoxal, and antioxidants (AOX)

14.3 Factors Affecting Photosynthesis

Many abiotic stressors have a negative effect on many photosynthetic components, resulting in significantly lower yield and its components. Plants convert light into carbohydrates through a series of complex chemical reactions known as photosynthesis. The resulting carbohydrates are either directly or indirectly the primary energy source for heterotrophic species, including humans. An important factor in the growth and production of plants is the process called photosynthesis. Photosystems, the light-based NADPH and ATP synthesis processes, and the dark reactions for CO_2 assimilation (also known as the Calvin-Benson or C3 cycle) are all components of the plant photosynthetic apparatus. Carotenoids and chlorophyll a, b are plants' photosynthetic pigments (Blankenship 2008; Stewart et al. 2020).

Drought is a major environmental factor that limits photosynthesis and plant development, as well as productivity (Kannan and Kulandaivelu 2011; Rahbarian et al. 2011; Batra et al. 2014; Liu et al. 2016; Meng et al. 2016). Crop yield decreases because of decreased foliage growth, which lowers photosynthetic productivity (Kannan and Kulandaivelu 2011). A decrease in carbon dioxide diffusion by stomata and mesophyll cells is the main factor contributing to the decline in photosynthesis caused by dryness in plants. Plants constrict their stomata in response to drought to prevent water loss, which enhances their capacity to utilize water effectively and lower transpiration rates (Ashraf and Harris 2013).

Plants are distressed by two types of salinity stress: electrolyte instability and salt overload (Hossain and Dietz 2016). As discussed in the drought section, osmotic stress causes conditions similar to water scarcity and drought-induced responses, such as the closing of the stomata, a decline in carbon dioxide capture, excessive electron transport chain reduction, and photorespiration stimulation, which results in the production of ROS (Abogadallah 2010). Moreover, osmotic stress has been shown to accelerate the respiration rate of the electron transport chain, apoplastic diamine oxidase, and mitochondrial respiratory burst oxidase linked to the cell membrane (Rejeb et al. 2015; Hossain and Dietz 2016).

Light is a major energy supplier and is among the most critical external stressors for growing plants (Naoya et al. 2008). In general, an increase in sunlight luminosity is associated with an increase in net photosynthetic rate. Increased light levels, on the other hand, results in a decrease in the net photosynthesis rate (Hogewoning et al. 2010). Changes in the light spectrum greatly affects the parameters of leaf structure, form, and composition (Macedo et al. 2011). Vegetation foliage capture approximately 90% of blue or red radiation existing in visible range (Terashima et al. 2009). As a result, blue and red light has a major influence on plant development and metabolism. While the blue spectrum enlarges the epidermal cells and palisade mesophyll cells, the red spectrum narrows the porous tissues and abaxial face (Macedo et al. 2011). The strength of PAR plays an essential role in deciding photosynthesis efficiency. Higher plants use photosynthetic pigments in the PS-I and PS-II photosystems to capture photo-synthetically active radiation, which is a portion of sunlight with wavelengths ranging from 380 to 700 nm. Photo-synthetically active radiation levels that are either too high or too low have an adverse influence on the photosynthetic machinery (Wimalasekera 2019).

Heat stress is becoming an increasingly common issue that reduces agricultural production, primarily due to growing atmospheric CO_2 concentrations. Heat shock or heat stress are terms used to describe a temporary period when temperature increase by 10–15 °C over the ambient (Wahid et al. 2007). Vegetation growth and development are significantly impacted by transient or ongoing high temperatures, which limits productivity (Song et al. 2014). The amount of chlorophyll in leaves is similarly affected by heat stress. Heat-stressed leaves contain low quantities of chlorophyll (Mathur et al. 2014). High temperatures limit plant growth and development by limiting output, including leaf chlorophyll content (Song et al. 2014). Heat-stressed leaves were found to have low chlorophyll levels (Mathur et al. 2014).

One of the long-term effects of elevated CO_2 on plants is an increase in photosynthesis and carbon assimilation in foliage. Another important function of carbon dioxide content is to regulate stomatal opening and closing. Stomata that are open allow water to escape the foliage and carbon dioxide to enter the leaves for respiration. Plants regulate the amount of stomatal opening in order to maintain a high rate of photosynthesis activity while minimising water loss. Plants can maintain high photosynthesis rates while maintaining comparatively low stomatal permeability as CO_2 levels rise (Taub 2010). Although the growth of C3 species frequently accelerates photosynthesis at high CO_2 levels, this can also have a negative impact on Rubisco content and photosynthesis (Ainsworth and Long 2005; Leakey et al. 2009). C4 plants can adapt to low ambient CO_2 concentrations because they have a special anatomical feature called the Kranz architecture, which concentrates CO_2 inside the cells and lowers RuBPcase oxygenase activity, lowering photorespiration and increasing photosynthesis. As a result, unlike C3 plants, C4 plants do not benefit from rising atmospheric CO_2 concentrations (Shanker et al. 2022). The C4 plants do not benefit from rising atmospheric CO_2 concentrations (Shanker et al. 2022).

Another environmental stressor is flooding. Flood-prone areas may be caused by natural occurrences like rainfall, snowmelt, or tidal floods, as well as human activity like building tidal reservoirs and hydroelectric generating plants (Liu et al. 2013). Flood stress alters the natural growing settings and circumstances in which plants are located, which substantially impacts plant development and physiological cycles. Major factors restricting plant survival, growth, and development include flooding's dramatic reduction in the amount of oxygen accessible to the roots (Oliveira and Joly 2010). Flooding causes stunted growth of new leaves, roots, and shoots, resulting in decreased plant progression; declines in photosynthesizing electron carriers proportion, net chlorophyll content, photochemical performance, and photosystem-II activity (Yi et al. 2006), ROS metabolism disorders (Lima et al. 2002), reductions in elemental uptake, and transport inhibition from roots to leaves (Smethurst et al. 2005). Other negative impacts of floods on plants include a decline in aerobic respiration in the roots, which hinders ATP generation and disturbs metabolism. In addition, soil flooding causes various physiological disturbances that change plant development, with hormonal imbalance, changed carbohydrate supply, inadequate nutrient absorption, premature leaves, and organ damage, sometimes leading to plant death. (Rodríguez-Gamir et al. 2011).

Soil compaction refers to a rise in the quantity of soil particles within a given volume. Soil compaction is also known to upset plant growth. Heavy machinery use in forestry management has increased significantly, compacting forest soils and potentially distressing seedling establishment and survival (Alameda and Villar 2012). Soil compaction inhibited yield, affecting plant growth and development. Stunning, leaf discolouration, shallow root system, and reduced plant height are the major structural effects related to soil compaction. In contrast, low nutrient absorption, carbon assimilation, abridged gas exchange, and low photosynthetic mass transfer are harmful effects of soil compaction (Shah et al. 2017).

Increased industrial and human activity produces heavy metals, which limit plant growth in a variety of ways, as shown in Table 14.2. Chromium (Cr), a heavy metal, is regarded as a major environmental pollutant in the biome. Compounds containing chromium are extremely poisonous to plants and detrimental to their development. Plant development and growth are also impacted by Cr's presence in the surrounding environment. Inhibition of plant development, chlorosis of new leaves, tip withering, loss of photosynthetic activity, root damage, and finally, plant death have all been linked to Cr (Sharma et al. 2003; Scoccianti et al. 2006).

Table 14.2 Effects of abiotic stresses on plant photosynthesis

Stresses	Optimum range	Effects	References
Heavy metals	0.01–1500 ppm	Effects on the ultrastructure of chloroplast, degradation of chloroplast	Kapoor et al. (2019)
Temperature	13–27 °C	Stomata closure, change in CO_2 effects on photosynthesis	Hussain et al. (2019)
Drought stress	RWC 60–80%	Reduction in chlorophyll florescence and contents of chlorophyll	Liu et al. (2018)
Light impacts	2700–7000 K	High light intensity damage to P-I and P-II	Faseela and Puthur (2018)
Salt stress	4.5–9 mmhos/cm	Mostly effects on the efficiency of P-II	Salma et al. (2023)
Pesticide stress	5.0 and 7.5 mL/L	Reduction of chlorophyll, effects on photosynthesis	Sharma and Zheng (2019)
Wind	0.3 m/sec	Stomatal limitation, reduction in photosynthesis	Feng et al. (2019)
Dust	<19.17%	Stomatal closure, effects on photosynthesis	Kaur et al. (2021)
CO_2	0–3.0% V/V	Low and high CO_2 both effects on photosynthesis rate	Molino et al. (2020)
Bulk density	<1.3 g/cm^3	Soil compaction hinders the root proliferation and uptake of required nutrition and water for photosynthetic activity/plant growth	Mukhopadhyay et al. (2019)

Although cadmium does occur naturally in soils, the main sources of soil pollution are anthropogenic emissions, primarily originating from mining, burning fossil fuels, the steel industry, and excessive use of phosphate fertilizers (Singh and Agrawal 2007). The stresses in plants causes various stress symptoms, including necrotic lesions, chlorosis, wilt, mineral dystrophy, and carbohydrate metabolism, which can significantly cut back on producing biomass (Azevedo et al. 2005; Santos et al. 2010). Reduced photosynthesis is a typical response in plants subjected to cadmium because the photosynthetic mechanism is vulnerable to cadmium (Burzynski and Klobus 2004). Zinc deficiency is one of the most prevalent crop and soil deficiencies (Alloway 2008). According to Balakrishnan et al. (2001), zinc deficiency inhibits plant development, specifically shoot growth and chlorophyll concentration, resulting in chlorosis and irregularities in leaf morphology and eventually affecting chloroplast form (Kim and Wetzstein 2003).

14.4 Photosynthetic Adaptation in Plants Under Abiotic Stress

Plants are exposed to a range of abiotic stressors, including dry conditions (Hui et al. 2018; Tanveer et al. 2019), high and freezing temperature (Sharma et al. 2020a, b, c), salinity, nutrient deficiency, ozone pollution, and some specific environmental factors (Zhenzhu et al. 2019). Abiotic factors are primarily nonliving variables that influence plant morphogenesis mechanisms in terms of environmental conditions. Poor plant conditions result from insufficient water availability, elevated temperatures, and inadequate or specific concentrations of available salts for plants growth. Any type of abiotic stress directly hits the photosynthesis process in plants by defacing and denaturing the outer layer of chloroplasts, bringing down the amount of chlorophyll in them (Sidhu et al. 2017). Photosynthesis is inhibited not only by temperature but also by the availability of water. For instance, when a plant has a limited supply of water, it can cause damage and structural problems in the organ (Ali and Ashraf 2011). Some plants exhibit ecological and biochemical responses to abiotic stress conditions as adaptive mechanisms in photosynthesis.

14.4.1 Ecological Aspect of Photosynthetic Adaptations

Photosynthesis is an important process in plants that transform sunlight into chemicals that produce energy (Chen et al. 2018; Demmig-Adams et al. 2018). Plants use this process to generate their own energy, establishing themselves as primary producers and contributing to the food chain for the entire ecosystem. Photosynthesis occurs in plant chloroplasts and involves light and dark photosynthetic reactions. Both photosystems (PS-I and PS-II), and electron transport chain chlorophyll biosynthesis are all negatively impacted by abiotic stresses like salt stress, stress of temperature, drought, and stress of heavy metals (Kalaji et al. 2016; Sharma et al. 2016a). Oxygen-free radicals are involved in plants' nutrition, providing immunity and protection against stress, particularly abiotic stress. The synthesis of oxygen-free radicals in different plant organs, participating organs are mitochondria, apoplasts, plastids, and peroxisomes. These synthesize, regulate and manage the network of genes in ROS.

Various ROS sensors decode distinct ROS signatures produced by multiple or combinations of different environmental abiotic stresses, triggering particular stress signals in impacted plants (Noctor et al. 2014). Research has shown that the light reactions in chloroplasts at the ETCs of both photosystems produce ROS, which is amplified when carbon dioxide availability and ATP synthesis are reduced (Nishiyama and Murata 2014; Tikkanen and Aro 2014). There are two possible suppliers of oxygen-free radicals during abiotic stress. The first is signaling ROS to a single transduction network as a reflex to abiotic stress (Tikkanen et al. 2014). The second type is metabolic ROS, which disrupts metabolic activity. Although ROS-detoxifying proteins such as SOD (superoxide dismutase), catalase, oxidoreductases, peroxiredoxin, and hydrogen-peroxide oxidoreductase reduce intracellular ROS levels, their specific scavenging system cannot completely remove them (Upadhyaya et al. 2011).

Plants have transcription factors (TFs) (Ashraf and Harris 2013). TFs are proteins that manage abiotic stress responses, plant immunity, and convert DNA to RNA to control plants' physiological and morphological development and growth and protect them against the impacts of environmental stresses. TFs primarily regulate photosynthesis; they are classified into families and do crucial work in many stomatas, metabolic activities, and the size of some stomatal and non-stomatal plants. Several plants adapt and respond to photosynthesis in such a way that they increase carbon dioxide even when there are stressed conditions (Zhenzhu et al. 2019). To prevent the photosynthetic stress, plants increase their surface area and arrange leaves, stomata, and cuticles.

The survival of plants is becoming more difficult as global temperatures rise. When the temperature rises above a certain threshold, it reduces yield and disrupts metabolic activities, biomass, and homeostasis (Sharma et al. 2020a, b, c). On the other hand, low temperature affects the folding and unfolding of stomata, the rate of respiration, the carbon cycle, and thylakoid electron transport (Hou et al. 2017). Temperature differences primarily influence the process of preparing food by the photosynthetic process (Centritto et al. 2014). Although plants are modified by their ability to photosynthesize in response to prolonged high temperatures, this can cause chlorophyll degradation and even permanently harm chlorophyll synthesis. Short-term high temperatures disrupt plastid chlorophyll biosynthesis and decrease chlorophyll accumulation (Antoniou et al. 2017).

Differences in light and shade have a significant impact on plant photosynthesis. If there is shade, the scenario will be different. Some plants absorb more light in the shade, resulting in a condition known as photoinhibition. However, if the plant's upper surface grows in the shade, the rate of photosynthesis slows, and there will be no adequate photosynthesis if sufficient light energy does not reach the plant body. Irradiance adaptations are classified into convergence, correlation, and cost–benefit analysis. These adaptations are beneficial. But the second of these three assumptions is that convergence is doubtful because RUBISCO has a higher irradiance level as well as a higher photosynthetic rate, both of which reduce thermal stress. Rubisco activase RCA, a protein with 4KDA (isoform) and 47KDA (isoform) molecular weights, has been shown to activate Rubisco in a variety of species (Jajoo and Allakhverdiev 2017), but as previously stated, the carboxylates present in Rubisco reduce photosynthesis. As a result, rubisco contentment is adapted to shady conditions and is associated with low irradiance levels and dark area respirations. For example, it is stated that in spinach and rice crops, the -RCA isoform is important in sustaining Rubisco's primary activity under normal conditions, whereas the-rubisco activase isoform leads to better photosynthetic adaptation to moderate thermal shock. The fact that the isoform is more stable in the heat than the isoform is a hint. General understanding of RCA gene regulation and the production of more isoforms aid in understanding the mechanism and procedure of rubisco optimization under stressed environmental conditions. Moreover, thermal stress or a temperature increase destabilises the structure of the plant's oxygen-evolving complex, light-harvesting complex, and reaction centre integrity. Heat stress has been shown to inhibit chlorophyll biosynthesis by lowering gene expression and inhibiting biosynthetic enzyme activity.

Salt stress reduces plant yield by 50%, stunts growth, and alters the metabolic and hormonal processes of plants (Gururani et al. 2015; Ahmad et al. 2019; Sharma et al. 2020a, b, c). The thylakoid layer is damaged by an elevated level of different solutes, anions, and cations in the chloroplast. Furthermore, inorganic salts cause irreversible changes in photophosphorylation and can limit electron transport across the thylakoid membrane (Mittal et al. 2012). Photosynthetic pigments in some species, including wheat, alfalfa (*Medicago sativa*), castor bean (*Ricinus communis*), and sunflower (*Helianthus annuus*), are affected by salinity stress. Drought stress also reduces photosynthetic functioning and limits plants' morpho-physiological growth, development, and yield (Hui et al. 2018; Tanveer et al. 2019). Inadequate water availability negatively affects the thylakoid membrane and reduces chlorophyll concentration (Smolikova et al. 2017; Smolikova et al. 2020).

Global warming is a major issue that is lowering groundwater quality and the water table, resulting in drought conditions worldwide. Plants struggle to survive in these harsh conditions because if there is an insufficient water supply for plants to run their photosynthesis process, how can they serve as the primary producers for the entire world? To deal with these conditions, some plants adapt to them, and some of them respond in such a way that they have a high chance of survival. Plants use a variety of strategies to ensure survival in these harsh conditions, including stomatal closure to reduce respiration and store as much water as possible in the plant body and osmotic adjustment (Sharma et al. 2019a, b, c, d). Xerophytes are the best plants for absorbing water and surviving in these conditions (Macková et al. 2013).

Heavy metals from industrial waste, sewage, traffic, volcanoes, incinerator emissions, and hard water reduce transpiration and photosynthesis by interfering with the stomata (Ghori et al. 2019). It also has an effect on the anatomical and biochemical processes of plants (Anjum et al. 2015; Handa et al. 2018; Shahzad et al. 2018a, b, c; Khanna et al. 2019; Kohli et al. 2020). Chlorosis of the leaf occurs when the size of the chloroplasts is reduced due to the uptake of heavy metals from the soil, such as Co, Cd, and Zn (Shahzad et al. 2016, 2017). Heavy metal stress has an impact on photosynthetic pigments; as the content of heavy metal Nickel in the vegetative tissues rises, so does the concentration of photosynthetic pigments, it inhibits pigment synthesis and interferes with the photosynthesis process (Soares et al. 2019, 2019; Shahzad et al. 2018a, b, c). According to Kohli et al. (2020), nickel can also inhibit chlorophyll activity and act as a strong modifier of the plant's lipid membrane.

Light intensity is required for balanced vegetative growth and development with high yield and biomass. Light is a necessary component of photosynthesis; any variation in light reduces photosynthesis, as well as changes metabolic and physiological functions (Wang et al. 2017; Sharma et al. 2020a, b, c). When there is a high intensity of light, it produces toxic oxygen radicals (Gururani et al. 2015), which have a direct effect on the light-harvesting complexes (LHC) (Erickson et al. 2015). Low light intensity leads to decreased photosynthesis, which raises oxidative stress, impairs stomatal function, and disrupts transpiration rate (Zhang et al. 2016; Pan and Guo 2016). Severe light stress negatively affects plants' photosynthetic apparatus. During this process, photons are excited in the chlorophyll of the plant, reducing the efficiency of the photochemical process. This is most common in tropical areas where plants are exposed to harsh light.

14.4.2 Overview of the Photosynthetic Adaptation Process

Plant photosynthesis refers to photochemical reactions that capture and convert solar energy into chemical energy. A protein web regulates the photosynthesis process. The process involves the ATP synthase complex, cytochrome b6f, and photosystems I and II. These proteins are significantly influenced by abiotic stress. The agriculture outputs and the security of the world's food supply are severely hampered by these pressures. Due to their detrimental impacts on overall photosystem efficiency, biosynthesis of chlorophyll, gaseous exchange characteristics, and electron carriers processes, and a range of other aspects, they frequently reduce plant photosynthetic efficiency (Paunov et al. 2018; Sharma et al. 2019a, b, c, d). Many toxic contaminants impede the photosynthetic process in natural plants, resulting in reduced plant growth and development.

External factors have an effect on photosynthesis (Kalaji et al. 2012). Photosynthesis is typically suppressed before other cell processes are compromised or impaired due to its susceptibility to extreme temperature stress. In higher plants, high-temperature stress primarily impacts the photosynthetic processes (Yang et al. 2020). The heat sensitivity of the main photochemical reaction mechanism in the thylakoid membrane often determines the heat tolerance threshold of higher plant leaves. While tolerance thresholds differ between genotypes, they are also adaptable. Rapid adaptive thermal stability adjustments that only take a few hours can be used to accomplish long-term acclimations. Increased heat tolerance stabilizes the light-induced proton gradient and enhances heat tolerance.

Along with irreversible effects, temperature elevations may have a significant rescindable impact on photosynthesis. High-temperature stress affects RuBisCo and Photosystem II, plastoquinone (PQ), and cytochrome b559 (Cytb559). PS-I, as opposed to PS-II, is more stable at higher temperatures (Fig. 14.3). Extreme temperature stress results in the creation of radical oxygen species and secondary compounds, as well as the development of heat shock proteins (Hasanuzzaman et al. 2020). Temperature challenges to most plants' photosynthetic rate are reversible for a wide range, generally 10 to 35 °C; however, the photosynthetic system may suffer irreversible damage if exposed to temperatures below or above this range. As a result, extreme temperatures can severely halt photosynthesis in addition to the intrinsic temperature effects on photosynthesis, which are unaffected by the probity of the photosynthetic apparatus. In order to adapt to temperature variations, plants use a variety of strategies, such as increasing membrane lipid unsaturation in high temperatures and lowering it in low temperatures.

Water stress reduces stomatal opening and leaf water potential, which causes photosynthesis-related genes to be down-regulated. It also influences photosynthetic rates through changes in photosynthetic metabolism or stomatal closure, reducing

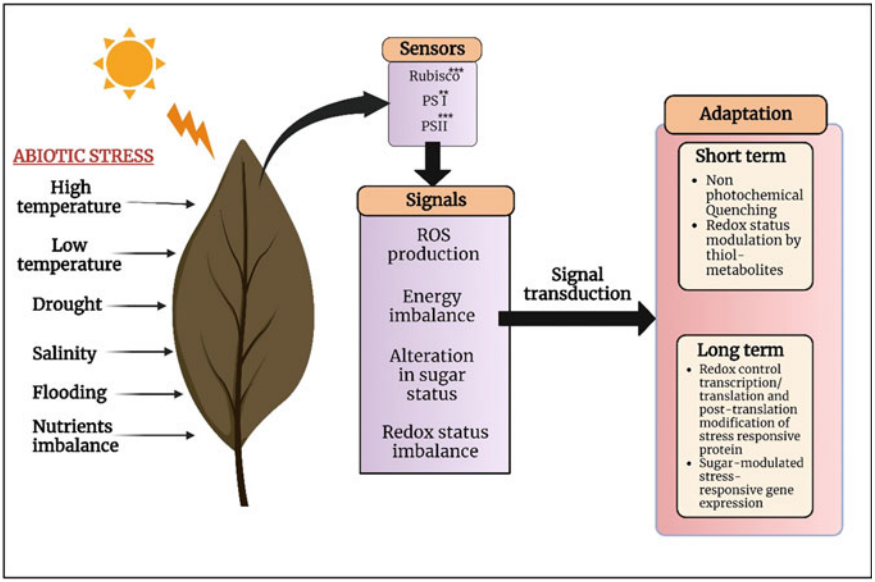

Fig. 14.3 The effects of abiotic stress on photosynthesis components (PS-I and II, RUBISCO), signal transduction, and adaptation to environmental stressors

CO_2 availability. Water scarcity disrupts the fundamental organizational structure, preventing carbon absorption and interfering with the photosynthetic mechanism (Wang et al. 2018).

Drought stress impairs plant development via a number of physiological and metabolic mechanisms, including respiration, antioxidant systems, potential ion uptake, stomatal closure, water potential, photosynthesis, plant hormones, and sugar and nutrient metabolism. In moderate drought, stomatal restriction causes a decrease in chlorophyll, while non-stomatal restrictions result in a reduction in photosynthesis. Plants in arid regions have evolved xeromorphic characteristics to reduce transpiration in drought pressure. Reduced transpiration can also be achieved under drought conditions through leaf abscission, size, leaf number, and branching (Khalvandi et al. 2021). Plants have evolved various adaptive responses to mitigate the damage caused to photosynthesis by drought, such as the xanthophyll cycle, the water cycle, detachment of light energy complexes from photosynthesis centers, and thermal tolerance of light energy.

Salinity impairs physiological functions, particularly photosynthesis, which has a adverse influence on plants net yield. The K^+:Na^+ ratio appears to be altered by the buildup of intracellular sodium ions during salt stress, which then affects the bio-energetic process of photosynthesis. It accelerates the buildup of sodium chloride in cyanobacterial cells or higher plant chloroplasts, slowing development, and is frequently linked with a decline in the performance of electron transport involved in photosynthetic reactions. Thus, plants respond to indications of salt stress over various mechanisms, such as control of ionic homeostasis, initiating osmotic stress passageways, amplification of plant hormone signalling, control of cytoskeletal dynamics, and composition of the cell wall (Zhao et al. 2021). Depending on their tolerance level, plants react differently to different abiotic stimuli.

14.4.3 Biochemical Regulation Stress

Due to immotile in nature, the plant faces several types of environmental stresses (biotic and abiotic). However, the severity of loss relies upon the plant's magnification and maturation stage at the span and severity of stress (Sharma et al. 2016a, b). Abiotic stress also affects biochemical processes in plants, especially photosynthetic processes, causing adverse conditions (Elsheery and Cao 2008; Ashraf and Harris 2013; Fidalgo et al. 2011; Kohli et al. 2018; Paunov et al. 2018; Sharma et al. 2019b; Soares et al. 2018).

The most important abiotic elements in an ecosystem are temperature and sunlight. Light and temperature stress affect plant biochemical processes by impacting chloroplasts and interrupting the photosynthetic electron transfer pathway functions (Yadav et al. 2018). According to recent research, the quality and amount of light can have a significant impact on the unbalanced activation of PS-II and PS-I, resulting in an energy mismatch between photosystems and the thermodynamic tuning of photosynthetic complexes (Schottler et al. 2015; Tikkanen and Aro 2014). This disproportion between the two PS-I and PS-II can lead to originate the unstable reactive intermediates, mainly ROS (Zavafar et al. 2015). The photosynthesis electron transport chain oxidises water in chloroplasts, which are found in plant cells (Croce and Amerongan 2014). ROS are released into the chloroplast through photosystem-I and photosystem-II processes by excess photons captured in the PS-II and electron sinks to molecular oxygen via PS-I (Apel and Hirt 2004; Triantaphylides and Havaux 2009). The ROS are produced by a diverse array of mechanisms in different compartments of the cell including peroxisomes, mitochondria, apo plasm, chloroplasts, and endoplasmic reticulum (Ashraf 2009). Under normal conditions, ROS formation is involved in important intra- and intercellular signalling processes and beneficial to antioxidant safeguarding systems and biological processes (cell proliferation, distinction, or stress adaptation mechanisms) (Mittler 2017). In general, abiotic stress affects the production of ROS in plant cells, as well as peroxide, superoxide, superoxide radical, and hydroxyl ions (Kaur et al. 2019; Sharma et al. 2019b). ROS generation can damage the oxidation process in chloroplasts and end up causing photoinhibition of photosystems, both of which severely limit plant growth. Plant trigger mechanisms of a buffer, such as circulating photosynthetic electron flux and energy-dependent quenching, to manage stable-state photosynthetic productivity and prevent ROS collection (Murchie 2017; Yang et al. 2018a, b). Plants further activate antioxidant mechanisms to scavenge ROS by boosting the enzymatic activity of glutathione synthetase, superoxide dismutase, and ascorbate peroxidase (Sharma 2016). According to the Mehler reaction, a sink for electrons is an important alternation in the chloroplast during photosynthesis, but as a byproduct, it produces superoxide. A membrane-bound superoxide dismutase quickly dismutates this active oxygen molecule to generate hydrogen peroxide, which is then converted to water by ascorbate peroxidase. This is known as the water-water cycle or the Mehler-peroxidase reaction. The removal of superoxide and H_2O_2 without further damaging the cellular section and thylakoids of plant cells is due to the Mehlar-peroxidase response (Foyer and Noctor 2009).

Soil salinity adversely affects the plant's photosynthetic activity and promotes the formation of reactive oxygen species (ROS), hence lesser plant growth (Khan and Bano 2018). The ion signalling pathway, osmolyte regulatory pathway, and signal transduction have three types of gene regulatory pathways under stress conditions (Nxele et al. 2017). An ionic stress-indicating pathway was introduced for message transmission under salt stress. Calcium (Ca^{2+}) plays a central role here and induces signalling of the plants' part to adjust under these stress conditions (Yuan et al. 2018). High Calcium concentrations in cytosol initiate various tasks that affect enzymatic activity, ion channel activity, and regulation of gene impression (Naseem et al. 2018). Applying calcium exogenously conducts K^+/Na^+ selectivity and salt adaptation by brushing signal transduction. Glycine betaine reportedly maintains signalling and ion homeostasis under salt stress conditions (Kumari et al. 2015). Glycophytes and halophytes have profound salinity effects at the cellular level by changing cytoplasm and cell membrane. As a survival tactic, the plant changes the composition and structure of the plasma membrane, particularly lipid and protein matters. Cell membranes are usually the first exposure target (Saha et al. 2015).

Salinity stress also alters the thickness and composition of the cell cytoplasm (Ali and Xie 2019). Salt causes severe abnormalities at the time of the cell division process. These are the metabolic processes that undergo significant changes in saline environments. In particular, the salinity-stressed environment changes leaf anatomization by affecting vacuoles, mitochondria, leaf surfaces, and stomatal diameter (Balal et al. 2017). The whole body of the plant face shows salinity tolerance by partitioning the harmful ions (Ahmad and Tariq 2021). This process allows plants species that tolerate salts to keep harmful concentrations of toxic ions within the vacuole, preventing them from interfering with metabolic activities in the cytoplasm. The distribution of sodium and chloride ions within the vacuole activate high concentrations of potassium ion and biological osmolytes in the cytosol to control ion osmotic pressure within the vesicle (Mehmood et al. 2018).

ROS levels rise dramatically during environmental stresses such as causing oxidation damage in proteins, Deoxyribonucleic acid (DNA), and lipids (Apel and Hirt 2004). ROS are highly reactive and are harmful to plants by promoting protein breakdown, lipid peroxidation, DNA breakage, and ultimately cell death. Moisture causes oxidative stress in plants by producing ROS (Farooq et al. 2009). ROS directly attacked the lipids in cell membranes, increasing lipid breakdown (Mittler 2002). Over a generation of reactive oxygen species by drought encouraging malondialdehyde (MDA) levels. MDA is regarded as an indicator of oxidative damage (Møller et al. 2007). Due to oxidative damage, it places demands on tissues to accelerate processes such as the production of ROS, particularly H_2O_2, in the photorespiration process via the glycolate oxidase reaction within peroxisomes at extremely high rates. The ability of antioxidant enzymes to scavenge ROS and mitigate their unconditional harmful effects may be correlated with plant drought tolerance.

Many enzymatic and non-enzymatic antioxidants must be present, and a functioning highly organized system to address continuous ROS production in plants. Ascorbate–glutathione cycle and metabolites all are important removal mechanisms (CAT, SOD). They are found throughout the plant cell, with the exception of catalase, which is only found in peroxisomes (Mir et al. 2018). SOD acts as the first line of defense against ROS attack because it rapidly hunts superoxide, the first ROS produced, and breaks it down into oxygen and H_2O_2. Although the conversion in this reaction is one ROS to another, and H_2O_2 immediately attacks the thiol protein, so H_2O_2 must also be destroyed. The primary enzymatic cellular scavenger of H_2O_2 is catalase and APX. However, they both appear to have different harmonies for this Reactive oxygen species aa dissimilar cellular roles in H_2O_2 scavenging.

Moreover, CAT has a less affinity for its H_2O_2 (mM range) than APX (mM range) (Mittler 2002). The above discussion led towards the hypothesis that APX, an enzyme found in cells in ROS formation parts, serves as a superior regulator for intracellular ROS levels, for the signaling process, and as a mass scavenger for excessive ROS production under stress conditions. Glutathione reductase (GR) is the final enzyme of the ascorbate/glutathione cycle, and it plays a crucial part in managing the intracellular glutathione pool in a reduced state (GSH) (Noctor et al. 1998). GSH like ascorbate acts directly (non-enzymatically) as an antioxidant by removing singlet oxygen, superoxide, and even hydroxyl radicals, or oxidizes ascorbic acid by the enzyme dehydroascorbate. It can work indirectly as a reducing agent to convert the reduced form of dehydroascorbate reductase.

14.4.4 C3, C4, and CAM Plants Comparative Response

Plants have C3, C4, and crassulacean acid metabolism (CAM), three types of photosynthetic processes that capture CO_2 in different ways. They differ from each other by structure and function, as well as their responses to various environmental abiotic stresses are also different. Climate change effect and increase the rate of photorespiration, CO_2 concentrations, heat, light, aridity, and salinity (Sage et al. 2018). The ecological grouping according to photosynthetic types along with temperature gradients is especially pronounced in grasses, where C4 grasses production increases at high temperatures and makes the pathway for C_3 grasses as the temperature cools (Bremond et al. 2012; Pau et al. 2013).

Energy absorbed by leaves is allocated to the sum of heat loss, photorespiration, and photosynthesis in C3 plant types exposed to varying degrees of drought. As compared to C3 plants, C4 plants exhibit higher photosynthesis rates, increased CO_2 fixation rates, as well as greater water use efficiency (WUE) and transpiration rates, highlighting their advantage. However, it's important to note that the photosynthetic process differs between C3 and C4 species under drought conditions (Taylor et al. 2011; Way et al. 2014; Hatfield and Dold 2019). Gas exchange in C4 plants was less affected by drought compared to C3 plants, as the earliest response to leaf water deficit is stomatal closure, which specifies the CO_2 diffusion limit into the chloroplast (Yan et al. 2016). CAM plants are adapted to protect against drought stress through their advanced internal organization by storing water, absorbing CO_2 throughout the day, and having high water-use efficiency (Drennan and Nobel 2000).

WUE is improved by shifting CO_2 absorption to night time hours when evaporative water loss is minimal as CO_2 is absorbed at night. Photosynthetic properties differ greatly in C3, C4, and CAM plants. This is due to adaptation to their specific growth conditions on the evolutionary timescales. The C3 plants have greater photosynthetic temperature adaptation over a wider temperature range, whereas CAM plants have a diurnal photosynthetic process with drastic temperature swings during the day and night because CAM plants are grown in tropical rainforest epiphytes, but it is also found in the desert in a variety of ratios. However, within C3 species, evergreen woody and perennial herbaceous plants show higher temperature homeostasis of photosynthesis. This means that photosynthetic acclimation is essential for perennial and long-lived species that experience increased growing season temperatures during the growing season. C3 plants have no specific mechanism to control photorespiration by performing carbon dioxide fixation and the Calvin cycle in separate cells. Conversely, CAM plants reduce photorespiration by working on carbon dioxide fixation and the Calvin cycle at different times. In addition, photosynthetic electron transport (PET) can be disrupted by sodium or chloride ions' toxicity which is induced by salinity (Mehta et al. 2010; Tomar et al. 2012), increasing the leakage of electrons to O_2. A decrease in Cl^- slows the process of the Calvin cycle and induces photorespiration (particularly in C3 plants), and leads to more H_2O_2 formation in peroxisome (Wang et al. 2018).

14.5 Planning to Combat Abiotic Stress

Environmental elements that have an impact on a plant's growth and development are referred to as stress in plants or production. Abiotic stressors, which include radiation, salinity, floods, droughts, extremely high or low temperatures, and heavy metals, among others, cause the loss of essential crop plants across the globe (Gull et al. 2019). The majority of people in undeveloped countries, where traditional agriculture is still practiced, face ongoing threats to their way of life from abiotic stressors and their interactions with biotic stressors (Calanca 2017). Abiotic stress poses a serious threat to agriculture and food security, particularly in areas affected by climate change and environmental degradation. For crop plants, abiotic variables are the primary yield-limiting factors. Around 90% of arable lands are vulnerable to one or more of the aforementioned stresses, leading to output losses in important food crops of up to 70% (Waqas et al. 2019). It is challenging to predict how abiotic stress would affect crop production accurately. Abiotic stress causes complex and dynamic plant responses that can either be reversible or irreversible (Yadav et al. 2020). In an effort to lessen the stress of environmental changes and satisfy the need of the rising population, crops must be able to withstand multiple stressors since, In the field, these stresses frequently coexist (He et al. 2018). For agriculture to maintain crop output throughout the year, regardless of weather variations, management measures for abiotic stress tolerance must be developed (Usman et al. 2023). This is a result of abiotic stress's wide-ranging effects as well as negative predicted changes in the world's climate (Oshunsanya et al. 2019). It is critical to identify the abiotic stressors, develop a plan to cope with them, and consider the likelihood of adaptation and mitigation. There are many methods for reducing abiotic stress; A few examples include agronomic methods, nanotechnology in agriculture, various climate-smart agricultural techniques, and the creation of cultivars that are resilient to abiotic stress. (Hossain et al. 2021).

14.5.1 Breeding of Crops

Crop breeding strategies aim to use various technologies under controlled and field circumstances to reduce the breeding cycles and produce more stress-resistant, high-yielding crop varieties for specified areas. Breeding initiatives often focus on cultivating early-maturing cultivars that are suited to short-season conditions and can withstand late-season stress (Maphosa et al. 2020).

The genetic diversity of agricultural plants provides the foundation for the ongoing development of novel varieties to address present and future issues. Plant breeders have a variety of reactions to stress:

- Selective breeding and backcrossing.
- Repeated selection of highly tolerant germplasm after extensive controlled stress screening tests.
- Making use of foreign genetic variation (Conserved Wild Relatives).
- Creating variants with specific adaptations to particular ecologies and breeding for early maturity (Gazal et al. 2018).

More stress-tolerant germplasm may be produced by enhancing the breeding process using screening technologies, quicker generational improvements, and parent recycling. Modern techniques for future plant breeding initiatives will be required, including transgenic strategies and marker-assisted breeding (Mondal et al. 2021).

14.5.2 Agronomic Practices

The use of agronomic practices can reduce abiotic stress on crops. Abiotic stress can be overcome using several techniques, including planting drought-tolerant plants at the right times of the year and applying precision irrigation. Drought-tolerant crops are developed to survive prolonged periods of drought and need less water for growth. Precision irrigation provides water to crops only when and where it is required, and optimizing planting dates helps crops avoid the worst abiotic stress periods. These methods have dramatically increased crop yields in abiotic stress-affected locations (Lopez-Marquez et al. 2019; Wang et al. 2020).

- **Soil Management**: Useful soil management techniques, such as nutrient management, soil amendments, and soil tillage, can help crops more effectively withstand abiotic stress. For instance, conservation tillage improves soil water retention and lowers soil erosion, which is especially advantageous in areas that are prone to drought (Lal, 2015). Additionally, soil additions like organic matter and biochar can promote nutrient availability and soil quality, which can help crops resist abiotic stress (Liu et al. 2019).
- **Genetic Engineering**: Crops with increased resistance to abiotic stress have been developed using genetic engineering techniques. For instance, transgenic crops that express osmoprotectant genes, like glycine betaine, have been demonstrated to have increased salt and drought tolerance (Sharma et al. 2020a, b, c). Likewise, genetic modification of photosynthetic pathways can increase carbon fixation efficiency and lessen abiotic stress's effect on crop yields (Lawson et al. 2020).
- **Crop Diversification**: Different crops are grown in rotation or as intercrops to lower the danger of abiotic stress. This procedure can aid in reducing soil-borne diseases, enhancing soil quality, and preserving yield stability under abiotic stress (Gan et al. 2015). Intercropping can also boost nitrogen cycling and decrease water

use, both of which are beneficial for crop growth and yield (Hauggaard-Nielsen et al. 2018).

14.5.3 Environmental Techniques

Environmental techniques are a collection of measures designed to mitigate the adverse effects of abiotic stress on ecosystems, natural resources, and crops. These approaches aim to restore health and sustainability to abiotically stressed natural and agricultural systems. The most promising environmental practices are soil and water conservation, reforestation, landscape restoration, and sustainable land management.

Reducing soil erosion and improving soil water retention are the objectives of water and soil conservation practices. Some of these techniques include mulching, conservation tillage, cover cropping, and terracing. By improving nutrient cycling and soil structure, these practices have the potential to improve soil fertility, which in turn can improve crop growth and yield. Additionally, conservation methods aid in preventing soil and water degradation, which can have long-term effects on ecosystem health (Lal 2014).

Another effective strategy for reducing the effects of abiotic stress on natural systems is reforestation. Ecosystem services like carbon sequestration, water regulation, and habitat preservation are provided by trees and other vegetation. By restoring degraded and deforested areas, reforestation can help to conserve biodiversity, reduce soil erosion, and increase carbon sequestration. Additionally, reforestation has the potential to enhance soil moisture retention, thereby lessening the detrimental effects of drought on crops and other vegetation (Parr et al. 2014).

Landscape restoration, a method of ecological restoration, includes the reintroduction of native vegetation and the restoration of natural ecosystems. This strategy is especially important in areas subject to abiotic stress, such as desertification and land degradation. Landscape restoration can boost soil fertility, lessen soil erosion, and boost water retention by restoring native plants. Furthermore, landscape restoration may provide ecosystem services such as carbon sequestration, animal habitat, and recreational opportunities (Chazdon et al. 2016).

Sustainable land management techniques also promote the long-term production and sustainability of agricultural systems. Crop diversification, agroforestry, integrated pest control, and environmentally friendly irrigation are a few of these techniques. These procedures may increase agricultural output and ecosystem resilience by reducing abiotic stress's harmful impact on crops and natural resources. Additionally, sustainable land management techniques may bring about economic and social advantages, including better food security, enhanced livelihoods, and less environmental damage (FAO 2018).

14.5.4 Abiotic Stress Tolerant Crops

Abiotic stress, which includes drought, salinity, and extremely high or low temperatures, is a significant obstacle to agriculture. These pressures can cause crops to lose a large amount of output, which can significantly impact food security. As a result, plant biologists now prioritize research toward developing crops that can withstand abiotic stress. Genetic engineering is one method for increasing crops' ability to withstand abiotic stress. According to Zhao et al. (2019), overexpression of the rice gene OsJAZ9 improved rice plant tolerance to drought stress. The researchers discovered that OsJAZ9 controlled the expression of several stress-responsive genes, increasing the ability of plants to withstand drought. By overexpressing the soybean gene GmWRKY54, Dong et al. (2020) demonstrated that soybean plants' ability to tolerate salt was enhanced. In order to boost salt tolerance, the researchers discovered that GmWRKY54 controlled the expression of several genes that are responsive to salt stress.

Plant growth-promoting bacteria (PGPB) have also been investigated to increase abiotic stress tolerance in crops in addition to genetic engineering. Inoculating maize plants with PGPB considerably increased their resistance to drought stress, according to a study by Rehman et al. (2021). The scientists discovered that PGPB boosted the osmoprotectant accumulation in the plants, which helped them adapt to drought stress. Similarlyly to this, Ahmad et al. (2019) found that inoculating wheat plants with PGPB increased their ability to withstand salt stress. The researchers found that PGPB boosted the activity of many antioxidant enzymes in the plants, which helped to alleviate the effects of salt stress.

Abiotic stress tolerance in crops can also be increased by using natural chemicals. A natural substance called chitosan was found to increase the tolerance of maize plants to drought stress (Viana et al. 2019). Chitosan increased the buildup of osmoprotectants in the plants, which enhanced their ability to withstand drought stress. Similarly, a study by Zhang et al. (2021) demonstrated that tomato plants were given a natural substance called salicylic acid to boost their tolerance to heat stress. Salicylic acid increased the activity of several antioxidant enzymes in plants, which the researchers discovered helped to mitigate the effects of heat stress.

14.5.5 Microorganisms

Microorganisms significantly influence plant responses to abiotic stress. Abiotic stresses like salt, dehydration and heavy metals have been proven to decrease plant development and boost plant resistance to specific microbial strains (Kumari et al. 2019). Microorganisms, such as bacteria, fungi, and algae, may promote plant growth, nutrient uptake, and stress tolerance by interacting with plants (Vurukonda et al. 2016). For instance, certain bacteria may produce plant hormones that encourage root growth and development, which might aid plants in better coping with drought and other abiotic stressors (Naveed et al. 2014).

Microorganisms could potentially help plants cope with salt stress by improving the absorption of crucial minerals like phosphorus and iron (Etesami and Beattie 2018). Certain fungi have the ability to form symbiotic relationships with plant roots, which may improve plant growth and survival under difficult circumstances (Sánchez-López et al. 2019). Furthermore, some microorganisms can detoxify heavy metal pollutants in the soil, minimising their detrimental effects on plant growth and development (Jaiswal and Dubey 2015).

14.6 Conclusion

Abiotic stressors can reduce plant vigour in a variety of ways by interfering with structural stability and cellular mechanisms required for plant development and growth. A sessile plant anchored in soil can face stressors such as water scarcity, an excess of salts, nutritional imbalances, and extreme weather conditions, which are largely due to the presence of persistent pollutants in the environment, rapidly fluctuating climatic conditions, and continuous anthropogenic activities that result in cellular structure deformation, deterring plant growth, and commotion of stomatal functioning, which affects the rate of photosynthesis. Phytohormones like abscisic acid, ethylene, auxin, gibberellin, salicylic acid, jasmonates, and antioxidants i.e., glutathione, peroxidase, carotenoids, flavonoids, etc. in a plant play an important role in the cell's defense by preserving biomolecules and suggesting alternate signaling pathways that help in increasing the tolerability of a plant against these stressors and minimizing the toxicity scale of abiotic stressors. Environmental stresses causes the production of proline to protect plant cell membrane structures and assist plant stabilization in harsh climatic conditions by maintaining cellular metabolism. Polyamines in plants also facilitate ion stabilization within plant cells. Carbohydrates can help in mitigating water stress as they can easily breakdown to produce water molecules. Backcrossing, recurrent selection, and the production of crop variants with the highest tolerable range to abiotic stressors are examples of modern crop breeding techniques. Other approaches to mitigating the impact of stressors may include managing natural resources by reducing soil erosion and water retention in the soil through eco-friendly techniques such as cover cropping, tillage, and terracing, as well as practising IPM; incorporating abiotic stressor-resistant microbes into the soil to enhance soil aeration and crop growth; and incorporating genetically engineered crop strains to alleviate the impact of abiotic stressors.

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Chapter 15
Use of Tissue Culture Methods to Improve Stress Tolerance in Plants

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Abstract Nowadays, climate change has become a worldwide concern as it affects global food production and security. Among the consequences of climate change are increasing abiotic constraints such as drought and salinity, and facilitating the invasion of pests and pathogens. Plant tissue culture would greatly help to mitigate climate change threats and foster biodiversity conservation. The major advances made in the field of plant micropropagation have played a key role in the rapid and large-scale production of stress-tolerant cultivars and constitute a powerful tool to develop stress-tolerant lines. In vitro mycorrhization is an interesting approach to improve tolerance to a variety of abiotic and biotic stresses while ensuring the mass production of plants. Tissue culture techniques would thus facilitate plant adaptation to an increasingly stressful environment. In the present chapter, the main achievements made in the field of plant micropropagation as a tool to produce stress-tolerant plants are presented and discussed. This includes the use of organogenesis for rapid and large-scale production of date palm plants resistant to bayoud disease and for palm grove rehabilitation, in vitro selection of abiotic stress-tolerant plants, morphological and physio-biochemical responses of plants to abiotic stresses under in vitro conditions, and the use of in vitro mycorrhization to improve stress-tolerance in plants.

Keywords Climate change · In vitro mycorrhization · In vitro stress · Micropropagation · Plant-environment interaction · Stress tolerance

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_15

15.1 Introduction

Climate change imposes a major threat to natural ecosystems and agricultural production. It is also a phenomenon that hampers the efforts aiming at reducing poverty and ensuring food security and sustainable development (Ahmed et al. 2023). The development of climate change-resilient agriculture is today a critical challenge for scientists and policymakers. Indeed, climate change affects all forms of life. Moreover, its negative impact on plant reproduction and biodiversity, and therefore on agricultural sustainability is no longer to be demonstrated (Bhadouria et al. 2019).

In recent years, different strategies have been implemented to cope with climate change, including advanced technologies. This was associated with agricultural practices that include increasing soil organic matter, improving cropland management, optimizing irrigation water use, use of local genetic diversity, use of biofertilizers, improving livestock management, use of mixed crop-livestock systems, use of microbial inoculation and intercropping systems (Kukal and Irmak 2018; Aryal et al. 2020; Harkousse et al. 2021; Sammama et al. 2022). In addition, significant progress in agricultural production resulted from biotechnological approaches that include rapid and large-scale propagation and genetic improvement of plants (Jan et al. 2018; Saraswat et al. 2022). However, despite the progress made, climate change remains a critical issue that affects agricultural systems. Indeed, with the sudden and continuous changes in environmental conditions, negative impacts on agricultural production are observed due to the direct and indirect effects of abiotic stresses (Singh et al. 2023a). Moreover, due to human activities and particularly the excessive use of fossil fuels and continuous deforestation, the concentration of greenhouse gases has increased. The concentration of CO_2 in the atmosphere has increased from 280 to 400 ppm, i.e., by about 45% since the industrial revolution and is expected to increase further to 1000 ppm by 2100. It is therefore predicted that the concentration of CO_2 will double by the end of this century (Hu et al. 2022). Emissions of pollutant gases, in particular CO_2, are the main factors causing the greenhouse effect and global warming (An and Zhu 2022).

Under natural conditions, plants experience environmental stresses such as salinity, drought, heat and cold (Raza et al. 2019). Climate change has increased the intensity of these abiotic stresses (Fatemi et al. 2022). High temperatures, increased evapotranspiration and limited rainfall are some factors that have enhanced soil salinity, reduced groundwater and consequently decreased agricultural productivity (Hussain and Al-Dakheel 2018). Hence, maintaining agricultural production and food safety is today a challenging task.

Current climate trends have affected agricultural production not only by increasing the intensity of abiotic stressors, but also the risk of exposure to pests and diseases (Bhadouria et al. 2019). Events of high temperature and reduced rainfall could facilitate the spread of crop pests. Moreover, high temperatures associated with drought may promote plant pathogen virulence and facilitate disease dissemination (Mazri et al. 2023).

In addition to the direct impacts of climate change on crop yield, there is also the altered timing of phenological events due to winter heat waves, the advance of spring and the late onset of autumn (Gremer et al. 2020). For example, the early bud break of woody plant species (Ladwig et al. 2019). Significant phenological shifts can also have strong impacts on ecosystem functions and plant productivity. For example, reduced seed formation, fruit set and yield (Bhadouria et al. 2019). The shifts of phenological events may affect plant distribution and abundance. In fact, many species will tend to leave their natural habitat to a new one with appropriate climatic conditions (Mazri et al. 2023).

It is a fact that today's agriculture is influenced by climate change and its negative impacts. This has led scientists, agronomists and food producers to use modern strategies to enhance crop yield and quality in a challenging environment (Raza et al. 2019). Biotechnological approaches are one of them, because they represent a potent and sustainable strategy that can guarantee continuous production systems, with no consideration for environmental or geographical constraints (Cabrera-Barjas et al. 2022; Sreelekshmi et al. 2023). Biotechnological tools are being increasingly used for fundamental and applied purposes, including functional genetic studies, commercial micropropagation of plants, production of transgenic plants with specific industrial and agronomic traits, plant breeding and crop improvement, virus elimination from infected plant material, germplasm preservation, rescuing endangered species, in vitro secondary metabolite production and production of innovative food ingredients.

Genetic and physiological challenges must be addressed to improve plant adaptation to adverse environments such as increased temperatures, salinity and drought. This can occur through understanding plant responses to adverse conditions at different levels. Thus, it is necessary to explore the genetic, physiological and biochemical mechanisms underlying the adaptation process of plants to unfavorable conditions. The use of modern agricultural technologies is also needed to develop and/or mass produce plant genotypes with enhanced tolerance to abiotic and biotic stresses.

This chapter is a review of the most significant progress made in the field of plant micropropagation as a tool to produce plants with enhanced tolerance to environmental stress. It provides overviews on in vitro regeneration systems and plant resistance mechanisms to stress. It reports data from the literature on the use of tissue culture to assess plant tolerance to abiotic stresses. It summarizes the Moroccan experience in the field of date palm micropropagation as a tool to control *Fusarium oxysporum* f. sp. albedinis, and the potential use of organogenesis for rapid and large-scale propagation of cactus pear cultivars resistant to *Dactylopius opuntiae*. Finally, it describes and outlines progress on in vitro mycorrhization as a novel approach to produce stress-tolerant plants.

15.2 Plant Micropropagation: An Overview

Since the beginning of the 20th century, plant tissue culture has made substantial contributions to agriculture, and is today an indispensable tool for agronomic sciences, and particularly for plant propagation, biodiversity conservation, genetic improvement and secondary metabolite production (Twaij et al. 2020). In recent years, climate change has broadened the field of application of plant tissue culture to be used as a tool for investigating the mechanisms that underlie the process of plant adaptation to stress and a powerful strategy for mass propagation of plants with enhanced tolerance to adverse environments.

Based on the United Nations reports, the world population is expected to increase to 9.9 billion by 2050, food production must therefore increase by about 60% to meet the needs of the world's growing population (Raghuvaran et al. 2023). Plant propagation through tissue culture (i.e., plant micropropagation) can guarantee continuous production of plants, with no consideration for environmental or geographical constraints (Abdalla et al. 2022). Indeed, plant micropropagation technologies allow for rapid and large-scale production of plants in a limited space and all year round (Abdalla et al. 2022). They can also be used for other purposes such as germplasm conservation and genetic improvement (Purwantoro et al. 2022; Rai 2022).

Plant tissue culture is one of the most important components in the field of plant biotechnology, since it can be used to overcome many problems that harm agricultural production and threaten global food security (e.g., global warming, desertification, salinity, water deficit) (Abdalla et al. 2022). Plant micropropagation can be achieved through different methods, among which somatic embryogenesis and adventitious organogenesis are known for their huge potential for mass production of plants, thus they have been widely used as potent tools for the genetic improvement of many species. Somatic embryogenesis and organogenesis are based on the totipotency and plasticity of plant cells, and their capacity to regenerate into complete plants (Desai et al. 2022).

Organogenesis is the in vitro regeneration process in which new organs are formed from an explant to further develop a complete plant (Tahiri et al. 2023). This method consists of several phases: adventitious bud induction (either directly on the explant or indirectly from callus cultures), shoot bud proliferation, shoot elongation, shoot rooting and plantlet acclimatization (Meziani et al. 2019). Somatic embryogenesis is a morphogenetic process in which somatic cells differentiate into embryos able to develop into complete plants (Mazri et al. 2020; Desai et al. 2022). Somatic embryogenesis consists of a transition from a somatic to an embryonic state. This transition involves changes at the cellular, biochemical, genetic and epigenetic levels that are induced and regulated by several factors, particularly plant growth regulators (PGRs) (Kumar and Van Staden 2017). Somatic embryo induction is followed by maturation and then the conversion into a complete plant (Mazri et al. 2020).

Somatic embryogenesis and organogenesis are powerful biotechnological tools that allow to manipulate the physical and chemical conditions at different stages of the regeneration process and to study their effects on plant production qualitatively and quantitatively. The conditions under which plant regeneration takes place would impact their adaptive capacity to environmental stress.

In vitro culture is a great tool to investigate the behavior of undifferentiated cells and the whole plantlets to environmental stress induced artificially. Somaclonal variation is another biotechnological tool that can be used for the in vitro selection of cells with enhanced tolerance to abiotic stress (Maleki et al. 2019).

15.3 Plant Resistance Mechanisms to Stress

Plant ecosystems are increasingly threatened by both natural and anthropogenic stressors such as climate change, natural habitat fragmentation, deforestation and increased incidences of pests and diseases. All these factors affect plants at the cellular, molecular, morphological, physiological and biochemical levels and consequently the overall developmental process of plants (Raza et al. 2020). In recent years, climate change has increased the global threats by influencing the suitability of a given region to grow specific crops and consequently crop productivity (Santos et al. 2017). Indeed, climate change has caused serious alterations of environmental conditions and biodiversity patterns, which led to major changes in ecosystem components. The alteration of the environmental conditions such as heat waves, changes in precipitation patterns and increased CO_2 concentrations have increased the magnitude of abiotic stressors, particularly salinity and drought, and caused the invasion of pests and the dissemination of pathogens and diseases (Mazri et al. 2023).

Global climate change has therefore exacerbated the severity of many abiotic constraints and increased the incidence of pathogenic microorganisms and the invasion of pests. These constraints may cause irreversible damage to plants, thus decreasing agricultural productivity and threatening global food security (Bhadouria et al. 2019). Stress can be defined as a sudden change in environmental conditions with the potential to cause substantial disturbances in plant growth and development at different levels (Kaur et al. 2023). Since climate change is a natural and unavoidable phenomenon with constantly growing impacts, plants must adapt to adverse environmental conditions by developing tolerance/resistance mechanisms. These mechanisms are reflected in a series of morphological, physiological, biochemical and molecular changes (Acosta-Motos et al. 2017; Akpinar and Cansev 2022). Along this line, various studies have been carried out to better understand the plant adaptation mechanisms to abiotic and biotic stresses, with the aim of ensuring agricultural sustainability through the selection and cultivation of stress-tolerant plants.

Among the different stages of plant growth, seed germination is the first process to be affected by abiotic stress. Low and high temperatures affect the viability of embryos and decrease the rate of seed germination due to protein denaturation, structure alteration, membrane degradation and tissue damage (Mazri et al. 2022a). The negative effects of extreme temperatures are enhanced when combined with other abiotic stresses such as salinity and drought. Drought is considered to be the most crucial environmental stress due to its severe impacts on plant viability, growth, development and yield (Francesca et al. 2021). On the other hand, the increased levels of salinity are major constraints to crop production. Plant exposure to high salt concentrations may cause several metabolic complications including osmotic imbalance, nutrient deficiency and excess of toxic ions which usually leads to overproduction of reactive oxygen species (ROS), and consequently to oxidative damage (Hasanuzzaman et al. 2020; Chaudhry and Sidhu 2022).

Plants are able to slow down their growth and alter their morphology under stressful conditions to survive and resist stress. These morphological changes include reduction of leaf area and leaf shedding in order to minimize water loss through transpiration and to avoid salt toxicity (Mishra and Tanna 2017; Chiconato et al. 2019; Mandizvo et al. 2021). The growth slowdown under stress can be reflected by the reduced number of leaves, reduced plant length, and decreased stem and root weights (Toscano and Romano 2021). Another aspect of plant adaptation to abiotic stress is observed at the root system (Angon et al. 2022). It has been reported that a deep and extensive root system promotes tolerance to abiotic stress since it allows to explore more soil layers, thus improving water and nutrient uptake (Salehi-Lisar and Bakhshayeshan-Agdam 2016). Additionally, leaf architecture may be subject to modifications in response to drought stress. Plants tend to produce hairy leaves under drought stress to maintain high water potential, low leaf temperature and reduced transpiration (Salehi-Lisar and Bakhshayeshan-Agdam 2016).

Stomatal regulation by the closure of stomata and the regulation of stomatal density and conductance is another indication of stress tolerance, aiming to minimize water loss through transpiration (Kiani-Pouya et al. 2020). However, the stomatal behavior differs from a species to another and within the same species, depending on the genotype, the leaf area and surrounding conditions (Cocco et al. 2020). Stomatal closure was reported to be one of the first responses to external stress, which causes a decrease in the level of photosynthesis, since the stomata are the mediators of gaseous exchanges (especially CO_2) between plant tissues and the surrounding environment (Akhtar et al. 2021). Abscisic acid (ABA) has been shown to be a primary factor in this regulation mechanism. The role of ABA is to induce stomatal closure, decrease the transpiration rate and the turgidity of guard cells by promoting the efflux of potassium ions, which allows stomata to close (Agurla et al. 2018; Liao et al. 2023). In addition, ABA plays a crucial role in the protection of photosystems by reducing ionic toxicity caused by the accumulation of sodium ions in leaf tissues. Indeed, salt stress not only inhibits photosynthesis but also inactivates PSI and PSII photosystems by altering photosynthetic proteins (Hernández 2019).

Based on physio-biochemical indices, a range of defense reactions are generated by plants in response to stressful environments in order to maintain cell turgor pressure, prevent membrane damage, protect cell structure and protect macromolecules such as proteins and enzymes against denaturation (Zulfiqar et al. 2020). The accumulation of compatible solutes is one of these protective reactions. These osmoprotectants are hydrophilic organic molecules characterized by a low molecular weight, which makes their accumulation at high concentrations does not alter the membrane structure of the cell, its metabolism and mechanisms (Wang et al. 2013; Sengupta et al. 2016). The compatible solutes that are accumulated by plants in response to stressful environments include proline, glycine betaine, polyamines and soluble sugars (Gao et al. 2008). These molecules help to maintain the plant water potential lower than that of the soil, protect membranes, eliminates ROS, facilitate water absorption and retention which helps to maintain cell turgor (Ali et al. 2020a; Kayak et al. 2022). Besides, they are involved in sustaining photosynthetic activities and in photosystem protection by stabilizing the thylakoid membrane (Ali et al. 2020b; Kayak et al. 2022).

Anthocyanin accumulation is another defensive strategy adopted by plants in response to environmental stress. Anthocyanins are water-soluble pigments belonging to the flavonoid family (Saikia et al. 2023). They are produced at the endoplasmic reticulum, and transported to the vacuole where they are stored (Samota et al. 2022). Several studies have suggested that anthocyanins act as non-enzymatic antioxidants, protecting cells against ROS-induced oxidative stress (Naing and Kim 2021). Besides, a positive correlation between the accumulation of anthocyanins and stress tolerance has been observed in many plant species (Mbarki et al. 2018; Mackon et al. 2021; Saad et al. 2021; Pang et al. 2023). Other protective molecules against the negative effects of oxidative stress and that facilitate the detoxification of ROS include antioxidant enzymes such as catalase (CAT), superoxide dismutase (SOD) and ascorbate peroxidase (APX) (Cruz de Carvalho 2008).

At the molecular level, several researches were carried out on *Arabidopsis thaliana* as a model plant, but also on other plants such as rice and soybean (Ma et al. 2005; Gao et al. 2008; Zhao et al. 2018). It was found that the adaptation process of plants to their environment is regulated by a cascade of molecular events such as the perception and transmission of an incoming signal through signaling molecules (e.g., Ca^{2+}, ABA), which leads to the activation of a set of resistance genes. The target cells perceive the first stress signals (i.e., stimuli) through receptors that recognize and transmit the signals of changing environment (Gao et al. 2008). These receptors are membrane proteins. They induce an ionic imbalance by cytosolic accumulation of Ca^{2+}. A series of signaling reactions is therefore mediated by protein kinases, calcium-dependent proteins and other mediators. Once the signal is perceived, several transcription factors are triggered. This initiates the expression of target genes (i.e., effector genes), which will induce physiological responses from the plant to mitigate the adverse effects of stress (Gupta and Huang 2014; Paes de Melo et al. 2022). There are several signaling pathways including the calcium-dependent protein kinase pathway, the mitogen-activated protein kinase pathway and the salt overly sensitive pathway (Gao et al. 2008). In order to activate their defense system and ensure their survival following exposure to an environmental stress, plants may engage different signaling pathways and express several genes that code for a set of protective proteins, including late abundant embryogenesis proteins and heat shock proteins (Villalobos-López et al. 2022).

In sum, environmental stresses may enhance the resistance of plants by stimulating their stress-resistance mechanisms. However prolonged exposure to stressors can cause irreversible damage to the structure and function of plant cells. The studies conducted so far have helped in identifying and understanding the response mechanisms of plants to environmental stresses at different levels (i.e., morphological, physio-biochemical and molecular levels). Combining this knowledge with the advances made in the field of plant micropropagation would make a great tool for rapid and large-scale production of plants with enhanced resistance to environmental stresses.

15.4 Morphological and Physio-Biochemical Responses of Plants to Abiotic Stresses Induced in Vitro

Among the different factors affecting plant growth and productivity is the ever-changing environment, which put plants under stress. This includes biotic stresses such as infection by pests and pathogens, and abiotic stresses such as drought, salinity, extreme temperatures and heavy metal toxicity (Mazri et al. 2023). Developing stress-tolerant crops is therefore a must for sustainable agriculture.

Plant responses to environmental stresses are diverse, from gene expression to physiology, from morphology to metabolism (Mareri et al. 2022). Besides, plant responses to environmental stresses also depend on the growth stage, and stress intensity and duration (Radi et al. 2023). In order to assess/improve plant tolerance to environmental stresses, in vitro experiments can be done by using stressors such as sodium chloride (NaCl) for salt stress, polyethylene glycol (PEG), sorbitol or mannitol for drought stress, and pathogen culture filtrate and phytotoxins for biotic stresses. In vitro culture under stress conditions would allow to understand plant mechanisms to adapt to stress and also to select lines with enhanced tolerance to environmental stress (Radi et al. 2023). In vitro culture experiments are conducted under controlled laboratory conditions thus provide a better understanding of the morphological and physio-biochemical responses of plants to environmental stress. In addition, complex interactions between plants and their environment can be controlled or suppressed, while the intensity and duration of stress can be precisely and conveniently controlled. All of these factors allow for in-depth analysis of the different aspects of plant growth and development under adverse conditions. Over the past two decades, in vitro studies were conducted in order to understand the mechanisms underlying plant responses to stress and to identify specific genes/metabolites that are responsible for tolerance and adaptation. These studies also aimed to improve tolerance to abiotic stresses in a variety of species including date palm (El Hadrami et al. 2011), tomato (Aazami et al. 2010), cactus pear (Radi et al. 2023), rice (Abdelnour-Esquivel et al. 2020) and potato (Laisina et al. 2021) among many others. This section provides information related to the use of tissue culture technology as a tool to understand the mechanisms underlying plant adaptation to abiotic stresses.

15.4.1 Salt Stress

Salinity is a very common abiotic stress that affects plant growth and development. Salinity stress is usually caused by excessive concentrations of Na^+ and/or Cl^- ions (Shelke et al. 2019). The problem of soil salinity has always existed. However, it was exacerbated by agricultural practices (Çavuşoğlu 2020). According to Sita and Kumar (2020), salinity affects about 20% of cultivated lands and 50% of world's irrigated lands, thus significantly reduces agricultural production and threatens food security.

Many researchers have added NaCl to the culture medium in order to assess plant tolerance to salt stress. Besides, different types of plant material (e.g., suspension cultures, calli, somatic embryos, shoot cultures) and various species of high economic importance such as tomato (Zaki and Yokoi 2016), potato (Ahmed et al. 2020), rice (Revathi and Pillai 2015) and maize (Balkrishna and Shankarrao 2013) were used to evaluate their aptitude to tolerate different levels of salinity.

Based on several studies, salt stress alters the morphological and physio-biochemical processes associated with plant growth and development, because salinity causes osmotic and oxidative stresses, which lead to ionic imbalance and nutritional deficiency (Kumari et al. 2021; Rangseekaew et al. 2022). According to Gupta et al. (2016), NaCl reduced the growth parameters (e.g., shoot proliferation and length) of *Stevia rebaudiana* explants. Similar results were observed in many other species including guava (*Psidium guajava* L.) (Rai et al. 2010), pistachio (*Pistacia vera* L.) (Raoufi et al. 2021) and cactus pear (*Opuntia ficus indica*) (Radi et al. 2023).

At the physio-biochemical and enzymatic levels, it was reported that salt stress increases the activities of antioxidant enzymes, promotes the accumulation of osmo-protectants such as proline and glycine betaine which are involved in the process of osmotic adjustment, and induces changes in other macromolecules depending on plant growth stage and the severity and duration of stress (Razavizadeh et al. 2023; Radi et al. 2023). Rai et al. (2010) reported that increasing the concentration of NaCl in the culture medium increased the proline and glycine betaine contents in guava (*Psidium guajava* L.) leaves, while it decreased those of chlorophylls and carotenoids. Raoufi et al. (2021) reported that increasing the level of salt stress enhanced the contents of proline and soluble sugars in pistachio (*Pistacia vera* L.), while the contents of starch and chlorophylls were reduced. In a recent study by our group (Radi et al. 2023), it was found that salinity caused a drop in proline, glycine betaine and total carbohydrate levels of cactus pear organogenic cultures. However, this drop was followed by the accumulation of these compounds as the intensity and duration of stress were increased. Besides, the concentrations of chlorophyll *a* and total proteins decreased with increasing stress duration. Razavizadeh et al. (2023) noted that salt stress stimulated the accumulation of proline and reducing sugars, and enhanced the activity of SOD, CAT and APX in seedlings and calli of *Carum copticum* (L.). According to Singh et al. (2023b), CAT, nitrate reductase (NR), peroxidase and indole-acetic acid (IAA) are all indicators of stress tolerance in sugarcane and play a crucial role in the protection of cellular structures against oxidative stress caused by salinity.

Another mechanism of plant defense against salt stress is the production of bioactive molecules and secondary metabolites. For example, Razavizadeh et al. (2023) reported that salt stress induced in vitro is a reliable and sustainable approach for the production of phenolic compounds and anthocyanin from seedlings and calli of *Carum copticum* (L.). Similarly, Raoufi et al. (2021) found that salt stress enhanced the malondialdehyde (MDA) content of in vitro cultured pistachio shoots. Gupta et al. (2016) regarded in vitro culture under salt stress conditions as an alternative method for the production of secondary metabolites, in particular steviol glycoside, a highly sweet non-toxic compound with negligible effect on blood glucose.

Micropropagation-associated stress conditions is also an interesting tool to improve resistance of micropropagated plants to salt stress. Along this line, potato cell lines were successfully selected by exposing potato callus cultures to increasing concentrations of NaCl (Queiros et al. 2007). These cell lines showed good cell proliferation, increased levels of soluble and insoluble proteins, ascorbic acid and MDA. Likewise, Hossain et al. (2007) demonstrated that a gradual increase in NaCl concentration is a reliable method to obtain salt-tolerant calli in *Chrysanthemum morifolium*. The selected calli were successfully used to regenerate plants tolerant to salt stress (Hossain et al. 2007).

15.4.2 Drought Stress

Drought (or water deficit) is one of the major abiotic stresses that inflicts significant damage to agriculture. Drought leads to a decrease in moisture content, a water deficit in the soil and a decline in water potential in plant tissues. In vitro culture can be used as a tool to select lines with enhanced tolerance to drought stress. This is based on the fact that in vitro and in vivo responses of plants to drought are assumed to be similar (Smith et al. 1985).

Drought stress is simulated by the addition of osmotica such as mannitol, sorbitol or PEG to culture media. These compounds lower the water potential of the medium. Consequently, it becomes difficult for plants to take up water, which leads to the reduction of water potential in plant cells and tissues (Piwowarczyk et al. 2014). The tolerance mechanisms generated by plants under drought conditions allow them to grow, or at least survive, at reduced water potential (Verslues et al. 2013). Previous studies showed that simulating drought stress under in vitro conditions is a feasible way to assess the effects of drought on plant growth and development (Bündig et al. 2017; Harun-Or-Rashid et al. 2021).

While many researchers have used PEG, mannitol or sorbitol as an osmotic stress agent to evaluate plant tolerance to drought and for in vitro selection purposes, PEG (especially that of 6000 molecular weight) has been the most widely used to mimic dry soil environments and create drought conditions in vitro (e.g., Wani et al. 2010; Kacem et al. 2017; Ahmad et al. 2020; Molnar et al. 2022). The morphological responses of plants to drought stress induced in vitro varied depending on the species. Generally, drought stress results in a negative impact on the morphological parameters of plants, especially in terms of shoot/stem length. For example, Acemi et al. (2018) noted that increasing the concentration of PEG decreased the shoot length of European Bluestar (*Amsonia orientalis* Decne.). Similar findings were reported by Razavizadeh et al. (2019), Hosseini et al. (2020) and Mansinhos et al. (2022). However, in other species, divergent results were observed. For example, drought stress had a negative impact on blueberry (*Vaccinium corymbosum*) shoot length, yet other morphological parameters such as shoot number and proliferation were improved as compared to PEG-free medium (Molnar et al. 2022). In cactus pear (*Opuntia ficus indica*), drought stress had a negative impact on shoot proliferation and growth, but promoted root formation and growth (Radi et al. 2023). According to Ahmad et al. (2020), drought stress induced by PEG improved the morphological parameters (nodal explant shooting, shoot length, node number, leaf number and fresh weight) of *Stevia rebaudiana*. Mehmandar et al. (2023) suggested to use PEG and sorbitol for accurate, rapid, and reliable in vitro screening to assess and identify potentially drought-tolerant genotypes of melon (*Cucumis melo* L.).

The capability of plants to withstand drought stress is achieved by antioxidative enzymes such as peroxidases and catalases, and the accumulation of compatible solutes, particularly proline (Mansoor et al. 2022). Generally, the findings from the literature show that increasing PEG (or any other drought stress-inducing agent) concentration in the culture medium resulted either in an increased proline content or in a drop in proline level followed by the accumulation of this osmoprotectant as the intensity and/or duration of stress increase. According to Pradhan et al. (2021), osmolytes such as proline play a major role in the process of plant adaptation to drought stress. Rahim et al. (2020) observed positive correlations between PEG concentration and proline content, APX and CAT activities in rice (*Oryza sativa* L.). Similarly, drought stress induced by PEG improved the contents of rebaudioside A and stevioside and increased the antioxidant activity in in vitro grown shoots of *Stevia rebaudiana* (Ahmad et al. 2020). In *Thymus lotocephalus*, increasing the concentration of PEG increased the proline content (Mansinhos et al. 2022). However, in melon (*Cucumis melo* L.), the proline content showed an increase followed by a decrease with increasing PEG and sorbitol concentrations to a certain level, while the content of MDA was positively correlated with PEG and sorbitol concentrations (Mehmandar et al. 2023). In cactus pear (*Opuntia ficus indica*), the opposite was observed since osmoprotectants (i.e., proline and glycine betaine) showed first a drop in their concentrations followed by their accumulation as the stress was prolonged, which was interpreted as adaptation to drought (Radi et al. 2023). These results could reflect different levels of tolerance or adaptation processes to drought stress among plant species. On the other hand, many researchers reported that drought decreases the amount of pigments. Along this line, Molnar et al. (2022) observed negative impacts of drought stress on chlorophyll and carotenoid contents in blueberry (*Vaccinium corymbosum*), as compared to PEG-free medium. In *Thymus lotocephalus*, increasing the concentration of PEG decreased the chlorophyll and carotenoid contents (Mansinhos et al. 2022). Likewise, PEG and sorbitol decreased the content of photosynthetic pigments in melon (*Cucumis melo* L.) (Mehmandar et al. 2023).

During the somatic embryogenesis process, many researchers found that moderate drought stress promoted somatic embryo maturation and subsequent germination. Indeed, moderate drought stress induced by PEG, sorbitol or mannitol would create a culture environment similar to desiccation (Zhang et al. 2007). Such environment was reported to induce osmoregulation and promote the accumulation of proline, proteins, lipids, amino acids and sugars by somatic embryos (Al-Khayri and Al-Bahrany 2004; Agarwal et al. 2004; Yaseen et al. 2013). PEG was therefore suggested for the maturation of somatic embryos of numerous species such as holm oak (*Quercus ilex* L.), papaya (*Carica papaya* L.) and date palm (*Phoenix dactylifera* L.) (Blasco et al. 2013; Vale et al. 2018; Mazri et al. 2019a, b, c).

15.4.3 Heavy Metal Stress

In recent years, soil contamination by heavy metals (e.g., cadmium (Cd), lead (Pb), chromium (Cr), arsenic (As)) has experienced a continuous increase due to anthropogenic activities such as urbanization and excessive use of fertilizers, which deteriorated the quality of agricultural soils. Heavy metals are defined as metals with an atomic density greater than 5 g/cm^3 (Mitra 2015). Some heavy metals such as zinc (Zn), manganese (Mn), copper (Cu) and iron (Fe) are necessary for plant growth but at low concentrations (Elango et al. 2022). At high levels, these elements become toxic and exert harmful stress on plants by disturbing plant metabolism (Elango et al. 2022). Some other elements such as Cd and As are non-essential for plants and exerts harmful effects even at low concentrations (Thakur et al. 2022). The toxicity by heavy metals induces a multitude of reactions and adaptive responses in plants. Similar to other abiotic stresses, in vitro studies have been carried out on several plant species in order to investigate and understand the effects of heavy metal stress on plant growth, development, physiological and biochemical traits, and also to select and regenerate genotypes tolerant to this type of stress.

Chaitanya et al. (2022) evaluated the effects of different concentrations (50–150 μM) of Zn, Cu and Cd on nodal explants of *Momordica cymbalaria.* It was found that 150 μM of Zn reduces shoot proliferation and growth. Regarding Cu, a concentration of 50 μM gave optimal responses. On the other hand, 50 μM of Cd led to callus formation with no signs of growth and development. Higher concentrations of Cd turned out to negatively affect shoot proliferation and growth and led to explant death. Moreover, increasing the concentrations of heavy metals in the culture medium decreased the chlorophyll content of shoots. The results of this study led to the conclusion that at low concentrations, Cu and Zn are essential for plant growth and development. This is in good agreement with the findings of Ali et al. (1998), Naik et al. (2015), Alam et al. (2020) and Martins et al. (2020). According to Ali et al. (1998), a Cu concentration higher than 100 μM negatively affected the morphological responses of *Bacopa monniera* by reducing shoot length, shoot number, rooting and fresh biomass. Naik et al. (2015) observed a positive effect of low concentrations of Zn (0.12 mM) and Cu (0.02 mM) on shoot proliferation and biomass accumulation in *Bacopa monnieri*. However, they found that the highest concentration of Cu (0.20 mM) promoted the accumulation of bacoside A, a chemical compound known for its neuroprotectivity. Thus, they suggested that in vitro heavy metal stress can be used to promote the production of bioactive molecules. According to Martins et al. (2020), a high Cu concentration (200 μM) decreased biomass accumulation of *Alternanthera tenella*, reduced cell sizes and caused partial inhibition of electron transport and photochemical activity of photosystem II. Samiei et al. (2020) evaluated the morpho-physiological responses of in vitro seedlings of *Climacoptera crassa* to different concentrations of Pb and Cd (0–2 mM). It was found that increasing the concentration of Pb and Cd to 2 mM negatively affected shoot length, leaf number, root number and length. Moreover, a concentration of Cd ranging from 1 to 2 mM led to plant death. Besides, the carotenoid and chlorophyll contents decreased with increasing the concentrations of Pb and Cd.

Proline accumulation was also reported as an adaptation mechanism to heavy metals. According to Zhu et al. (2020), high Cu concentrations (e.g., 200 mg.L^{-1}) rapidly activate the self-protection mechanism of *Belamcanda chinensis* calli by promoting proline accumulation. Ali et al. (1998) observed a positive correlation between Cu concentration and proline content in *Bacopa monniera* shoots. Likewise, Samiei et al. (2020) found that increasing the concentration of Cd and Pb in the culture medium promoted the accumulation of proline in *Climacoptera crassa* leaves. Sharma et al. (1998) suggested that proline protects enzymes such as glucose-6-phosphate dehydrogenase (G6PDH) and NR against Zn and Cd toxicity, probably through the formation of Zn-proline and Cd-proline complexes. Proline accumulation was therefore considered as a protection mechanism against heavy metal toxicity.

15.5 In Vitro Mycorrhization: A Novel Method to Produce Stress Tolerant Plants

In recent years, many studies were conducted to highlight the importance of telluric microorganisms and their application in modern agriculture. Among these beneficial microorganisms, mycorrhizal fungi have been widely studied and suggested as an alternative to chemical fertilizers and pesticides (Sammama et al. 2022).

Mycorrhiza is a symbiotic association between the roots of a higher plant and a soil fungus (Geetha and Dathar 2022). This symbiosis is characterized by a mutually beneficial relationship for both plants and fungi (El Amerany et al. 2020). It has been reported that mycorrhizal infection dates back 450 million years ago when plants started transition from aquatic to terrestrial environments, hence the importance of this interaction in plant life cycles (Brundrett and Tedersoo 2018). Under natural conditions, 80 to 90% of plants are colonized by mycorrhizal fungi (Han et al. 2019; Kamal et al. 2020).

There are two major types of mycorrhizae depending on the type of fungus-root association formed: ectomycorrhizae and endomycorrhizae (Huey et al. 2020). In ectomycorrhizae, an intercellular network of hyphae known as the Hartig net is formed. In this case, the fungal hyphae do not penetrate the individual cells of plant roots. Less than 5% of plants are associated with ectomycorrhizal fungi, including some perennial and wood-producing species of economic importance such as Pinaceae and Fagaceae, and some shrubs and members of the Basidiomycota and Ascomycota (Bucking et al. 2012; Waterman et al. 2013; Iannaccone and Buhagiar 2021). In endomycorrhizae, the hyphae penetrate the cell wall and invaginate the cell membrane of roots (Huey et al. 2020). Endomycorrhizae are the most widespread type of mycorrhizal association occurring in plants, with different categories, namely monotropoid, orchid, ericoid, arbutoid and arbuscular mycorrhizae (Kamal et al. 2010). Arbuscular mycorrhizal symbiosis is the most common symbiosis between plants and soil fungi (Bentrad and Bouhired 2022).

Unlike plants, fungi are unable to produce their own organic matter, thus they need reduced carbon as an energy source to sustain their growth and metabolism. This makes mycorrhizal completely dependent on host plants (Jansa and Treseder 2017). In return, the host plant receives mineral nutrients (Genre et al. 2020). Indeed, mycorrhizal fungi increase the absorption surface of plant roots and therefore the efficiency of water and nutrient uptake. This is due to the formation of an extended filamentous network around roots (i.e., the mycelial hyphae), which can penetrate deep into the soil and reach levels that are otherwise inaccessible by roots to absorb more water and mineral nutrients, in particular those with low mobility such as phosphorus (Mathur et al. 2019; Püschel et al. 2021).

Other benefits of mycorrhizal symbiosis include improved water-use efficiency and yield under stress conditions (Askari et al. 2019). Indeed, it is well known that climate change has aggravated the effects of abiotic and biotic stresses on agricultural productivity and threatens global food security. Along this line, plant-mycorrhiza association was suggested to enhance plant tolerance to environmental stresses (Inbaraj 2021). To cope with biotic and abiotic constraints and to improve plant growth and nutrient uptake, many plant species of great economic value, such as grapevine and argan were subjected to mycorrhizal inoculation (Aguilera et al. 2022; Soufiani et al. 2022). Many Other studies aiming to improve plant growth and productivity under stress conditions were undertaken (e.g., Ruiz-Lozano et al. 1995; Yooyongwech et al. 2016; Manga et al. 2017; Zardak et al. 2018). The findings of these investigations revealed greater nutrient uptake by mycorrhizal plants under stress conditions, particularly phosphorus, potassium and nitrogen, compared to non-mycorrhizal controls. Besides, higher concentrations of proline, carbohydrates and proteins were found in the tissues of mycorrhizal plants compared to non-mycorrhizal controls. Such accumulation of osmoprotectants and macromolecules allows osmotic adjustment of cells exposed to stress as a physiological mechanism to sustain growth and productivity under stress and reflects plant adaptation to adverse environments (Lilius et al. 1996; Wang et al. 2012; Fu et al. 2019). As a result, mycorrhizae have a well-established role in enhancing the stress tolerance of plants.

Given that in vitro culture is a powerful biotechnological tool for rapid and large-scale production of plants, and that mycorrhizae have positive effects on plant growth and development under stressful conditions, in vitro mycorrhization has attracted great interest in recent years thanks to the beneficial effects of mycorrhizal fungi on root growth under in vitro conditions, plant acclimatization and subsequent growth and development under normal and adverse environmental conditions. Consequently, a higher tolerance to the stress caused by plant transfer from in vitro to ex vitro conditions (Kapoor et al. 2008; Soumare et al. 2021; Cantabella et al. 2022). In vitro mycorrhization would allow for homogeneous and rapid colonization by mycorrhizae in an environment free from other undesirable contaminations. It is also a tool for large-scale production and commercialization of mycorrhizal fungi.

In vitro mycorrhization can be achieved through different culture systems:

- The autotrophic culture system for in vitro mycorrhization (ACS), which consists of a mono-compartmental Petri dish containing a sucrose and vitamin-free culture medium (e.g., modified Strullu-Romand (MSR) medium (Declerck et al. 1998), on which mycorrhizal association is established between the roots of an autotrophic plant and mycorrhizal fungi. The growing shoot is developed through a hole in the lid or an opening in the sidewall of the Petri dish (Voets et al. 2005). This system allows for high sporulation and colonization rates, and is well suited for mycorrhizal proliferation due to the ability of spores produced in vitro to colonize new seedlings under the same conditions (Voets et al. 2005).
- The half-closed arbuscular mycorrhizal-plant (HAM-p) was developed based on the ACS system. The difference lies on the fact that in HAM-p a bi-compartmental Petri dish is used instead of a mono-compartmented one. In HAM-p, the roots of the host plantlet are placed on the surface of the medium in the first compartment (i.e., root compartment (RC)). Isolated spores are inoculated with the roots of the host plantlet. The plantlet shoot grows outside of the Petri dish through the hole previously made in the lid or the opened sidewall. In the second compartment (hyphal compartment (HC)) only the extraradical hyphae are allowed to proliferate (De Boulois et al. 2009).
- The mycelium donor plant (MDP) (also known as mycorrhizal donor plant) method is the most used system for in vitro mycorrhization (Table 15.1). It consists of two Petri dishes of different diameters; for example, 55 and 145 mm (Koffi and Declerck 2015). Both Petri dishes are filled with the same culture medium; for example, modified Strullu-Romand (MSR) medium (Declerck et al. 1998) without vitamins and sucrose. In this system, a donor plant is used to facilitate and boost mycorrhization of the host plantlet. The small Petri dish (RC) is placed inside the biggest one (HC). RC is where the roots of the donor plant are placed along with mycorrhizal spores. *Medicago truncatula* is generally used as a donor plant since it is a strong mycotrophic plant (Koffi and Declerck 2015). HC is where the fungal hyphae develop and where to culture the host plantlet. The extraradical mycelium bearing spores moves from RC to colonize the roots of the host plantlet in HC. This system was successfully applied for banana (Koffi and

Declerck 2015), potato (Fernández et al. 2017), pear (Lotfi et al. 2019), date palm (El Hilali et al. 2021) and argan (Ganoudi et al. 2021).

In vitro *mycorrhization* is also a tool for large-scale production and commercialization of mycorrhizal fungi. Along this line, the root organ culture (ROC) system was developed for the in vitro culture of mycorrhizae. This system consists of culturing Ri T-DNA transformed root segments on a culture medium (generally M (Bécard and Fortin 1988) or MSR media) to promote the growth of lateral roots (Declerck

Table 15.1 Mycelium donor plant (MDP) culture system used for in vitro mycorrhization of some economically important species

Host plant	Donor plant	Culture medium	Mycorrhizal fungi	Reference
Rubber tree (*Hevea brasiliensis* Müll. Arg.) genotype Prang Besar PB 260	*Medicago truncatula* Gaertn. cv Jemalong A17	Semi-solid modified Strullu-Romand medium without vitamins and sucrose	*Rhizophagus irregularis* strain MUCL 41,833	Sosa-Rodriguez et al. (2013)
Banana (*Musa acuminata*) cv. Grande Naine	*Medicago truncatula* Gaertn. cv Jemalong A17	Semi-solid modified Strullu-Romand medium without vitamins and sucrose	*Rhizophagus irregularis* strain MUCL 41,833	Koffi and Declerck (2015)
Potato (*Solanum tuberosum* L.) cv. Desirée	*Medicago truncatula* Gaertn. cv Jemalong A17	Semi-solid modified Strullu-Romand medium without vitamins and sucrose	*Rhizoglomus intraradices* strain MUCL 41,833	Fernández et al. (2017)
Pear (*Pyrus communis* L.) cv. Arbi	*Medicago truncatula* Salsa	Semi-solid modified Strullu-Romand medium without vitamins and sucrose	*Rhizophagus irregularis* strain INCAM11	Lotfi et al. (2019)
Date palm (*Phoenix dactylifera* L.) cv. Boufeggous	*Medicago truncatula* Gaertn. cv Jemalong A17	Semi-solid modified Strullu-Romand medium without vitamins and sucrose	*Rhizophagus irregularis* strain MUCL 41,833	El Hilali et al. (2021)
Argan (*Argania spinosa* (L.) Skeels)	*Medicago truncatula* Gaertn. cv Jemalong A17	Semi-solid modified Strullu-Romand medium without vitamins and sucrose	*Rhizophagus irregularis* strain MUCL 41,833	Ganoudi et al. (2021)

et al. 1996; Verdin et al. 2006). Mycorrhizal association between fungi and root cultures is thereafter established. Ri T-DNA transformed carrot roots are the most frequently used as host for monoxenic cultivation of mycorrhizal fungi. Transformed roots are used because they allow greater mycorrhizal colonization, promote and sustain extraradical hyphal development and stimulate fungal production (Danesh and Tufenkci 2017). This system is very efficient for the mass production of mycorrhizal spores (Declerck et al. 1996). Different species were used for the in vitro culture of mycorrhizae, including *Daucus carota* (L.) (Declerck et al. 1996), *Solanum lycopersicum* Mill. (Diop et al., 1994), *Cichorium intybus* (L.) (Verdin et al. 2006) and *Linum usitatissimum* L. (Rodrigues and Rodrigues 2015).

Up to date, in vitro mycorrhization has been successfully achieved in a number of plants. In vitro mycorrhization improved the morphological and physio-biochemical characteristics of plants (e.g., rooting, stem and root growth, acclimatization, fresh and dry weights, chlorophyll content, proline content, etc.) and accelerated the field transplanting process. This leads to the conclusion that this method could be proposed as a promising and powerful tool for rapid propagation of plants with enhanced tolerance to abiotic and biotic stresses. In vitro mycorrhization would also allow for rapid multiplication of mycorrhizal fungi and sustainable production of spores. Additionally, in vitro mycorrhization can be an interesting area for further in-depth research on plant-microorganism interaction to better understand mycorrhizal symbiosis.

15.6 Use of Tissue Culture Methods for Rapid and Large-Scale Production of plants Resistant to Biotic Stressors: Cases of Date Palm (*Phoenix dactylifera* L.) and Cactus Pear (*Opuntia* spp.) in Morocco

One of the main goals of plant tissue culture is the rapid and large-scale production of plants. Under conditions of abiotic and biotic stresses, plant micropropagation could be a powerful tool for the production of stress-tolerant plants. Among the different micropropagation methods, organogenesis allows for the rapid and large-scale production of uniform plants. In this section, we describe the Moroccan experience in controlling the date palm Bayoud disease by using organogenesis for mass production of Bayoud-resistant cultivars and to preserve the elite susceptible ones, and the potential use of this method in the case of cactus pear to rapidly and efficiently propagate the cochineal-resistant cultivars.

15.6.1 Date Palm

Date palm (*Phoenix dactylifera* L.) belongs to the Arecaceae family. It is native to Mesopotamia (modern Iraq) and is primarily grown in the Middle-East and North-Africa (Johnson et al. 2013). In Morocco, date palm groves cover a total area of about 60,000 ha, with more than 450 cultivars and 2.6 million khalts (i.e. spontaneously regenerated seedlings), and is mainly located in the Draa-Tafilalet region (MAPMDREF 2023a, b). Date palm plays important socio-economic and ecological roles in arid and semi-arid regions by generating employment, providing local populations with food and other products, and creating microclimates suitable for crop growth and ecosystem function (Jain 2012). Unfortunately, Moroccan date palm has suffered for decades from a wilt disease called Bayoud. This disease is caused by fungus *Fusarium oxysporum* f. sp. albedinis. Bayoud has caused the loss of more than 10 million date palms in Morocco during the 20th century and the disappearance of many high commercial value cultivars. Moreover, the best date palm cultivars such as Mejhoul, Boufeggous and Bouskri are very sensitive to Bayoud and have experienced significant losses in their populations (Mazri et al. 2017, 2018).

Propagation by tissue culture, namely direct organogenesis, is the main method used in Morocco for date palm propagation (Mazri et al. 2021a; b). Organogenesis is utilized to achieve two purposes: (i) grove rehabilitation by planting each year thousands of date palms that are resistant to Bayoud, and (ii) preservation of Bayoud-susceptible cultivars by creating new orchards in Bayoud free-areas (Mazri et al. 2022b).

Date palm propagation by organogenesis: a powerful tool to control Bayoud and preserve susceptible cultivars

In date palm, organogenesis can be achieved from either shoot tip or inflorescence explants (Mazri and Meziani 2015). In both cases, the regeneration process comprises the following steps: adventitious bud induction, shoot bud multiplication, shoot elongation and rooting and plantlet acclimatization (Meziani et al. 2019) (Fig. 15.1). Generally, the production of rooted shoots takes at least 15 months: 9 months for induction, 3 months for multiplication and 3 months for elongation and rooting. However, to maximize plant production, the multiplication phase can be extended up to 15 months.

In order to control Bayoud and preserve the best date palm cultivars, Morocco has chosen a strategy based on the rapid and large-scale propagation of two categories of date palm cultivars: those resistant to Bayoud; for example, cv. Najda, and high commercial value cultivars that are susceptible to Bayoud and thus planted in Bayoud free-areas; for example, cv. Mejhoul.

Selection and multiplication of Bayoud-resistant date palm cultivars

Since the 1960s, Morocco has undertaken a date palm rehabilitation program based on prospection, selection and multiplication of date palm genotypes characterized

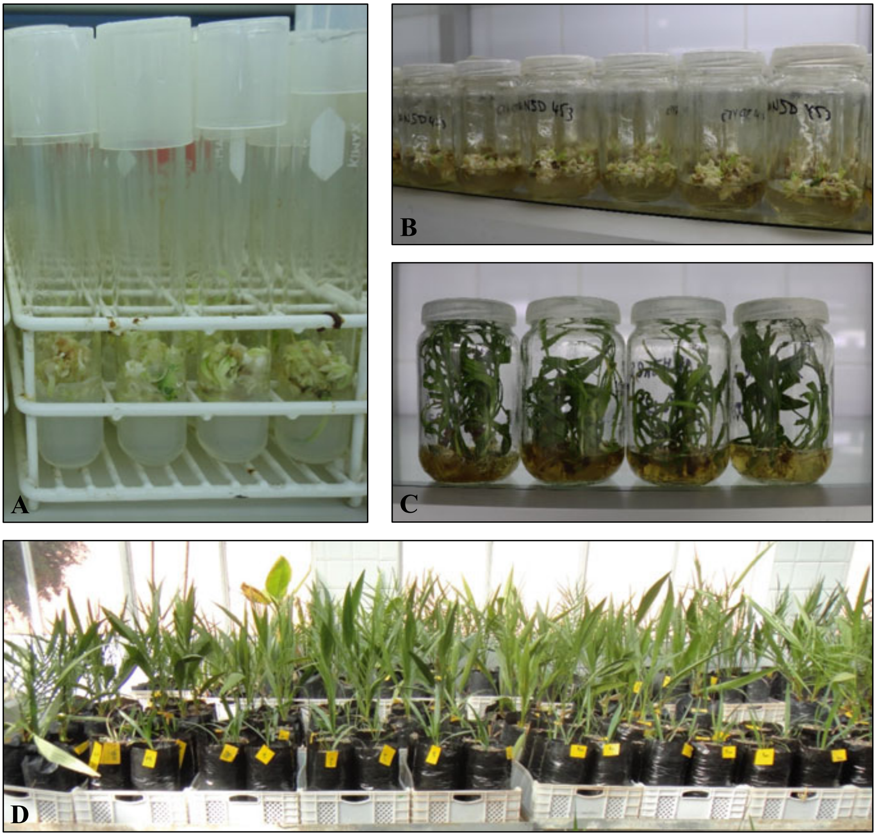

Fig. 15.1 Date palm (*Phoenix dactylifera* L.) propagation by organogenesis. **a** Adventitious bud induction. **b** Shoot bud multiplication. **c** Shoot elongation and rooting. **d** Plantlet acclimatization

by Bayoud resistance and good fruit quality. Prospections and selection were mainly performed among khalt populations. Afterwards, screening for Bayoud resistance was performed both in the field and under laboratory conditions (Sedra 2011). As a result of these investigations, many genotypes characterized by high fruit quality and resistance to Bayoud were selected. For example, Sedrat (INRA-3003), Najda (INRA-3014), Al-Amal (INRA-1443), Daraâouia (INRA-1445) and Al-Fayda (INRA-1447) (Sedra 2011). Among all these cultivars, cv. Najda was the most adopted by farmers and most appreciated by consumers.

Use of tissue culture to preserve Bayoud-susceptible cultivars

In order to preserve the best Moroccan date palm cultivars that are susceptible to Bayoud; for example, cvs. Mejhoul, Boufeggous and Bouskri, and to enhance and sustain their productivity, new and modern date palm orchards were created in Meski-Boudnib (Drâa-Tafilalet region, Morocco) (El Bakouri et al. 2021). This region known as "extension zone" is characterized by favorable climatic conditions for date palm cultivation and is free of Bayoud. Up to date, more than 1.3 million tissue culture-derived date palms have been planted in the extension zone (MAPMDREF 2023a, b). Besides, Morocco aims to plant 1.4 million date palms in this region by 2030 (MAPMDREF 2022).

Optimization of culture media and conditions for date palm organogenesis

It is well known that successful micropropagation and regeneration of plants depends on many factors including the genotype, explant type, culture medium and culture conditions (Koufan et al. 2022). Based on our own experience, successful micropropagation of date palm is genotype-dependent. Along this line, several experiments were conducted during the last decade to optimize the culture medium and conditions for the best date palm cultivars, both those threatened by Bayoud and those selected for their resistance to the Bayoud disease. As a result, efficient micropropagation and regeneration systems were developed for cv. Mejhoul (Mazri et al. 2016, 2018), cv. Boufeggous (Mazri 2015), cv. Bouskri (Mazri et al. 2021a, b, c), cv. Najda (Mazri 2012; Mazri and Meziani 2013), cv. Aziza Bouzid (Elmaataoui et al. 2020) and cv. Al-Fayda (Mazri et al. 2019c).

Moroccan strategies to develop the date palm sector: Green Moroccan Plan (2008-2020) and Green Generation (2020–2030)

Date palm has been at the center of past and present Moroccan strategies to develop the agricultural sector. In 2008, Morocco has launched the Green Moroccan Plan (Plan Maroc Vert, PMV) as a national strategy to develop Moroccan agriculture. Regarding the date palm sector, one of the major purposes of PMV was the plantation of 3 million date palm plants. This objective was reached in 2019 by using organogenesis as a tool for mass-production of date palm plants (Mazri et al. 2021a). The main cultivars planted were cv. Mejhoul, cv. Boufeggous, cv. Bouskri and cv. Najda. The outcomes of the PMV clearly show the effectiveness of in vitro propagation, particularly organogenesis, in controlling a major biotic stress such as Bayoud and preserving susceptible and elite cultivars. It worth noting that organogenesis has been chosen over somatic embryogenesis in order to avoid the production of somaclonal variants, which would be catastrophic for small farmers (Ferry 2011). Indeed, direct organogenesis allows for the production of true-to-type plants (Mazri et al. 2019c). After this successful experience, Morocco has launched a new strategy called 'Green Generation' for the current and upcoming years (2020–2030) with the purpose of planting 5 million date palms (MAPMDREF 2022). In addition to the above-mentioned cultivars, other date palm cultivars will be used for mass propagation. Plant propagation will be made by organogenesis.

15.6.2 Cactus Pear

Cactus pear (*Opuntia* spp.) is a multipurpose plant genus native to the tropical and subtropical regions of America but cultivated in many countries with different soil and climatic conditions (Mazri 2021). The genus *Opuntia* (Cactaceae) consists of about 300 species, among which *O. ficus indica* is the most economically important one (Palevitch et al. 1993; Pinedo-Espinoza et al. 2017). Cactus pear is cultivated for many purposes including human and animal consumption, as food additive, to prevent deforestation, soil degradation, erosion and environmental destruction, to preserve biodiversity and ecosystem function, and for cosmetic and pharmaceutical applications (Mazri 2018). Many cactus pear species suffer from the cochineal scale insect (*Dactylopius opuntiae*) (also known as *Opuntia* cochineal scale and prickly pear cochineal). This insect may cause severe damage to cactus pear plantations (Bouharroud et al. 2016). Since its introduction to Morocco in 2015, the cochineal has caused drastic losses in cactus pear plantations, with more than 80,000 ha of cactus pear being completely destroyed (Bouharroud et al. 2016; Hortimedia 2022).

Selection of resistant cultivars and conventional propagation

For years, Morocco has been the home of a great cactus pear phylodiversity with many species (but mainly *O. ficus indica*) and hundreds of genotypes and ecotypes (El Kharrassi et al. 2017). Unfortunately, since 2015, Morocco has experienced the loss of a great part of its cactus pear genetic patrimony because of the cochineal scale insect *Dactylopius opuntiae* (Mazri 2018). Thus, strict and emergency actions were initiated by the Moroccan department of agriculture to control the cochineal scale insect. They include the use of natural enemies, natural and chemical products as well as mechanical methods that consist of removing and burning infected plants (MAPMDREF 2017; Mazri et al. 2023). However, the most pertinent and relevant result was the selection of eight resistant cultivars to the cochineal scale insect. These cultivars that belong to different cactus pear species were baptized Marjana, Belara, Karama, Ghalia, Angad, Cherratia, Melk Zhar and Aakria (Sbaghi et al. 2018). Afterwards, a large-scale multiplication and planting program was started and is currently underway to rehabilitate Moroccan cactus pear areas (Sabbahi and Hock 2022). This propagation program is based on conventional propagation by cladode cuttings. The use of tissue culture methods, particularly organogenesis, would certainly help to quickly achieve the objective outlined by the Moroccan department of agriculture (Mazri et al. 2023). Thus, research activities are currently underway to develop efficient micropropagation systems for the cactus pear genotypes resistant to the cochineal scale insect.

Cactus pear propagation by organogenesis

In cactus pear, organogenesis is initiated from areoles. Areole explants (i.e., cylindric segments each containing one areole) are grown in appropriate culture medium and conditions to promote shoot formation. This initiation phase generally takes 2 months. The areole-derived shoots are then cut into small segments and used as secondary explants (Bouchiha and Mazri 2022). Starting from this point, the regeneration process is similar to that used for date palm and comprises the following steps: adventitious bud induction (2 months), shoot bud multiplication (6 months), shoot elongation and rooting (3 months) and then plantlet acclimatization (Bouchiha and Mazri 2022) (Fig. 15.2).

Development of tissue culture systems for rapid and large-scale propagation of cactus pear

In addition to the planting program of cochineal-resistant cactus pear cultivars, that is based on conventional propagation by cladode cuttings, studies are currently underway to develop efficient in vitro regeneration systems for the resistant cultivars. The aim of these studies is to develop rapid, large-scale and reproducible protocols

Fig. 15.2 Cactus pear (*Opuntia* spp.) propagation by organogenesis. **a** Shoot development from areole explants **b** Adventitious bud induction from shoot explants. **c** Shoot bud multiplication. **d** Shoot elongation and rooting. **e** Plantlet acclimatization

based on organogenesis and somatic embryogenesis. Preliminary results have shown that 6 out of 8 cultivars can be propagated by direct organogenesis. The success of these in vitro multiplication experiments would greatly contribute to the control of the cochineal scale insect and the rehabilitation of cactus pear plantations in Morocco.

15.7 Conclusion

Due to the growing demand for food and the increase in the world population along with the challenges posed by climate change, many recent studies have been directed towards the development of rapid and efficient methods for the selection and mass multiplication of plants tolerant to environmental stress. Indeed, environmental stresses cause severe damage to plants at the morphological, physiological and biochemical levels, which negatively affects crop growth, yield and quality. Adaptation to climate change is essential for the sustainability of agriculture and to support food requirements of a growing world population. The establishment of an agricultural system more resilient to climate change requires the adoption of agricultural practices that would increase productivity and enhance tolerance to environmental stresses.

One of the strategies to deal with environmental stress is the selection and mass multiplication of plants that are tolerant to multiple stressors. Along this line, in vitro culture methods seem to be the most appropriate choice for plant breeders and horticulturists due to the numerous advantages they provide. Plant tissue culture not only offers the advantage of growing a large number of plants in a small space, but also offers possibilities for in vitro selection and genetic transformation. Under in vitro conditions, plants seem to respond to abiotic stress in the same way as in natural conditions. The response of plants to abiotic stress is done in a variety of ways, including the accumulation of osmoprotectants that protect macromolecules from damage, stabilize cellular structures, promote water absorption and retention and maintain cell turgor through osmoregulation. In addition, in vitro environment allows for more efficient monitoring and evaluation of the effects of abiotic stress as well as the development/selection of lines with enhanced tolerance to stressors. Another in vitro approach that allows for mass propagation of plants, reducing the effects of abiotic stresses and improving the growth and development of plants under stressful conditions is the use of certain microorganisms in vitro, particularly mycorrhizal fungi. In vitro culture is also a relevant strategy to control biotic agents such as pests and pathogens. In fact, micropropagation allows for the rapid and accurate screening of plant resistance to biotic stressors by using pathogen culture filtrate and phytotoxins, and also the rapid and large-scale multiplication of pest- and pathogen-resistant crops. In vitro culture therefore plays important roles in the development and mass multiplication of genotypes with enhanced tolerance to abiotic and biotic stresses, thus promoting agricultural sustainability and food security under adverse and changing environments.

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Chapter 16

Research Challenges in Sustainable Cultivation of Important Medicinal Plants in Oman; Insight into the Plant Environment Interactions Based on Different Climatic Zones

Shamshad Ahmad Khan, Aahd Mohammed, and Priyanka Verma

Abstract The different climatic condition plays a very important role in interaction of plants to a specific area and more importantly it effects the yield and productivity of a plant. Oman has its territories covered with different plant species specifically in areas such a Jabal Akhdar, a hilly region and Dhofar governorate. Environment conditions in these regions are quite different as the Dhofar region has various mountain ridges in combination with coastal areas of Arabian sea. The nature of the soil in these areas helps in the growth of plant species such as *Boswellia sacra, Anogeissus dhofarica, Adansonia digitata* and other plant species. Several varieties of *B. sacra* are present in this specific region depending upon the sesquiterpene exudate from the bark of this plant. Jabal Shams is also an arid mountenous area in Oman and according to zone wise vegetation plants such as *Acacia tortitilis, Euphorbia larica, Moringa peregrine, Ziziphus spina-Christie, Fagonia indica* and *Rhyza stricata* can be found in this region. Jabal Akhdar which is a part of Al Hajar mountain chains present in the Dakhliyah region also is rich in plant communities with presence of succulent, drought desiduous plant species such as *Convolvulus acanthocladus, Grewia tenax, Maerua, crassifolia* and *Moringa* species. The woodlands species such and *Sideroxylon mascatense, Olive* species, *Dodonanea viscosa* and *Myrtus communis* can also be found in this area with the presence of medicinal plants such as *Teucrium mascatense* and *Ephedra pachyclada.* The chapter discusses the different environment parameters and their effect on the vegetation of these plants with significance of Aflaj system of irrigation which demonstrate long lasting sustainable use of water resources for the cultivation in extremely arid desert lands.

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_16

Keywords Medicinal plants · Climatic zones · Aflaj system · Plant-environment interactions · Plant metabolites

16.1 Introduction

The different climatic condition plays a very important role in interaction of plants to a specific area and more importantly it effects the yield and productivity of a plant. Oman provides different climatic and ecological zones thus its territories are covered with different plant species specifically in areas such as Al Hajar mountain ranges, coastline of Al Batinah area and distinct areas of Dhofar governorate. Environment conditions vary in these regions are quite different as the Dhofar region has various mountain ridges in combination with coastal areas of Arabian sea. The nature of the soil in these areas are shallow and it helps in the growth of plant species such as *Boswellia sacra, Anogeissus dhofarica, Adansonia digitata* and presence of scrublands with *Boswellia* species. Amongst these species the *Boswellia sacra* has been found to be a unique species in Dhofar area commonly known as Frankincense and used in various medicinal and perfumery industries. Several varieties of *B. sacra* are present in this specific region depending upon the sesquiterpene exudate from the bark of this plant. Jabal Shams is also an arid mountainous area in Oman and according to zone wise vegetation plants such as *Acacia tortitilis, Euphorbia larica, Moringa peregrine, Ziziphus spina-Christie, Fagonia indica* and *Rhyza stricata* can be found in this region.

Jabal Akhdar which is a part of Al Hajar mountain chains present in the Dakhliyah region also is rich in plant communities with presence of succulent, drought deciduous plant species such as *Convolvulus acanthocladus, Grewia tenax, Maerua, crassifolia* and *Moringa* species. The woodlands species such and *Sideroxylon mascatense, Olive* species, *Dodonanea viscosa* and *Myrtus communis* can also be found in this area. Important medicinal value containing plants such as *Teucrium mascatense* and *Ephedra pachyclada* can also be found in this hilly area. The present chapters will discuss the different environment parameters and their effect on the vegetation of these plants with an insight into Aflaj system (included in world heritage site 2006), an ancient engineering technology that demonstrate long lasting sustainable use of water resources for the cultivation in extremely arid desert lands. These watercourses are built tapping into springs on the sloppy mountain, hand digging tunnels to reach underground water sources. The channels were built with stones and mortar to flow the water downhill to houses and terraced cultivated areas (Fig. 16.1). A large agricultural area of the country is still under this irrigation system.

Fig. 16.1 A general view of water channelization through falaj in different regions in Oman. (Pic courtesy: Mohd. Taleb Sulaiman Al Shaqsi, Taif Rashed and Arwa Khamis Juma Al Dawdi)

16.2 General Vegetation in Oman

The trend in the Agricultural sector of Oman indicates the productivity was at peak until late 1990s and after that subsequent decline has been noticed for which the major reason was attributed to poor water management strategies on the productive coastal regions. According to Economic vision 2020 the key agricultural objectives were to develop Omani human resources to deal with the technological developments and to develop growth in the private sector and attain competition at the international level. Considering these objectives, in Oman overall growth of agricultural sector seems to have lowered down as the relative share of this sector was down from 2.0% in the year 2000 to more decreasing 1.2% in the year 2010 of the overall gross domestic production. Interestingly it was noteworthy that agricultural sector's absolute value has contributed almost double since 1990 to 2010 as this sector's contribution is approximately 930 million USD in the year 2010. Apart from these data, Agriculture is the leading sector which provides employment as it is reported that out of 2.4 million population in 2005 a major percentage of (13%) was active in the Agricultural sector economically providing objective opportunities to Omani and expatriate workers. The productive land area in Oman is very limited (7.07%) with major areas divided in to seven areas geographically. Out of 5.29 million feddans of productive land in Oman only 1.88 million feddans are considered suitable for cultivation without any major management related issues. A major land area of 3.41 million feddans has been considered marginally suitable of agricultural purposes because of limitations in terms of reduced productivity. Almost 65% (0.162 million feddans) is attributed to coastal zones with major areas being Al Batinah coastal stretch.

The ecological and climate diversity in Oman provides chances to grow off season crops which are of high value. The vegetation in Oman is influenced by African and Asian continents as Oman is situated South Eastern location of Arabian Peninsula. Majorly northern Oman has been influenced more by Southwest Asia as here the vegetation is quite similar to this region whereas the South part of Oman is mostly impacted by East and North African vegetation (Pickering and Patzelt 2008). A total of seventy-seven vascular plants have been considered to be native of Oman among which Aloe species such as *A. whitcombei, A. collenetteae, Ziziphus hajarensis* and *Dionysia mira* are few to be mentioned here. More to add to this list are *Euphorbia momccoyae, Hyocyamus gallagheri, Limonium sarcophyllum* and *Salsola omanensis* plant species. Altogether 1239 vascular plant species and ferns were recognized (Patzelt et al. 2014) out of which approximately 716 plant species have been reported from Northern part of Oman. The central part of Oman has reported 254 species which is around 18% total flora and Southern region of Oman covered maximum plant species with approximately 817 plant species, covering 58% of the total floral distribution in the area (Patzelt 2015). Oman because of its interesting position in between tropical and subtropical zones has been rich by a good number of vascular plants whose number approximately reaches up to more than 1200 (Patzelt et al. 2014). The details of types of vegetation and plant varieties found in community is not well studied with restricted study on ecological effect of the individual plants as well as studies of population parameters. The extremely unique ecological areas in Oman have contributed in development of various range restricted species and endemic species with certain habitats such as Southern Oman's mountains and Al Hajar mountains in north contributing maximum to this cause. As mentioned earlier that more than 1200 endemic plant species have been identified in Oman and this number may reach up to 1400 or above as more invasive investigations are taking place (Patzelt et al. 2014) with distribution of these endemic species more in southern areas followed by northern Oman and a comparatively less area in the Central Oman. The Wahiba sands represents another extreme climatic zone of Oman (Fig. 16.2).

The arid conditions with cold nights and hot days create fogs. Those fog conditions favor many plants to survive. The main ones are *Heliotropum, Halopeplis* and *Calligonium* spp. But mostly found tree is Ghaf tree (*Prosopis cineraria*) which can survive long durations without water supply. They are drought tolerant medicinal trees that can provide food and shelter to livestock in harsh arid conditions. They are used against scorpion and snake bites and treat rheumatism, bronchitis and asthma.

The main agricultural land can be divided into Northern and Southern Oman with Northern Oman having major cultivation areas such as Al Batinah coastal plains, Interior Oman and Al Dhahirah plain, Jabal Akhadar or Saiq Platea and Al Sharqiya plain. Whereas in case of Southern Oman, Salalah plains, Dhofar jabel and Najd are the areas which are productive and suitable for cultivation (Oman Salinity Strategy Report 2012).

16.3 Productive Agricultural Areas of Northern Oman

The northern area of Oman has one of the most productive areas in form of Al Batinah coastal plains which are situated between Gulf of Oman and Hajar mountains constituting more than fifty percent of area for the production of agriculture in Oman

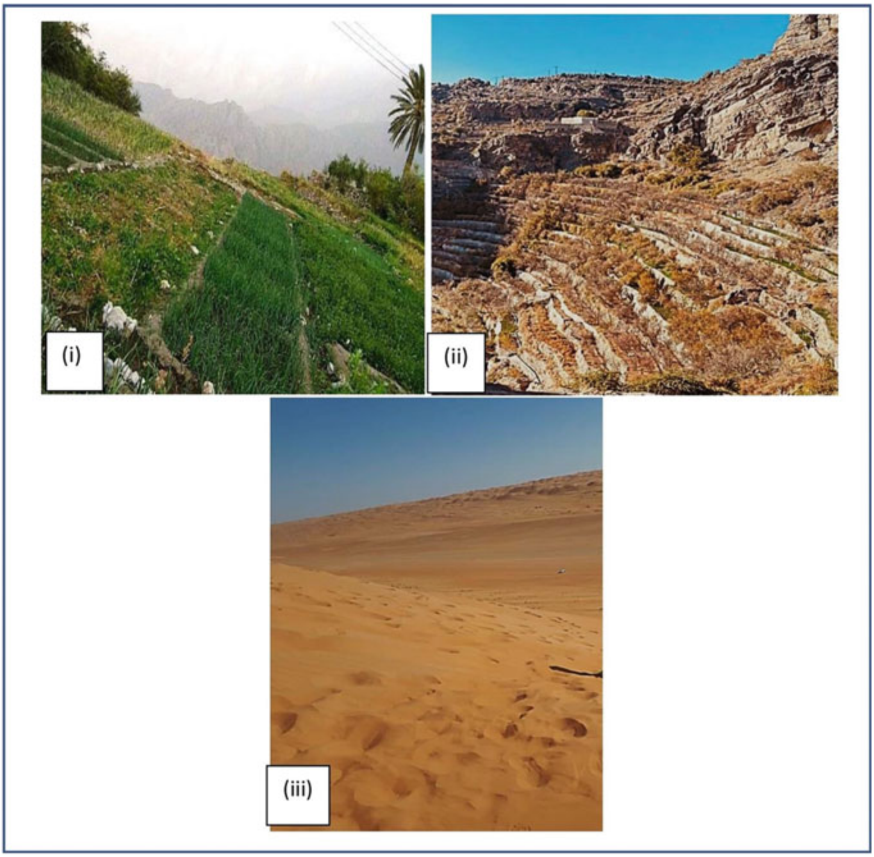

Fig. 16.2 Contrasting climatic zones of Oman (i)–(ii) Agricultural land and hill cropping area in Al Elya Wadi Bani Kharous area in Al Batinah, Oman. (iii) Wahiba sands in Sharqiya region of Oman. Pic Courtesy: Arwa Khamis Juma Al Dawdi, Mohd. Taleb and Salma Salem Al Kharousi)

(Fig. 16.3). The main crops which are grown in this area are fruits, vegetables, dates with the presence of forage crops such as *Rhodes* grass and *Alfalfa.* The temperate and tropical shorelines in Oman are very much covered with sandy beaches The most productive agricultural land of Al Batinah is a 200 km stretch of land area. The sandy beaches constitute most of the shoreline. Cash crops such as tomatoes, melon, watermelon and cabbage are grown in this area with other crops such as pepper, bitter gourd and cauliflower. Most of the fresh water resources are used for the cultivation of these crops and ground water pumping is generally implied to provide water to the crops. The over pumping of ground water has caused immense loss as it has resulted in intrusion of sea water in to this productive land area causing soil salinization issues (Al Said et al. 2007). The soil salinization persistence has led to various research-based studies in Al Batinah area and one among the strategies is analyzing the ground water salinity. For this purpose, the water wells in this area from the year 1990 until

2018 have been assessed based upon their type and their operational status. The salinity levels of the ground water were put in to five different categories on the basis of electrical conductivity (EC) status. The five different types of water used for the study were good quality irrigation water, low, medium and high salinity water and fresh water. The following study depicted that increased water salinity is due to over pumping of the water from wells and that because of increasing urbanization (Abulibdeh et al. 2021).

Other major areas for cultivation in Oman is Interior Oman and Dhahirah plains where inner plains are situated in the Al Hajar mountain's foothills and cover the areas of Ibri, Al Buarimi plain, Bahla, Nizwa and Wadi Quriyat. Traditional falaj system and wells are used for irrigation in these areas with dates being the main crop followed by *Alfalfa*. One more productive area is Jabal Akhdar in this zone which is known for growing nuts and temperate deciduous fruits because of lower temperatures (around 30°) and good annual rainfall of around 300 mm. Because of these climatic conditions the fruits such as peaches, pomegranate, apricots, pears and apple are grown in this area with some nut cultivation also such as almonds and walnuts (Fig. 16.3) (Oman Salinity Strategy Report 2012).

The Al Sharqiya plains have also been seen as an area which could be developed into productive lands. In Northern Oman, area of around 1500 ha covered for crops with the presence of 26 oasis using traditional falaj system for irrigation. The agricultural activities in this area are concentrated in Wadi Al Batha covering the areas of Ad Dariz, Ibra, Al Wafi and Al Ghabbi. The Waadi Batha plain consist of proper ground water availability and soil is also suitable for cultivation with special areas of focus in Al Wafi and Al Kamil in District Jalan. (Oman Salinity Strategy Report 2012).

16.4 Productive Agricultural Areas of Southern Oman

The southern part of Oman is quite diverse with the presence of woody hills which reaches up to 1500 m coastal plains consisting of Salalah plains. The southern part covers up approximately one third part of whole Oman and the Dhofar area gets benefits for the monsoon which help falls in the months between July and August. As mentioned earlier the precipitation rate in Dhofar area is quite satisfactory with annual rainfall reaching up to even 600 mm to 700 mm in areas of Dhofar Jabal which helps in establishing quite diverse and permanent vegetation in these areas with Jabal Qara and Jabal Qamar having rainfed pasture lands approximately half million hectares of the land.

The Dhofar region which is situated to the distant south western location of Oman with unique kind of vegetation (Fig. 16.4). The largely desert plain area has sparse vegetation and ranges of limestone mountains at coastal regions. The climatic conditions and topography play a major role in development of vegetation in these areas. The topographical factor which are to be considered are soil type, rainfall amount,

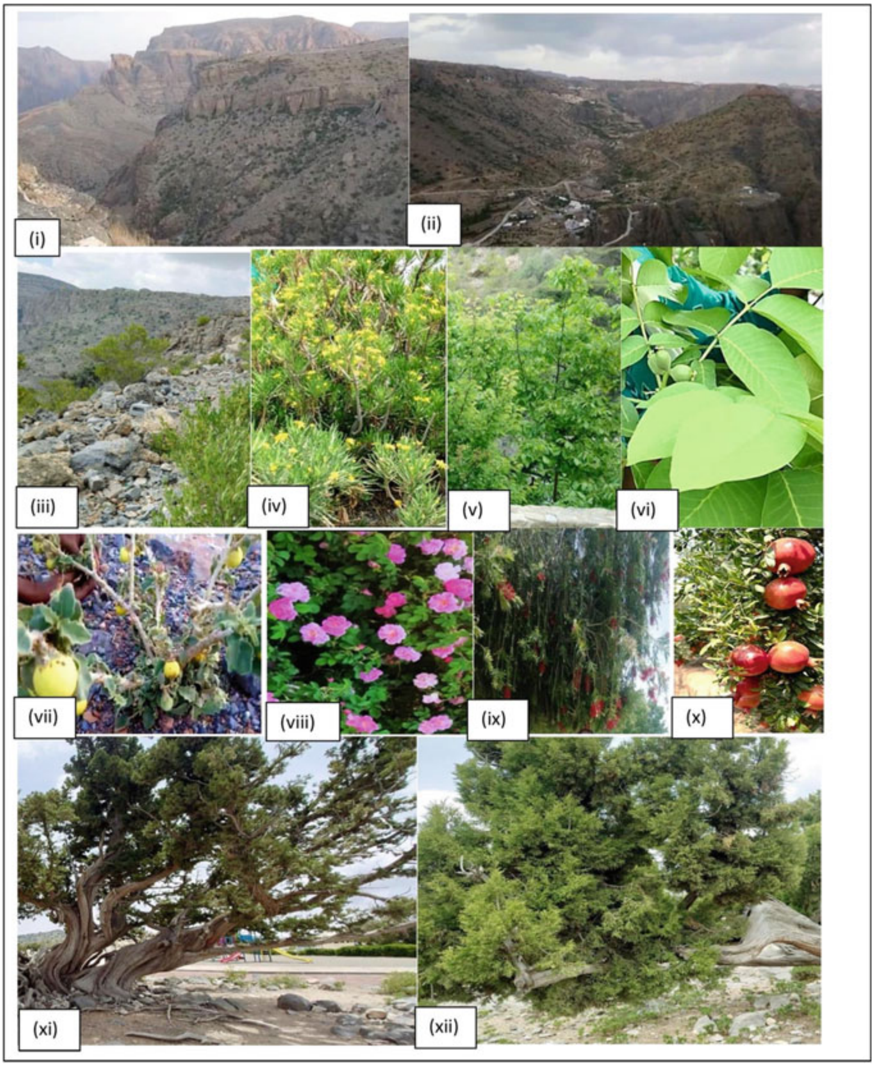

Fig. 16.3 Varied kind of dominant plant varieties seen in Jabal Akhdar region. (i)–(iii) Mountainous range of Jabal Akhdar at the height of around 2000 m above the sea level. (iv) *Limbarda* sp. (v) Apricot (vi) walnut (vii) *Solanum linnaeanum* (viii) *Rosa* sp. (ix*) Callistemon* sp. (x) Pomegranate (xi) *Juniperus osteosperma* (xii) *Juniperus phoenicea*

distance from the sea, aspect and elevation which decides the type and of vegetation (Ghazanfar 2003). The Jabal Samhan mountain range in Dhofar region found the presence of woody herb communities with certain endemic plant species of *Salvia hillcoatiae, Lavandula hasikensis* and *Campylanthus pungens.* The presence of *Acacia* tree may also be characterized on the summit with presence of *Pistacia*

Fig. 16.4 Varied kind of dominant plant varieties seen in Dhofar region. (i)–(iii) Frankincense land and Al Baleed Archeological site showing Frankincense trees; (iv)–(v) Mountainous sites (Darbat fall) showing vegetation rich in mosses, (vi)–(viii) coastal vegetation rich in coconut palms, papaya and banana trees

falcata and *Dracaena serrulata* plant species on the cliffs and sheltered valleys (Miller and Morris 1988a, b).

One more area of interest in Southern region is Najd as this area has been identified with presence of fossil groundwater which may work well for the potential agricultural activities despite of the fact that rainfall in this area is not very good (Oman Salinity Strategy Report 2012).

16.5 The Endemic and Range Restricted Plants in Oman

At least 64 different endemic plant varieties have been reported from Al Hajar mountains which mostly includes varieties such as *Teucrium mascatense, Ziziphus hajarensis, Dionysia mira* and *Campylanthus hajarensis*. Examples of distinct varieties may include plants such as *Ceratonia oreothauma* which is a key species in the area of Eastern Hajar mountains but generally absent in Western Hajar and Musandam areas. Same is the case with plant variety of *Olea europaea* sub species *cuspidata* which is absent generally in Musandam area and rarely found in Eastern Hajar mountains but it's considered as key species in the western area (Patzelt 2015).

The range restricted endemic varieties in Oman represent more than 13% of the overall flora of the Sultanate with precisely 77 varieties of plants strictly restricted to this country. If geographical boundaries are to be considered then more than 50 plant varieties are in near endemic zone where two countries are involved in one geographical entity. If threatened species are also categorized in this area then, more than 65 plant species fall in this area as well as more than 60 plant species considered endemic to Arabian Peninsula.

There could possibly be categories of the range restricted plants depending upon the local centers where plant endemism can be observed (Miller and Nyberg 1991). One of them is Jabal al Qara and Jabal al Qamar mountainous area which are in the southern Oman and mostly are affected by monsoon. This category could lie with mostly dry areas of Jamal Samhan which also contains wadi systems. Other category could be the limestone rich area of central Oman with area covering up to coastal areas of Jiddat al Harasis/ Huqf. These categorized areas can be further subdivided into Jabal al Samhan as well as Jiddat Al Arkad areas which fall under Southern and central Oman and can be taken as separate category respectively with increasing the local endemic area from three to five now. Lower and medium altitudes are profoundly rich in endemic species with major species belonging to Asteraceae followed by Apocynaceae and Lamiaceae. These families of plants are further followed by Plantaginaceae, Euphorbiaceae and Convolvulaceae and others. The Hajar mountains which is mostly arid to semi-arid ranges from southern Arabia and reaches up to Southwest Asia region. Earlier the characteristic plantations have been identified from Al Hajar mountains as whole but now it has been recognized that plantation can be subdivided in to three major areas with Western Hajar mountains covering the highest of the peak with up to 3000 m followed by Musandam mountains with peak as high as 2008 m. The Eastern Hajar mountains are at lowest amongst this category with peaks of 2000 m. Among these areas, the Eastern Hajar areas and Musandam receive very low precipitation but western Area receives a considerate amount of rain and this results in difference in the occurrence of vegetation in these areas (Patzelt 2015).

16.6 The Coastal Vegetation in Oman

The coastal area in Oman can be assessed in two categories with the first one containing beaches with sand and salt marshes. This area is mostly present with coastal dunes species and halophytic plants (Ghazanfar 2003). The second type of coast can be characterized by rocky steep habitat with the presence of mangrove species *Avicennia marina*, succulent shrubs that are perennial in their growth and with presence of reed mace *Typha*, *Phargmites* and other related vegetation which are aquatic in nature (Pickering and Patzelt 2008). According to Ghazanfar (1999) the coastal vegetation in Oman can be divided in to four different types with the first category belonging to northern Oman which can be characterized by presence of plant communities of *Limonium-Zygophyllum* type vegetation. The second category is of *Suaeda—Limonium* type vegetation covering the North Eastern coastal regions in Oman. The third classification is of offshore island vegetation which mostly has *Suaeda* community with the presence of sabkhas and flat sandy beaches. The fourth category is of *Limonium-Sporobolus-Urochondra* type community which covers up the Southern coasts of Oman. The coastal vegetation in Oman is generally salt tolerant belonging to Plumbaginaceae family (with example of sea lavenders) and *Amaranthaceae* such as Pigweed family leading the way followed by certain *Juncaceae* and *Poaceae* family examples such as rush and grass families. Mostly *Avicenia marina* plants categorized as Mangrove plants are commonly found in estuary zones. The coastal dunes are largely rich in plant varieties such as *Sphaerocomum aucheri*, *Tetraena quatarense* and *Halopyrum mucronatum* with inland salt deserts rich in plant varieties such as *Suaeda moschata* and *Limonium sarcophyllum* which are Omani endemic plants (Patzelt 2015).

The coastal region of Oman is also rich in plant diversity and the type of plants can be divided into at least four different zones based upon the salinity level, topography, sea water intrusion level and substrate of the coast. If Northern zone of coastal area is considered, plants such as *Limonium* species and *Zygophyllum* species is majorly found whereas when North East area of Oman is taken the species of *Suaeda vermiculite* and *L. stocsii* is found in abundance. The flat and sandy beaches with off shore island which have more fine sand and graded mud provides chances for the growth of plants like *Atriplex* species and *Suaeda* species (Patzelt 2015). As far as the southern coast of Oman is concerned, *Urochondra* species, *Sporobolus* and *Limonium* species are found. Mangrove plants can often be observed specially on different salinity levels abruptly in Oman with major identified variety named *Avicennia marina* (Ghazanfar 1999).

The tree species of *Juniperus seravschanica* is also one of the species which is mostly absent in the area of Musandam and Eastern Hajar mountains but is considered a key species in the western areas of Hajar mountains. Same way many perennial shrub species are there such as *Withania coagulans* which are absent in Musandam and western Hajar areas but can be rarely found in Eastern areas, whereas *Artemisia sieberi* also is a key species in Musandam but found generally absent in West and East Hajar areas (Patzelt 2015).

16.7 Ethnobotanical Plant Species and Their Uses

Oman has undergone several botanical studies and out of it the most significant one is by Miller and Morris (1988a, b) which was conducted in the Dhofar region. It is apparently considered that an elaborative study related to ethnobotanical information of traditional plants in a better way with threat facing wild plants that have not been illustrated in Oman specially in the area of Western Hajar Mountain area. For endemic plant varieties Jabal Al Akhdar has been seen as the source or center which is covered under Al Hajar Mountain area in northern Oman (Ghazanfar 2003). From ecological point of view these areas are covered under "vulnerable" category and henceforth has been listed among the 200 ecoregions globally by WWF which is named "Arabian Highland Woodlands and Shrublands" (Brinkmann et al. 2009). A thorough study was conducted in this area to evaluate environment conditions of open woodlands with grazing gradient and its effect on the vegetation. Study indicated that a total of five vegetation groups can be formed based upon the cluster analysis out of which *Sideroxylon mascatense-Dodonaea viscose* is on grazed pleateu sites whereas Olea europaea-Fingerhuthia africana was on the ungrazed pleateu. The wadi sites were with *Ziziphus spina-christi-Nerium* oleander group. More importantly it was highlighted that intensity of grazing and altitude of the landform were the variable considered to distinguish between these clusters (Brinkmann et al. 2009).

The plant *Dodonaea viscosa* which in Arabic is called Zaitun Al Ramal and in local Omani language referred to as "Shahs" is a flowering plant of medicinal value. Is has been used in ethanomedicine to treat various diseases with specific occurrence to the region such as Northern Oman, Al Jabal Al Akhdar, Salalah and Al Hamra (Hussain et al. 2013). Locally in Oman the plant leaves are used to treat itching, swelling and rash, disorders of bone, rhuleumatoid arthritis and sometimes as relaxants of muscle (Al-Oraimi and Hossain 2016). Other parts are also beneficial in treatments such as root segment is used mixed with leaf for relieving tooth pain, diarrhea, headache, indigestion and constipation (Meenu et al. 2011). *Senna* and *Aloe* are used in constipation cases as a laxative and *Teucrium mascatense* which is endemic plant to Oman has antimicrobial activities. One more plant which has prominent anti-inflammatory and antipyretic properties in *Lycium.*

Other medicinal plants that are in use in Oman are *Commiphora quadricincta* which is used as a medicinal gum, *Ephedra intermedia* used as oilment for the treatment of sores and *Cassia sophera* which is used in drinking form in tea for the treatment of stomach ache. Other minor medicinal plants which are used are *Ecbolium viride* which in general is used in tooth cleaning process and *Olea africana* which is used in making poultices for the wounds of livestock and treatment of their sores. The plant *Monsonia helitropoides* is generally used as a remedy in snake bites.

The traditional plants which are in use for ethanomedicinal uses are Thyme (Zaater), Cinnamon (Qurfa), True myrtle (Yas), Juniper (Arar) Miracle tree (Shu) and Spurge tree (Labna) to mention a few. The Miracle tree (*Moringa peregrina*) know in Oman as "Shu" is used for various purpose with main use in nutrition, constipation and other stomach related disorders. The oil can be extracted and generally used for bone setting purposes. *Lycium shwaii* commonly known as “Gharqad” is used as a purifying agent and helps in detoxifying the circulatory and digestive systems. For cleansing purpose also one more plant is used traditionally in Oman which is *Aloe barbedensis* This plant’s dried leaves are used for wound healing and antimicrobial purposes. General laxative plants which are available in Oman are *Senna* and *Aloe* with major antimicrobial plant such as *Teucrium* species, *Ocimum* and clove. For sedation purposes *Cannabis* and Datura seeds are used. *Acacia, Ficus, Ocimum* and *Euphorbia* species are used for the treatment of burns, bites and boils (Divakar et al. 2016).

The major plant varieties in Jabal Akhdar region range lands at a height of 1580 to 2000 m are woodland mostly consisting of *Sideroxylon mascatense* in a mixed manner with *Dodonaea viscosa*, *Olea europaea* sub species cuspidata, *Euryops arabicus* and *Sageretia thea* (Ghazanfar 1991). The ground is covered dominantly at 1580 to 2000 m or even at higher altitudes by *Cymbopogon schoenanthus* dominantly. At the altitude of more than 2000 m, mostly *Ephedra pachyclada, Juniperus excelsa* and *Teucrium mascatense* can be identified as vegetation components (Ghazanfar 1991). To assess the agro-biodiversity of the mountain oases in Oman, Al Hajar range was chosen and three of the mountain oases were surveyed based upon GIS field surveys with interviews of the farmers. Interestingly the agro climatic conditions were found to be different on different elevations which included the highest as Jabal Akhdar (1750 to 1930 ma.s.l) to Maqta (930 to 1180 ma.s.l) and Balad seet (950 to 1020 m ma.s.l.). Balat Seet was found consisting of most fruit species and Maqta at the lowest with an overall identification of 107 different crop species which included a total of 33 fruit species. Majorly *Agave americana, Vicia faba* and *Lens culinaris* were identified as major vegetation species (Gebauer et al. 2007).

The western Al Hajar mountains which includes Jabal Shams and Jabal Asarah have also been ethnobotanically considering more than forty wild plant species. The wild species included trees, shrubs, herbs, grasses, large shrubs and climbing plants. It showed that as peruse 30% of the plants were used for medicinal purpose, followed by use for fuel and fodder which represented 14 and 12% respectively. Interestingly 9% of the plants were used for food purposes, a total of 7% for production of honey and rest of it for construction and various other purposes such as livestock care, tool making and utilitarian purposes (Hatmi and Lupton 2021). Overall, 27 plant species were identified out of which Rhamnaceae was considered most useful followed by other orders such as Asteraceae, Oleaceae, Fabaceae and Lamiaceae. The climatic changes such as less precipitation and raised summer temperatures in combination with socioeconomic developmental efforts have significantly affected the traditional plants and knowledge which needs to be improved in these plant rich areas in Oman (Hatmi and Lupton 2021).

16.8 Irrigation System in Oman: Falaj and Its Types

The irrigation in Oman is an important aspect to look in to as the rainfall is limited up to 100 to 200 mm in a year (Norman et al. 1997). The ground water has been the support for supplied water for which the source has been falaj system. Oman is still have actively working falaj system (3,108) out of 4,112 falaj available. These falaj systems approximately is covering around 26,500 hectares area (Al Hatmi and Al Amri 2000). According to the Ministry of Regional Municipalities and Water Resources 2008 statement, the falaj system is responsible for 30% of all the water that is used for agricultural purposes and rest of the 70% covered up by the ground wells.

The falaj system history dates back to 500 AD approximately but interestingly evidences from archaeology even reveals that falaj system could be even existing 500 to 1000 years than 5000 AD. The development of falaj system came naturally from the source that annual rainfall in Oman was less. The well based irrigation was conducted by the help of animals such as donkeys and bulls (Bentham 2021, Al-Marshudi and Salim 2007). Naturally because these methods of water extraction were time taking and required human interventions hence falaj system was developed in which gravity-based water movement was involved in to the agricultural areas which ultimately was less man power involving and required less supervision (Sutton 1984).

The word “Falaj” which literally means “to divide” is a technique of distributing the water whether the water is of wadi base flow ones, referred to as “Ghaili Falaj”, spring type one, referred to as “Aini Falaj” or for simple “Qanat” based irrigation system which are called the “Daudi Falaj” (Al-Ghafri 2018). The basic differences between the different falaj system in Oman is their source of water which in case of Aini falaj is natural spring water and used for agricultural and domestic uses with the help of canals. The Ghaili falaj system is more commonly found and water source in this system is basically gravity flow of upper stream of a wadi. The third type of falaj is Iddy or Daudi Falaj in which the water source is deep dug mother well in the bottom of a wadi. A complicated and difficult falaj to construct, this Daudi falaj system provides stable water flow among all the falaj systems as its driven by a water table (Birks 1984).

The Daudi falaj system has an interesting history in Oman as its believed that Prophet Suleiman bin Daud stayed in Oman for 10 days (tenth century BC) as ordered the jinn to construct 1000 qanat type aflaj every day and hence the name Daudi falaj named (Wilkinson 1987). The most used falaj system in Oman is Daudi falaj with 22% and second to it, is Aini falaj with 11% followed by Ghaili falaj which is used in 8% cropped areas. Rest of the cropped area in Oman is covered by wells with (59%).

A typical falaj system has three components with first being the source that could be upper wadi areas from which the water is diverted and channelized on the basis of gravity. The kinds of source could be a spring or a qanat based source. The second component of a falaj system are generally a conveyance system which can be defined as a cement covered or open arch ditch with the third component being the delivery system which takes the water to different areas based upon its allocations.

The source based falaj system could be of three types:

1. Gaily Falaj: The ghaily falaj system could be understood as the canal-based diversion where the water source is the wadi flow. This system collects or transfers the water resource through open channels and since its dependency is on shallow water tables, it generally gets dried up in case of long drought durations.
2. The Daudi or Qanat based falaj involves longest channels up from 16 to 45 km as this falaj system utilizes deep channels. Considered as the ancient falaj system the Daudi falaj takes the advantage of movement of water table by gravity.
3. The Aini falaj has springs as the water source and involves simple canalization to distribute the water.

The important aspect of water distribution by falaj is to transport the water to a long distance and more importantly to distribute the water equitably as the communal distribution was a key aspect of falaj development. Henceforth various shareholders received equitable amount of water distribution through falaj which was used for array of purposes from use in agriculture field to use of water domestically. Interesting to avert the problem of contamination of water the priority was given is usage for religious use of water, drinking purpose, domestic washing and for these purposes access points in the falaj system were provided through legal rules and social norms (Sutton 1984).

Probably one of the best examples of community-based administration, the falaj system has been covered with legality also. As if one wants to use falaj for irrigation then the concerned person must hold the water rights. Water rights have been shared by all the communities which permits them to use water from falaj for domestic use (Slim et al. 2008).

Despite being unique and ancestral in use the falaj system, Oman is facing challenges from urbanization as well as from the advent of Oil wealth development. The twenty-first century development has taken its toll from falaj system also, as many traditional areas have seen people moving towards urban areas and resulting in poor local maintenance of falaj. For the protection and conservation of these falaj systems several projects are underway one of which is “Aflaj Research Unit” by University of Nizwa which involves documentation of contribution of falaj system and its role in traditional knowledge, heritage, culture and the help it provided to the economy (Bentham 2021). The ministry level actions have also been taken to conserve various falaj system by protecting the mother wells by the concept of protection zones and well licensing. The Ministry of Regional Municipalities and Water Resources has constructed more than 900 support wells and spent approximately 15 million USD to support under 700 maintenance projects involving falaj systems. (Al Sulaimani et al. 2007) With the efforts of government strategies, five Omani aflaj systems namely Falaj Daris in Nizwa, Falaj Al Khatmeen in Niabat Birkat Al Moaz (Nizwa), Falaj Al Malaki situated in Izki, Falaj Al Mayassar located it Rustaq and Falaj Al Jeela in Sur Willayat have been included in the world heritage sites of The United Nations Educational, Scientific and Cultural Organization (UNESCO).

According to policies and legislation in Oman, Royal decree no.83/88 (1988) considers and declares water as national resources. To the purpose of protection of falaj no permission can be granted to construct the well within the areas of 3.5 km where the mother well or source of falaj is present. Apart from it for the construction of new wells, permission is required and Ministry of Regional Municipalities, Environment and Water Resources (MRWEMR) is also involved in drilling and well digging contractor renewal on yearly basis (OSS 2012).

According to the strategies and national priorities related to Water Resources in Oman, the aspects needed to focused for improvement of water resources are (1) improvement requirement for various data collection related to water resource and their uses (2) An elaborative and in-depth assessment of all the water resource available and (3) specifically the demand of water and its spatial distributions. The report also highlights the need to use of all the available water resource at optimum and necessity to explore new water resource possibilities in Oman. The report also emphasizes on construction of hydrological structures and recharge dams for conservation and storage of rainfall water. More importantly it also focuses on agricultural sector and importance of conserving the water for this purpose various ways. One of the possibilities by which water can be made available to agricultural sector more is by shifting the more water consuming crops to the brackish water areas. Other possibilities are restricting the cultivation of more water demanding crops and annual grasses and promoting the seasonal crops more.

Re-use of the waste water is also an important aspect which has been discussed in the report with improvement extension of waste water collection measures and possibilities of increased use of desalinated water domestically. The qualitative and quantitative importance of ground water resource management and intrusion of saline water control in the productive agricultural areas were also the key points discussed in the strategy related to Water Resources in Oman.

Water shortage planning in Oman figures out the challenges that Oman is facing in the water sector that include overall shortage of water as domestic sector being the most water consuming sector. Another major challenge that Oman faces in the water sector is desalination industries which involves a lot of energy (Water Challenges in Oman 2018).

16.9 Commercially Viable Crops of Oman and Future Prospects

Oman as such is covered by arid areas with limited agricultural land with scarce water resources and very high temperature reaching up to 50 degrees in summers. Out of the 7.07% of agricultural land the soil conditions are at compromising level with most land containing alluvial or sandy soil with poor water holding capacities. The soil of Oman according to the Ministry of Agriculture and Fisheries is organic in nature which ideally is not well suited for economic cropping production hence inorganic fertilizer supplementation is a must in these kinds of soils. The main productive lands of Al Batinah areas have been suffering from soil salinization problems also as the lands in these areas are titled towards the sea. Though the Ministry has taken the effort to categorize these areas in to different zones such as high saline to medium and low saline zones so that cropping can be adopted based upon these zones. Related salt tolerant tomato varieties and pearl millet have also been tested on these zones with other engineering efforts taken into consideration to reduce soil erosion due to salinization in these areas. Apart from these areas the other areas are also assessed to bring sustainability in the agricultural sector with the recent allocation of 6000 acres of land to Al Buraimi areas for growing various crops. Out of these lands 3500 acre of the land belongs to Niyabat of Al Rawdah, 2000 acres to wilayat of Al Sunainah and rest 700 acres in wilayat of Mhadah. According to the reports these areas has been selected because of better suitability for agricultural purposes and stable presence of ground water. The natural water presence has always been the preference of a traditional Omani hence valleys has always played a role in running the falaj irrigation system. Interestingly it's considered that Barley (*Hordeum* species), wheat (*Triticum* species), date palm (*Phonenix dactylifera*) and Frankincense (*Boswellia sacra*) are four major plants which have been considered basic to Omani prosperity and played a role in their life. The agricultural sector in Oman was pivotal to the economy prior to the finding of oil and main commercial crops that are grown here are dates, tomatoes, limes, eggplant, banana and carrots. The main agricultural area for cultivation is Al Batinah area which is situated in the Northeastern area in between Muscat and area of Diba al-Hisn covering approximate area of 101,000 acres.

In tropical and sub-tropical areas date palm (*Phoenix dactylifera*) is recognized as a medicinal fruit with immense nutritional benefits besides providing high energy value and nutrition. Date palm is considered one of the major crops of Oman with approximately eight million plants present in this area (Fig. 16.5). Recently a study related to dates as a potential antioxidant has been reported by Sultan Qaboos University which discussed the importance of dates as a functional food in the daily diets. Two different dates named "Umsellah" and "Khalas" were identified and studied for their antioxidant abilities, nutritional and carbohydrate values and their physical traits. The study findings revealed dietary fibers and carbohydrates with the presence of antioxidant and other photochemical compounds in high composition in both the date varieties. Among both the varieties Umsellah showed the presence of phenolic content more than Khalas variety with a satisfactory presence of gallic acid as an antioxidant. Among other components the caffeic acid, syringic acid, coumaric acid and sugar content were all found to be better in Umsellah variety compared to Khalas variety. Nutrient value also was found very high with potassium level ranging upto more than 450 mg/100 g in both of the varieties but dietary fiber again was better in Umsellah as compared to Khalas variety. Both the varieties are considered suitable in Oman to be used for organic diets as well as for their use in other by product preparation (Siddiqui et al. 2020).

Recently a Food Innovation Complex project has been discussed in Oman which deal with the innovation system of food sector and reaching out with the products to the markets whether the local ones and the international markets also. The project will also focus on enhancing the local added value and will also provide platform for jobs as well as businesses. Agreements have also been signed for coconut tree

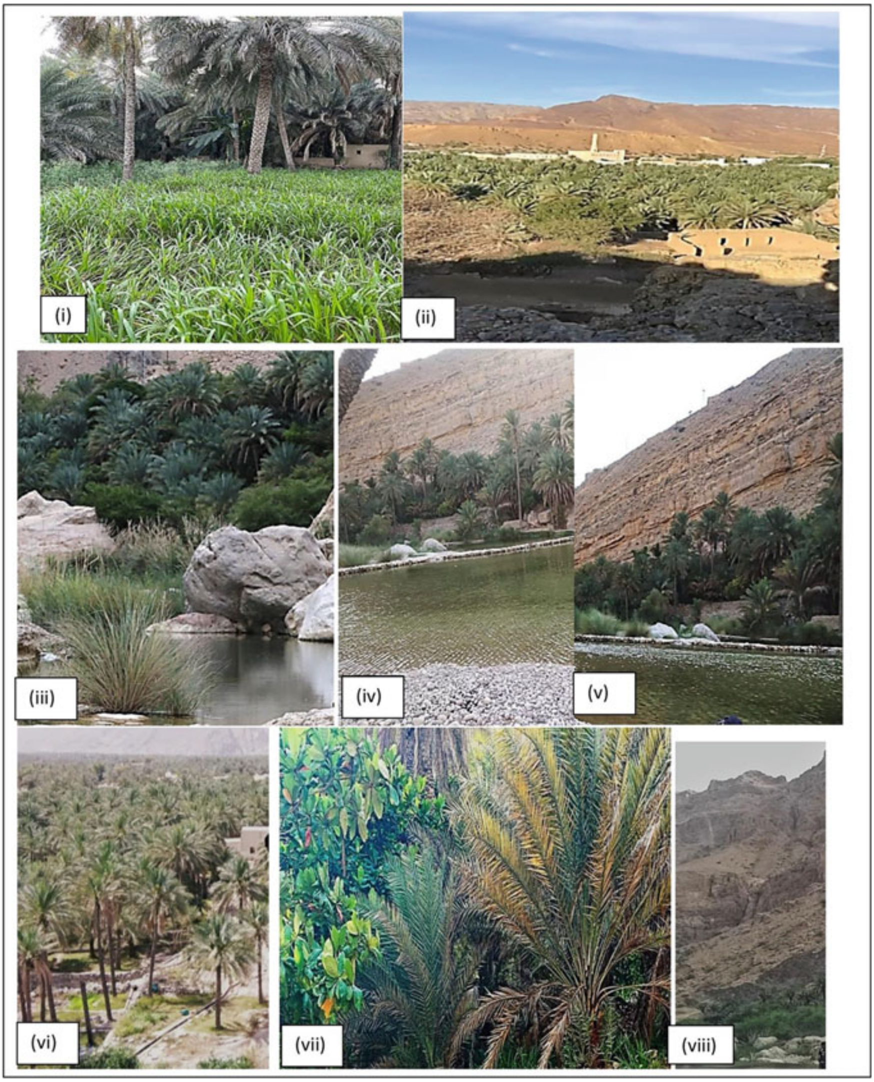

Fig. 16.5 Date palm cultivation in different zones of Oman. View of a date palm farm in (i) Tahwa, Al Sharqiyah Governorate (ii) Rustaq (iii)–(v) at the banks of wadi Bani Khalid, and wadi Shab (vi) Nizwa (vii) wadi Tiwi

planting in the Dhofar region and also a contract has been made for a project related to banana cultivation at commercial level in South al Batinah's Mussanah wilayat.

Dhofar region is also known in Oman as the "Land of Frankincense" and its significance has been recognized by UNESCO as in year 2000. It has been inscribed on World Heritage Site (Fig. 16.5). The plains of Dhofar which has a coastal stretch of around 20 to 25 km between Arabian sea and mountain ridges is consisted of limestone gravels aeolian and marine sand. Network of many wadis are also present with soil supporting xerophytic plants. In Al Fazayeh region of Dhofar governorate a xerophytic plant has been reported named *Caralluma flava* which is been used in stomach related disorders, general tonic and to suppress hunger (Divakar et al. 2016).

The best quality resin known by the name of "Royal Hojari" is produced from here by endemic variety of Boswellia. The medicinal values and importance of Boswellia sacra commonly known as Frankincense has been well recognised as the unique weather conditions support the growth and production of high-quality resin from this plant system in Dhofar. Boswellia sacra an endemic plant to Oman and known as olibanum producing tree in which the plant exudate is collected and used for various purposes. The odor, color, texture, clump size and shape plays major role in deciding about the quantity of Frankincense in which color plays a vital role. The golden color Frankincense is the most expensive one and considered of very high quality.

Generally, Frankincense has 65–80% alcohol soluble gum, 5–9% oil and rest of it gum which is water soluble. The Frankincense tree grows well on the higher pleateu with age duration between nine to ten years shall be completed for better quality resin production. The best quality Hojari Frankincense is mostly found in Jabal Samhan in the altitude range of 1000 to 1500 m.

One of the recent additions to Omani plants is Olive tree as it is an appreciated plant because of its religious and historical importance. From the earlier times the exchange of dates and Frankincense in place of Olive oil is occurring in Oman with the neighboring countries such as Egypt, Iran and Syria, Jordan and Lebanon. Due to unfavorable climatic conditions the cultivation of Olive was not possible but certain areas in Oman have been selected to introduce this plant's cultivation. One of the suitable place selected for this purpose is Al Hajar mountains in the North of Oman. The Southern areas in Oman such as Dhofar region have also shown conducible atmosphere for Olive growth as water scarcity is also not a problem in these areas. The Olive trees could be found here as a wild plant at the altitude between 900 to 2300 m. The Al Jabal al Akhdar region has semi temperate conditions in Al Hajar mountain range. Because if these prevailing conditions, olive cultivation is introduced at small farm and garden level. The first plantation started in 1994 and as of now 15,957 trees have been grown on approximately 36 hectares of the land area.

16.10 Conclusion

Oman with a very diverse climatic zones amongst different areas have been focusing on new crop cultivation idea with the traditional cropping. The lower temperature and good rainfall condition has helped in growing certain new crops such as olive and saffron cultivation. The traditional medicinal value plants have also been grown with variety improvement in tree species such as Boswellia sacra which will definitely help Oman in not only boosting the perfumery industry but medicinal industry also as characterization of various new compounds have been conducted from the mentioned plant system. With the recent advancements in cropping operations and focusing on lowering on soil salinity problems in certain area Oman is also advancing in new agricultural land preparations so that self-reliance in food industry can be achieved.

Many factors are responsible for overall biodiversity loss in Oman with major factors being resource overexploitation, urbanization, invasion of foreign species, overgrazing and industrial developments. According to the latest reports overall 40% plants are worldwide are facing extinction threats (World Economic Forum, State of World's plant and Fungi 2020). The active participation of Oman towards nature conservation can be seen with becoming member of various international treaties such as Global Strategy for Plant Conservation (2010–2020), Convention on Biological Diversity (2010–2020) and International Treaty on Plant Genetic Resources. A total of 18 different nature reserves have been established in Oman in an effort to conserve the plant genetic resources. Still efforts have to be taken to conserve medicinal plant species in Oman as there is no in situ protected areas to conserve these plant species. Traditional knowledge and ethnomedicine practice are one major area where Oman has been working rapidly in documenting the medicinal values of certain plants species which have been used from generation to generation through oral prescriptions. An in-depth study of these traditional knowledge based medicinal plants through molecular and photochemical based study will definitely result in characterizing many unknown useful compounds as Oman represents more than 430 medicinal plants. This medicinal plant exploration could lead to development of various important drugs as these plants are exposed to extreme climatic conditions and non-available of water resources in certain regions which may lead to stress related secondary metabolite development in these plants. The bio saline strategy is also in its budding stages in Oman as there is still a demand of skilled man power development, infrastructure development and involvement or more research-based approaches so that certain salinity effected areas can be recovered in terms of land productivity.

Acknowledgements Authors highly acknowledge the financial assistance provided by Ministry of Higher Education, Oman and UTAS-Sur, Oman during the writing of the chapter.

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Chapter 17
Impacts of Particulate Matter Pollution on Plants

Devendra Singh and Sunil Kumar Verma

Abstract In the current Anthropocene era of rapid urbanization and industrialization, air pollution is one of the major issues the world is currently facing. Particulate matter pollution, in particular, poses a risk both to the environment and public health. The biochemical, morphological, and biological status of green plants, as well as their responses, have been significantly influenced by the altered ambient environment caused by the particulate matter pollutant in urban areas. It turns out to be a useful indicator of the overall impact of particulate matter pollution as well as the detrimental effects of this pollution on vegetation when considering the context of the plants (wide distribution, increases the contact area, etc.). The chapter discusses how particulate matter pollution affects morphological characteristics like stomata structure, leaf area, flowering, growth, leaf number, as well as reproduction, along with biochemical parameters like pigment content, protein, enzymes, and sugar as physiological aspects like pH as well as relative water content. A brief overview of the effects of this matter on species diversity as well as climate change is also provided in the chapter. Additionally, the review highlights the genotoxic effects of particulate matter on plants.

Keywords Particulate matter · Bio-monitors · Plants · Climate change · Heavy metals

17.1 Introduction

The high speed of industrialization and urbanization in the recent Anthropocene approach has resulted in particulate matter (PM) pollution (US EPA 2009). Dust, commonly known as particulate matter, is actually a solid substance that has both natural and manmade origins. There is ample documentation in the literature regarding the size fractionation of PM along with its detrimental effects on health

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_17

(Brookmeyer et al. 2007; Brook et al. 2017). The air pollutants may negatively affect some biochemical factors, which would therefore slow down the development and growth of plants as a whole (Farooqui et al. 1995). Several investigations have been organized throughout the years to determine how different air contaminants affect plants' biochemistry and physiology (Ferreira-Baptista and De Miguel 2005). Reduced stress and increased utilization of both internal and external resources are benefits of these modifications for plants (Yadav et al. 2023; Govindjee 2004; Foyer and Halliwell 1976). Urban areas' changed atmosphere triggered by PM pollution has had a significant impact on plants' morphology, biochemistry, physiological state (McDonald et al. 2007; Theodor Keller 1983).

Nevertheless, it's possible to come across some significant references to gaseous pollution in certain places. Plants are the main apprehension sites for both gaseous and particle contaminants of the atmosphere because of their frequent exposure to air (Gostin 2009; Wang et al. 2017). Large amounts of foliar surface area in terrestrial plant species serve as a natural sink for contaminants, particularly particle ones. In the case of particle matter, vegetation is a particularly good marker of general consequences of air pollution (Escobedo et al. 2008). Numerous investigations had already established and validated that particulate matter has a damaging effect on vegetation (Farooqui et al. 1995; Ernst 1982; Erice et al. 2006; Eller 1977).

17.2 Biomonitoring Using Plants

By calculating projected air pollution tolerance index (APTI) as well as pollution index, ecologists can choose best bio-monitors by examining outcomes of PM on biochemical, physiological as well as morphological characteristics of plants (Eamus et al. 1989). Parameter, such as APTI are exercised in order to measure the air pollution impact on plants (Theodore Keller 1986). The ability of plants to withstand stress caused by pollution is expressed by the species-dependent plant attribute acknowledged as APTI (Tiwari et al. 1993; Singh et al. 2022a, b; Chauhan et al. 2023).

The air pollution tolerance index assessment offers a trustworthy way for evaluating the susceptibility of a large number of plants to air contaminants (van Heerden et al. 1996; Doğanlar and Atmaca 2011). Without the use of any expensive environmental monitoring equipment, this straightforward strategy is very easy to deploy in many types of outdoor situations (Dmuchowski and Bytnerowicz 1995). Vulnerable species could serve in role of biological indicators, whereas tolerant species could act as air pollution sinks (Alidoust and Isoda 2013). Only the biochemical parameters are affected by pollution, according to the air pollution tolerance index. Numerous socio-economic aspects are also taken into account while developing green belt growth in a specific location to prevent air pollution (Dizengremel et al. 2008; Dineva 2004; Delfino et al. 2011; De Santo et al. 1979). The API is determined for various species by integrating the resulting air pollution tolerance index values alongside certain pertinent socioeconomic and biological characteristics. Plants are assigned various grades (or) based on these characteristics (Mingorance and Oliva 2006; Singh and Singh 2022). A tree is only allowed to obtain highest of sixteen good points under the present grading scheme. The category has been evaluated based on the score received, which is scaled to a percentage system. Researchers enlist the criteria to evaluate the performance and evaluation categories, accompanied by results for a specific tree species. *Cassia fistula* (amaltas), *Delonix regia* (gulmohar), *Mangifera indica* (mango) and *Azadirachta indica* (neem) were the four plant species studied by Thawale et al. (2011). They determined that *Azadirachta indica* was the utmost tolerant species and may perhaps suggested in favor of green belt plantation (Iqbal et al. 2010; Chandarana and Amaresan 2023; Darrall and Jager 1984).

In terms of pollution indicators, there are two types: accumulator species, which concentrate the pollutant in their bodies, and sensitive species, which reveal the pollutant existence by developing lacerations or abnormalities (DaMatta et al. 2010; Everse and Grisham 1990; Cotrufo et al. 1995). There is yet another classification, namely species that multiply and increase in abundance in contaminated places (Mehler 1951; Verma and Kumar 2022). For the vast number of persistent pollutants in urban contexts, several plant species are required. All of these plant species, have the ability to function in the same way as pollution bio-monitor of specific elements in addition to can distinguish between the way plants the ability to respond to air pollution determine the air's quality as well as possibly detect trends in air pollution early on (Conklin 2001; Constantinidou and Kozlowski 1979; Duxbury et al. 1997). Lichens and higher plants are examples of potential biomonitoring technologies (Table 17.1).

17.3 Particulate Matter's Effects on Plants

Acute and chronic damage are the 2 major categories of unswerving harm which particulate matter pollution could do to vegetation. Severe damage is caused by contact to extreme gas concentration for a brief interval of time and is characterized by obvious, observable foliage symptoms, frequently in necrotic lesions form (Maxwell and Johnson 2000; Pandey et al. 2021, 2022; Dhiman et al. 2022). Chronic injury, which arises due to extended exposure to reduced gas concentrations besides manifests as growth and/or yield losses, is much subtler than this kind of injury and is frequently difficult in identifying. Pollutants in the environment are constantly absorbed, accumulated, and incorporated into the systems of plants (Choudhary et al. 2011; Chen et al. 1991; Carreras et al. 2006; Cape 2008). According to the article, plants can exhibit apparent changes depending on their level of sensitivity, including changes to metabolic processes or an accumulation of specific metabolites (Calatayud et al. 2011). Pollutants can harm vulnerable plant species' leaves, stomata, and senescence prematurely, diminish photosynthetic activity, interfere with membrane permeability, and inhibit growth and production (Masuch et al. 1988; Devendra Singh and Agarwal 2021). Invisible damage is caused to plant leaves by longstanding, low concentration air pollution exposures. Many researchers have carefully examined the cement effects, automotive exhaust, coal dust, fly ash, petro-coke dust, as well as

Table 17.1 List of effective bio-indicators and bio-monitors for each type of PM pollution source

Pollution source	Plants as bio-monitors	Effect	Reference
Massachusetts coal-burning station	Lichens on *Populus deltoids* and *Acer saccharinum*	Close to a coal burning station, the lichen cover has diminished	Murphy and Jana (2002)
India's Lucknow, where there is automobile pollution	*Thevetia neriifolia* and *Ficus religiosa*	Plants' leaf area and the structure of their foliar surfaces, as well as changes to the photosynthetic pigments in those tissues	Verma et al. Singh (2022)
Domestic heating and vehicle traffic in Siena	Fifty seven different types of lichen	Bioindicator along with showed an improvement in the quality of the air since 1995	Loppi et al. (2004)
Particulate pollution from human activity, especially urban mobility, throughout Europe and North America	Acer pseudo-platanu, *Eucalyptus globulus, Ficus nitida* and *Alnus glutinosa*	Effective for capturing dust in dry and semi-arid environments in both developing and developed nations	Alfani et al. (2000), Anna Alfani et al. (2001)
Traffic flow and significant industrial facilities in Naples' metropolitan area	*Quercus ilex*	Plant leaves have high concentrations of Cd, Cu, Ni, as well as other elements	Krommer et al. (2007)
Hong Kong's heavy metal pollution	*Bauhinia blakeana*	Served as bio-monitors for metals, sulphate of Sulphur, as well as total suspended particles	Lau and Luk (2001), Singh et al. (2022c)
Polycyclic aromatic hydrocarbons	*Quercus ilex*	Quantity of PAHs in *Q. ilex* leaves was fairly high overall	Anna Alfani et al. (2001)
Metal contamination in Galicia	*Pinus pinaster needle* and *Quercus robur* leaves	A regulated capacity to bio accumulate the investigated elements	Mingorance and Oliva (2006), Keane et al. (2001)
Air pollution issue in Cubato, SE industrial complex Brazil	*Mangifera indica, Psidium cattleianum* and *Psidium guajava,*	*Psidium guajava* and *Psidium cattleianum* can be utilized by means of an accumulative indication	González et al. (2012), Chen and Yen (2007)

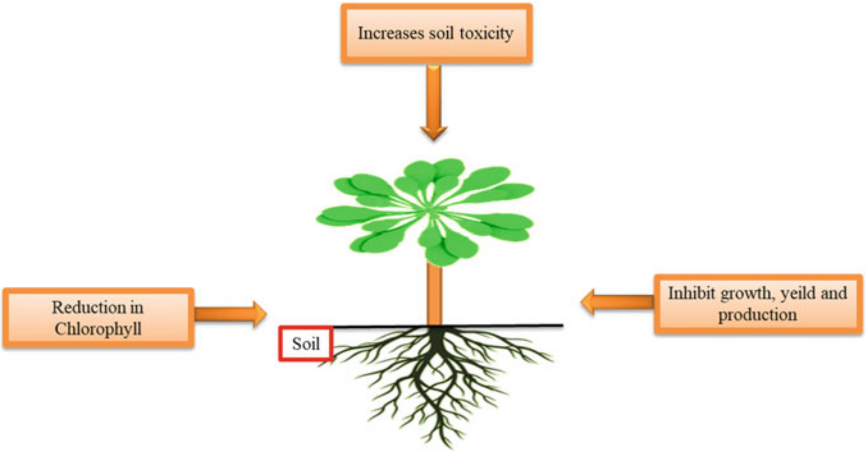

Fig. 17.1 A systematic representation showing the different effect of PM on plants

further airborne particles on a variety of physiological and morphological constraints in diverse plants (de Marco and Roubelakis-Angelakis 1996). Figure 17.1 shows the adverse effect of PM on plant.

17.4 Plant Morphological Effects of Particulate Matter

The principal receivers for both PM and gaseous contaminants in the troposphere are plant leaves. These pollutants interrelate in conjunction with the foliar surface and modify its structure before they reach the leaf tissue (Mariani et al. 1992; Mansfield and Majernik 1970). Dust deposition on leaf surface, consisting of ultrafine and coarse particles, shown reduction in plant development due to its influence on leaf gas exchange, blooming and reproduction of plants, number of leaves and leaf area, one of the most prevalent driving factors in growth assessments (Bytnerowicz et al. 1987; Bystrom et al. 1968; Bussotti et al. 2011). Reduced leaf generation and increased senescence could be to blame for the reduction in leaf number and area. Additionally, dust toxicity interferes with plant physiological processes, for instance hormonal imbalance, late flowering, growth inhibition and photosynthesis rate (Bucher and Schenk 2000; Sarnat et al. 2006; Bolsinger et al. 1991). When overall photosynthesis is inhibited, assimilate translocation is also inhibited, which leads to a decrease in leaf area (Du and Elemento 2015; Kumar et al. 2022; Bermadinger et al. 1988; Bermadinger et al. 1990). According to research by Shukla et al. (1990), *Brassica campestris* (Mustard) plants exposed to cement dust showed consistently lower growth rates, yields, and oil contents than control plants, all of which contributed to the plant's lower biomass (Kozioł and Whatley 2016).

17.5 Impact on a Plant's Physiology and Biochemistry, or on Plant Leaves

17.5.1 *pH*

Depending on their physical and chemical makeup, airborne particulate matter has a negative impact on the growth and development of plants (Bergamaschi et al. 2007; Bennett and Wetmore 1999). Plants' leaf extract pH may change as a result of dust. The sensitivity of the stomata to contaminants in the air may be impacted by changes in leaf-extract pH (Madamanchi et al. 1991; Singh and Agarwal 2022). On hydration, cement dust releases calcium hydroxide, which in some situations can raise the pH of the leaf surface alkalinity to 12. By hydrolyzing wax and lipid constituents, penetrating the cuticle, along with denaturing proteins, this level of alkalinity can plasmolyze the leaf. The leaf extract's low pH demonstrated a relationship with the sort of pollutants in the air (Ma et al. 2014). The pH of leaves is dropped when an acidic pollutant is present, and in delicate plant species, this decrease is more pronounced. The cement dust alkaline composition reduces the soil's ability to absorb minerals, which causes physiology and morphology alterations in plants (Batalha et al. 1999). Cement dust's alkaline composition, which damages chloroplasts, is what causes the change in leaf pH. Dusts with pH values of Z9 can harm plant life directly by depositing on leaf tissues or indirectly by changing the pH of the soil. Dusts that include poisonous soluble salts will also harm plants (Loppi et al. 2004; Verma and Kumar 2022) (Table 17.2).

17.5.2 *Relative Water Content*

A plant's water intake and release are balanced out by its relative water content. A plant's high water content may assist it retain its physiological equilibrium when exposed to the stress of air pollution. Plant resilience is favored by high relative water content. Schuppler et al. claim that a plant with enough water content can nonetheless increase its overall leaf area. According to Keller (1986), The increased cell permeability brought on by air pollution causes the early senescence of leaves and the loss of dissolved nutrients and water. In light of the physiological impacts of cellular water deprivation, leaf relative water content (RWC) is the appropriate indication of plant water status (Loewus 1999).

17.5.3 *Stomata, Photosynthesis, and Pigment Content*

Green plants' chloroplasts contain chlorophyll which is a photosynthetic pigment, which can be referred to as a photoreceptor and an indicator of productivity (Liang

Table 17.2 PH fluctuations impact stomatal behavior and photosynthesis

Plants	pH range	Effect	Reference
Poplar (*Liriodendron tulipifera*)	4.0–5.6	Decreased stomatal conductivity and photosynthesis	Forkmann and Martens (2001), Freer-Smith and Taylor (1992)
Spruce (*Picea abies,* two clones)	4.0–5.6	Stomatal conductance and photosynthesis in one clone were reduced. Impens and Van Elsacker	Eamus et al. (1989), Freer-Smith and Taylor (1992)
Spruce (*Picea rubens)*	2.5–5	Prolonged reduction in transpiration	Freer-Smith and Taylor (1992), Freer-Smith et al. (2004)
Beech *(Fagus sylvatica)*	3.0–5.5	Stimulation of nighttime closure and increased stomatal conductivity	Barnes et al. (1990)
Spruce *(Picea abies)*	3.5–5.5	Minimum stomatal conductance rose and maximum conductance decreased	Chauhan et al. (2022), Mahady et al. (1998)
Mangifera indica	5.0–6.5	Reduce photosynthesis and have an impact on chlorophyll	Musarrat et al. (2010)
Psidium guajava	5.5–6.5	Decreased stomatal conductance and photosynthesis	Joshi et al. (2009), Joshi and Patil (2017)
Ficus religiosa	7.0–9.0	A greater rate of hexosugar to ascorbic acid conversion	Saxena et al. (2012)

et al. 2011; Lau and Luk 2001). The pigments used in photosynthesis are particularly susceptible to harm from air pollution. Several workers also noted that photosynthetic pigments were degrading due to air pollution.

As chlorophyll is crucial to plant metabolism, measuring it is a crucial step in determining how air contaminants affect plants. Plant growth is directly correlated with changes in chlorophyll content. Starch accumulation can fluctuate depending on factors that have a greater or lesser impact on growth than photosynthesis, which “dilutes” nutrient concentrations in organs like leaves (Lakshmi et al. 2008; Verma et al. 2023).

According to Puckett et al. (1973), chlorophyll pigments exist in a highly organised state and can undergo a number of photochemical reactions under stress. As a result, every variation in chlorophyll content has the potential to impact how the plant behaves morphologically, physiologically, and biochemically. The various pollutants have a substantial impact on the photosynthetic activity that is inhibited, which may lead to a decrease in the amount of carotenoid and chlorophyll in the leaves of different plants. Reduced photosynthesis and gaseous exchange were seen in Viburnum tinus leaf tissue in response to an increase in black dust (Armbrust 1986; Larcher 2003).

Group of naturally occurring fat-soluble pigments known as carotenoids is mostly found in plants, algae, and bacteria that produce photosynthetic material. Carotenoids are essential for the photosynthetic process (Klumpp et al. 1994). Higher plants use them as auxiliary pigments. Reduced carotenoid content associated with air pollution has been documented by several researchers. Chlorophyll is guarded by carotenoid from oxidative damage. Specifically as photoprotective agents in the chloroplasts, carotenoids serve a crucial purpose (Tapiero et al. 2004). Light-catalyzed processes that result in the synthesis of epoxide from the oxidation of carotenoids are then reduced by an enzyme-catalyzed reaction in the absence of light. Such epoxide cycles do exist, according to Krinsky (1966), who also noted their importance in preventing photo-oxidation of chlorophyll.

17.5.4 Ascorbic Acid

An important factor in plants' ability to tolerate pollution is ascorbic acid, a naturally occurring antioxidant (Sharma et al. 2022). It is important for the light reaction of photosynthesis, triggers the body's defensive mechanisms, and can substitute water in the light reaction II under stressful conditions (Kuki et al. 2008; Verma et al. 2021). Ascorbate has a reputation as an air pollution detoxifying antioxidant molecule (Foyer and Halliwell 1976). Previous studies have demonstrated a clear association between plants' ascorbic acid concentration and their resilience to pollution. Ascorbic acid is present in higher concentrations in resistant plants than in sensitive plants (Loewus 1999; Keller and Schwager 1977). When exposed to pollutants, this acid's level decreases. Thus, plants that retain a higher level of ascorbic acid despite being in polluted environments are thought to be air pollutants resistant (Krupa and Baszynski 1995). Strong reductant ascorbic acid activates variety of defence and physiological systems, as well as its concentration straightforwardly affects how much reducing power it has. The impact of specific contaminants on the ascorbic acid levels of different species of plant have produced conflicting results in the literature (Krommer et al. 2007; Krajíčková and Mejstřik 1984).

17.5.5 Enzyme

Everyone is aware that the ascorbate–glutathione cycle, in which SOD catalysis is the process that removes damaging peroxide from chloroplasts (de Marco and Roubelakis-Angelakis 1996; Antonyuk et al. 2009; González et al. 2012). In contrast to growth characteristics, Lagriffoul et al. (1998) showed through their thorough lab research that determining enzyme activity possibly be incorporated as early biomarkers in a plant bioassay to evaluate the phytotoxicity of Cd-contaminated soils on maize plants. In Turkey when subjected to urban and industrial pollution, certain plants like *N. oleander* (Oleander), *Platanus orientalis* and *Acer negundo*

(Boxelder) showed decreased total soluble protein coupled with pigment concentrations and increased activity of peroxidase enzyme (Dineva 2004; Valsecchi et al. 2011).

17.5.6 Sugar Content

Soluble sugar serves as a critical building block and a source of energy for all living things. Plants create and decompose this organic substance during photosynthesis and respiration, respectively. Hardening conditions, which are brought on by pollutants like SO2, NO2, and H2S, can hasten the loss of soluble sugars in the leaves of plants grown in polluted environments (Khan and Malhotra 1982; Theodore Keller 1986). It's likely that the reduction in the total sugar content of injured leaves was accompanied by a photosynthetic inhibition or boost of respiration rate. Tree species that can withstand air pollution were shown to have a higher respiration rate (Keller and Schwager 1977). Due to chlorophyll deterioration, higher respiration and a reduction in CO2 fixation are the likely causes of the crop's lower sugar content near the cement dust-polluted area. The reduction in sugar overall is a reflection of the interference with light absorption brought on by dust buildup on leaf surfaces (Keller and Lamprecht 1995).

17.5.7 Protein

Most prevalent important plants foliar biochemical, protein is necessary for all plant species' enzymatic function (Alamgir 2017; Mora et al. 2008). The protein composition of plants responds to pollution stress in one of two ways, depending on the plant type and its natural resistance to pollution. A reduction in the amount of foliar protein was also seen in the contaminated regions. Protein degradation or a decline in protein synthesis from scratch are likely to blame for the protein content of the foliar tissues declines (Keane et al. 2001; Joshi and Patil 2017). Decreased photosynthesis may also be responsible for the decline in protein content. Pollutants harm plants in a number of ways, including by destroying color, reducing cellular lipids, and peroxiding polyunsaturated fatty acids. Plant produces reactive oxygen species, which lead to the per oxidative destruction of cellular components and the harmful effects of the contaminants. Similar results were observed by Baszynski et al., who noted that protein synthesis decreased as a result of the low chlorophyll diminished leaf area surface (1980). Fly ash particulate matter caused certain plants to have significantly less protein than others. Verma and Singh witnessed noteworthy changes in foliar tissue protein content and photosynthetic pigments as a result of auto exhaust pollution (Joshi et al. 2018; Kumar et al. 2022a, b).

17.6 Effects of PM on Climate Change Coupled with Biodiversity

Particulate matter may have a negative impact on biodiversity, especially when it comes to urban woods. According to reports, the deposition of fine particulate matter into jungles might serve nutrients source, on the contrary it alters the qualities of the leaf surface, lengthening the time that the surface is wet and changing the habitat for epiphytic organisms, raising the risk of diseases (Loppi et al. 2004). Additionally, when settling on an organ's surface, particulate matter can directly impair photosynthesis by leaf abrasion, stomata obstruction, and leaf smothering. Modification of the soil's qualities on a chemical and physical level may be considered an indirect influence (Iqbal, Jura-Morawiec, et al. 2010). A species' success in establishing itself can be hampered by environmental stress (Iqbal et al. 2010a, b). The dynamics of the vegetation are likely to be impacted by this state, leading to additional ecological issues. Additionally, it has been noted that particulate matter directly deposited on soil can affect nutrient cycling, particularly that of nitrogen, via influencing the rhizosphere's bacteria and fungus. According to reports, particulate matter deposition has an impact on the phyllo sphere's microbial community, which is crucial for the breakdown of litter fall (Iqbal et al. 2000).

Due to shared precursors, sources, and climatic processes, ground-level ozone and particulate matter 2.5 are tightly connected. Due of this intimate connection, modifications in one pollutant's emissions can affect ground-level ozone or particulate matter concentrations. The wind has the ability to transport particulate matter and their predecessors over great distances before depositing them on the land or in bodies of water (Inglis and Hill 1974; Singh et al. 2023).

17.7 Effects of Particulate Particles on Plants' Genotoxicity

Concerns about the genotoxic effects on ecosystem of particulate matter pollution (Huttunen 1994). Plants consist of a substantial subdivision of biosphere which are a fundamental constituent of the food chain, so impacts of toxic substances and the following genotoxic consequences on them are particularly important (Huang et al. 1996; Hirano et al. 1995). To assess the harm to the ecosystem and plant health, it is essential to estimate the Geno toxicity of particulate matter (Grantz et al. 2003).

It has been shown that a number of particulate matter contaminants have genotoxic effects on both plants and people (Grant 1999). For instance, even though polycyclic aromatic hydrocarbons are largely chemically inert substances, they can interact covalently with DNA's nucleophilic centres thanks to metabolic activation of their electrophilic derivatives (Hernández-Jiménez et al. 2002).

17.8 Conclusions

Despite the fact that plants have certain stress-tolerance mechanisms built into them, a significant amount of harm is done to them due to particulate matter or dust deposition, which inhibits photosynthetic activities and protein synthesis and makes them more vulnerable to harm from microbes. A crucial step in separating and screening tolerant plants from sensitive ones is to evaluate the biochemical, physiological, and morphological modifications that occur after exposure to particulate matter pollution. Tolerant bio meters may be employed and advised for the construction of green belts to address the issue of particulate matter pollution.

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Chapter 18
Physiological Approaches to Improve the Productivity of Crops Under the Climate Change Conditions

Mohammad Javad Ahmadi-Lahijani

Abstract The changing climate and increasing global population, two major challenges in the 21st century, along with limited arable land, threaten the world's food security. Increasing environmental stresses owing the climate change and the pressure on natural resources to enhance crop yield to meet the world's food demand have made the situation even worth. Recent advances like what occurred in the Green Revolution have improved food security and reduced poverty through increasing agricultural productivity. However, the continuation of this approach would have a great impact on environmental resources such as soil and water and will cause their gradual degradation or destruction. Therefore, improving the efficiency of environmental resource utilization by plants and adaptation to agricultural systems that have optimal consumption of resources are among the key goals of crop improvement. Crop improvement in a sustainable crop production system help in solving the emerging challenges of food security worldwide. To achieve sustainable production where plants are under various biotic and abiotic stresses, in addition to agronomic and crop management approaches, physiological and crop improvement approaches should also be considered. The physiological approaches to advance crop productivity under the future changing climate are discussed in the current chapter.

Keyword Phenotyping · Water use efficiency · Stomatal clustering · Canopy temperature depression · Water potential · Osmotic adjustment · Nitrogen use efficiency · Light use efficiency

18.1 Introduction

Climate change consequences such as drought and extreme temperatures have negatively affected crop productivity. Human intervention such as industrialization, deforestation, desertification, and overgrazing, which began in the early seventeenth

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_18

century, intensified the drought worldwide (Held et al. 2005). In addition, the altered precipitation amount and distribution resulting from increasing greenhouse gases emission further reduced the crop yield. Global warming has risen the earth and seawater temperatures which directly impose limitations on photosynthesis. Photosynthesis is a vital process for maintaining life on the planet, in which radiant energy is absorbed and converted into storable chemical energy in the set of processes of green plants, algae, and blue-green algae. The main factors that determine this process are sunlight, CO_2, water, and temperature. The maximum energy efficiency of photosynthesis is only ~6%, which is rarely obtained in agricultural products (mainly between 1 and 3%) (Sadras et al. 2016). Therefore, water scarcity and high-temperature limitations further increase evapotranspiration and reduce the conversion efficiency of photosynthesis.

Crop yield is a quantitative trait that is controlled by many polygenic traits (Wu et al. 2012). Increasing the genetic potential of plant yield through traditional breeding, such as increasing the yield of wheat by encoding the dwarfing gene of plants in the Green Revolution, has been very successful (Hawkesford et al. 2013). However, the success rate of traditional plant breeding, generally defined as “selection for yield”, is highly dependent on the availability of a wide range of parents, the selection of successful crosses, and the skillful evaluation of obtained genotypes (Donald 1968). Traditional plant breeding is limited by time and resources and is, therefore, less efficient in terms of the progress that is achieved, as desirable traits are introduced more randomly without the physiology of which being fully understood.

Selecting new cultivars with improved potential yield in a target environment, such as future climate changes, is a different and challenging task because understanding the physiological basis of the yield potential in a changing environment is required. It is difficult to select the desired traits and precise combinations of traits for future development and to evaluate the performance of the new variety in future climatic conditions. Hence, introducing plants based on advanced knowledge of crop physiology and evaluating their performance in the target environment can help to improve products with high yield potential under climate change (Fischer 2007).

Improved plants based on advanced knowledge of crop physiology and evaluating their performance in the target environment can help to improve crops with high yield potential under climate change. Recent advances in crop physiology have provided greater information for crop breeders and new tools for crop improvement to increase productivity (Tuberosa and Salvi 2006). Plant physiology along with molecular biology and genomics approaches improve understanding of the complex network of traits related to stress tolerance and selection efficiency and help identify the candidate genes and quantitative trait loci (QTLs) associated with these traits. In the present chapter, the physiological approaches to advance crop productivity under the future changing climate are discussed.

18.2 Water Use Efficiency (WUE)

Drought tolerance is related to WUE and is often characterized by higher water use efficiency. A small part (less than 5%) of the water absorbed by plants is used in synthesizing carbohydrates or the composition of plant tissues because most of it is lost due to evapotranspiration. Therefore, increasing the efficiency of water consumption, i.e., producing more dry matter per water consumption, is one of the possible options for improving productivity and increasing plant production. A wide range of water consumption efficiency definitions is used depending on the scale of measurement. At the plant leaf level, physiologists define WUE as the ratio of CO_2 absorption to transpiration through stomata (Sinclair et al. 1984). From the physiological point of view, WUE is defined as a function of the water consumption per unit of carbon absorbed on a leaf or plant surface, which can be intrinsic or instantaneous.

18.2.1 Stomatal Clustering

In most plant species, stomata are separated by at least one epidermal cell layer to create a cellular space for gas exchange (Ullah et al. 2019). Normally, the stomata are placed at a distance from each other, which provides enough space for the function of the guard cells of the stomata. However, in some plant species, stomata are arranged in clusters (Gan et al. 2010). This arrangement is completely different from the natural stomatal patterns. Stomatal clustering is an abnormal pattern that is created by two or more stomata in the epidermis of the leaf and has been found in more than 60 types of terrestrial plants, dicotyledons, and monocotyledons, including some begonia species, Crosulaceae, Sonrataceae, and Moraceae families (Gan et al. 2010; Lehmann and Or 2015). Many plant species with stomatal clusters live in dry, salty, or unfavorable environments. For example, stomatal clustering has been observed in sweet clover, the halophyte plant Sonneratia alba belongs to the Sonneratiaceae family, and the Sedum plant, which has a CAM photosynthetic system, which is very resistant to drought stress. These types of stomata have also been observed in crop plants, among which legume families such as sweet clover, *Vicia faba*, and some tomato mutants can be mentioned (Gan et al. 2010; Ahmadi-Lahijani and Erwin 2016, Unpublished data).

The formation of cluster stomata is proposed to reflect adaptation to harsh environments to reduce water loss from plant leaves. The stomatal clustering increases the resistance against water vapor diffusion (~10%). The reduction of gas exchange due to stomatal clustering shows that the function of the guard cell is impaired, which limits the stomatal opening. There are two different types of cluster stomata; “contiguous clusters” and “non-contiguous clusters”, according to the characteristics and distribution pattern (Gan et al. 2010). Contiguous cluster stomata have two (or more) stomata that are in direct contact (without the intervention of epidermal cells between

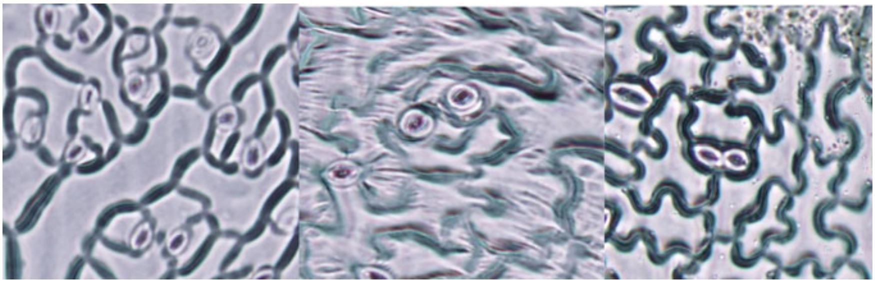

Fig. 18.1 Stomatal clustering in various plant species: **a** non-contiguous stomata in *Arabidopsis thaliana*, ade mutant [heat tolerant, ABA over expression]; **b** Non-contiguous stomatal clusters in *Arabidopsis thaliana*, accession Colombia; **c** contiguous stomatal clusters in tomato *Solanum tuberosum cv*. 1994

adjacent guard cells), but non-contiguous clusters are formed by groups of stomata which may not be in contact with each other (separated by sub-cells) (Fig. 18.1).

Environmental signals, such as signals from old to younger leaves to reduce the stomatal density under water shortage, or the formation of cluster stomata in some plants that grow in dry environments, may regulate the pattern of stomatal development (Wang et al. 2007). Studies showed that drought and salinity stress significantly increase stomatal density and stomatal index. In addition, the contiguous clusters also increased with the severity of drought and salinity. These results show that stomatal clustering might be related to environmental stimuli (Gan et al. 2010). Drought and salinity stress caused the formation of cluster stomata in the epidermis of *Vicia faba* plant leaves (Gan et al. 2010). Compared to the control plants, the stomatal density increased by 30 and 21% under mild and severe drought stress, and the stomatal index increased by 10.7 and 14.3%, respectively, which shows that more stomata were gathered in a certain area under drought stress. Similar results were observed under salt and heat stress conditions. In Arabidopsis and tomato plants under heat stress conditions, it was observed that the heat-resistant mutants had clustered stomata, while the heat-sensitive genotypes had a uniform distribution of stomata (Ahmadi-Lahijani and Erwin 2016, Unpublished data). The effect of stomatal clustering on the leaf conductance of different accessions of the Arabidopsis plant, which indicates different stomatal patterns, was investigated and the results showed that the diffusive conductance of leaves with cluster stomata was ~60% less compared with those with a uniform stomatal distribution (Dow et al. 2014).

Stomatal clustering is one of the environmental adaptation strategies in certain species that creates a lower transpiration requirement (Papanatsiou et al. 2017). Min et al. (2002) observed a positive relationship between cluster stomata and multilayered epidermis and stated that stomatal clustering is an important adaptation against drought. Over the past 50 years, it has been established that the two-dimensional distribution of stomata during leaf expansion is closely related to the living environment; for example, plants that grow in dry areas have fewer stomata (Zhang et al. 2003). Also, an increase in the concentration of atmospheric CO_2 often leads to a decrease in stomatal density (Woodward 1987), although no change (Ahmadi-Lahijani 2017) and even an increase (Lawson et al. 2002) have also been observed in the number of stomata under elevated CO_2. However, few studies are available to answer questions such as, why do some plants have cluster stomata? Are cluster stomata an environmental response or is it just a phenomenon during the growth and development of leaves in some terresterial plants? Or what is the ecological importance of stomata cluster in the natural environment? This can be considered a new indicator for the adaptation of plants to climate change and should be given special attention in future multi-breeding programs to increase the efficiency of water consumption.

18.2.2 Canopy Temperature Depression (CTD)

The plant's water status is a direct indicator of the plant's response to drought. Transpiration is the main cause of changes in leaf temperature, and there is a direct relationship between leaf temperature, transpiration rate, number of stomata, and stomatal conductance (Rebetzke et al. 2013). The difference between the canopy temperature from the ambient temperature is known as the CTD (air temperature (Ta)—canopy temperature (Tc)), which is considered an indicator of the water status of the plant and used to evaluate the plant response to environmental stresses such as high temperature and drought (Balota et al. 2008; Sofi et al. 2019).

Canopy temperature can be related to the genetic potential capacity of roots to explore soil moisture and can be used as an alternative trait to analyze root growth and biomass allocation under drought stress conditions (Hammer et al. 2009). Canopies with lower temperature show higher plant access to water through deeper roots. Genotypes with a cooler canopy had 30% more yield and 40% more root dry weight (Lopes and Reynolds 2010). Canopy temperature is affected by several environmental factors, including the amount of sunlight on the canopy, soil moisture, wind speed, temperature, and relative humidity (Mason et al. 2013). The CTD is positive when the canopy is cooler than the air and is related to the increase in crop yield. In wheat and soybean genotypes, a decrease in CTD had a direct relationship with crop yield and resistance to drought stress (Ahmadi Lahijani and Emam 2013; Kumar et al. 2017). The drought-sensitive genotypes which had relatively higher yield reduction under stressful conditions showed a warmer canopy in the middle of the day (Fig. 18.2).

Canopy temperature under field conditions is related to physiological traits and provides a low-cost measurement for selecting tolerant genotypes (Reynolds et al. 2009). In recent years, CTD has been widely used to study the response of genotypes to environmental stresses. In a study on wheat genotypes, an appositive correlation was observed between the CTD and grain yield under both stressful and unstressed conditions (Ahmadi Lahijani and Emam 2013) (Fig. 18.3). Studies on beans and chickpeas have shown that CTD can be used to evaluate the plant's response to stressful conditions (Sofi et al. 2019). Genetic variations in canopy temperature are due to changes in the plant's ability to transport water through the vascular system,

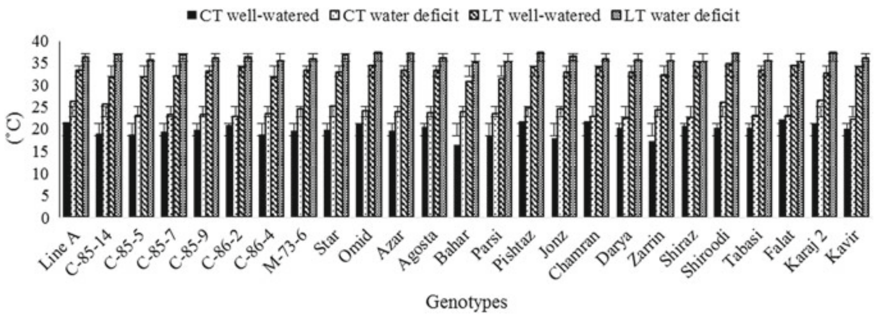

Fig. 18.2 Leaf temperature (LT) [°C] and canopy temperature (CT) [°C] for genotypes during the grain filling period. Genotypes are arranged on the x-axis in order of overall mean values. The bar above each column is the SE (n = 9) for comparing irrigated and non-irrigated means in each genotype

differences in stomatal physiology, root biomass and depth, metabolism, and source-sink balance (Saint Pierre et al. 2010).

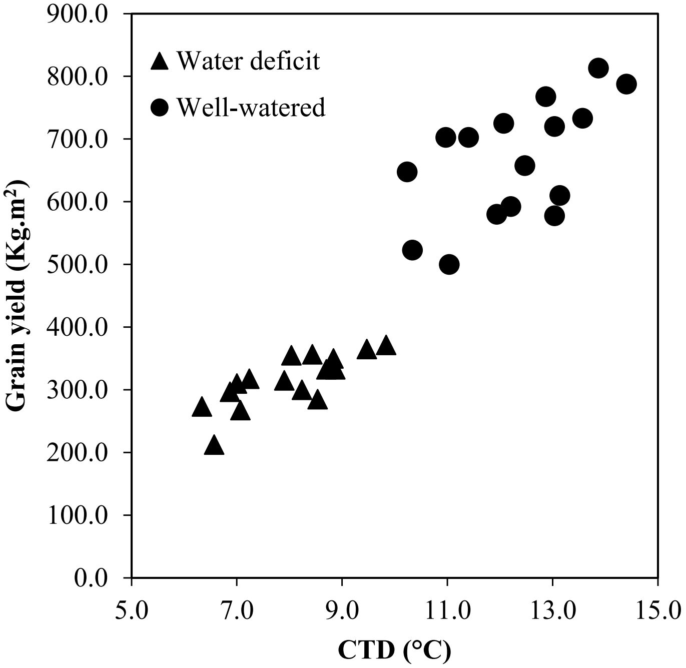

Fig. 18.3 The relationship between canopy temperature depression (CTD) and grain yield under well-watered and water deficit conditions in wheat genotypes

18.2.3 Leaf Water Potential and Osmotic Adjustment

Stomata play a double role in controlling the exchange of carbon absorption and water loss, and therefore, they play an important role in determining the WUE of plants. The dynamics of stomatal aperture control with environmental changes such as light intensity and quality, humidity, and CO_2 concentration regulate the process of gas exchange (Shimazaki et al. 2007). Transfer and accumulation of osmotic active compounds and lateral movements of guard cells are also important in stomatal movement control. Therefore, the species with higher osmotic adjustment ability will provide higher WUE, and under the condition of soil water shortage, which decreases the soil water potential, will be able to absorb more water and tolerate adverse conditions.

Leaf water potential shows the overall water status of the plant. Maintaining a high leaf water potential is associated with water deficit prevention mechanisms. Leaf water potential can be used as an easy and fast method for screening drought-tolerant genotypes. Before flowering, plants prevent dehydration in their organs by maintaining higher leaf water potential, while after flowering, they prevent dehydration by maintaining higher water pressure at a certain level of moisture stress (Rosenow and Clark 1995). Osmotic adjustment is defined as the active accumulation of solutes in plant tissues (roots or shoots) in response to the reduction of soil water potential, which helps plants maintain the pressure of shoots and roots due to water stress (Morgan 1984). In addition to its role in osmotic regulation, osmotic solutes protect plants against stresses, especially drought and high-temperature stress by scavenging reactive oxygen species (ROS), and stabilizing cell membranes, the structure of enzymes, and proteins (Farooq et al. 2009). Tangpremsri et al. (1995) found that the adverse effects of water stress can be reduced by selecting sorghum genotypes with high osmotic adjustment ability. Kafi et al. (2021) also observed that higher leaf water potential was associated with higher salinity tolerance of potato plants. Similar results were also observed in tomato plants (Nabati et al. 2021). It seems that species with the ability to osmotic adjustments and maintain a higher leaf water potential will be more successful in stressful conditions and future climate changes, which will be accompanied by an increase in temperature and water deficit.

18.3 Nitrogen Use Efficiency (NUE) and Remobilization

Chemical fertilizers, especially nitrogen (N), are one of the most important factors in increasing crop production in agricultural systems (Li et al. 2009). Nitrogen is an important nutrient for all living organisms and, in general, it is the most limiting nutrient for agricultural products (Rosolem et al. 2017). However, high N consumption to increase crop yield has been one of the main causes of environmental pollution, including soil, water, and air, and it is also considered one of the causes of global warming. Uncertainty in rainfall patterns and long-term droughts are expected to intensify worldwide and increase the demand for irrigation water to maintain production levels. Water availability not only determines the availability of N for crop production but also controls the entire geo-bio-chemical cycle of N (Gonzalez-Dugo et al. 2010). Lack of water affects N absorption even if it is available in the root environment because water is the factor in transporting dissolved minerals from the soil to the roots.

One of the practical solutions to reduce N consumption is increasing the NUE, either at the plant or field level. The NUE is determined by two components: nitrogen absorption efficiency (the amount of N absorbed by the plant relative to the available N in the soil) and nitrogen utilization efficiency (the amount of dry matter produced per unit of N absorbed) (Moll et al. 1982). The increase in NUE can be achieved through agricultural approaches, including crop rotation, management of irrigation, fertilizer sources and methods, and physiological approaches.

From a physiological point of view, understanding the physiological mechanisms that regulate the N absorption by plants, grains, and roots, the process of N absorption and redistribution in the cell, and the leaf structure, can help to improve the NUE. For example, N uptake and leaf area index are directly related (Hirel et al. 2007). This is of special importance, especially in the conditions of N and water limitation. Overexpression of the downstream gene of N absorption has increased the absorption and NUE in rapeseed and rice (Shrawat et al. 2008). The production of larger and deeper roots, which can absorb N in the soil profile, increases N absorption by plants. Also, plants with deeper roots will have the ability to absorb more N in sandy soils, where N is more prone to leaching (Liao et al. 2006).

Simultaneously with the vegetative growth of the plant, N is remobilized from old to younger leaves and reproductive organs. The remobilized N from the stem and old leaves (lower leaves) to the upper leaf layers is very important to maintain the N content of young leaves. The number of grains per spike in cereals and the beginning of tuber formation in potatoes is influenced by N and its remobilization. Grain N content is the result of the interaction between N remobilization from the aerial parts in the reproductive stage and the total N absorbed, the N harvest index, grain yield, and grain N percentage (Ciampitti and Vyn 2013). Identifying the physiological characteristics that regulate the balance between the N dedicated to photosynthesis and the remobilization of N to physiological sinks can be useful for improving the NUE.

Increasing the N transportation to the target organs such as leaves or grains can significantly improve the N uptake index and the overall NUE. Improving the photosynthetic NUE (photosynthetic capacity per leaf N unit) can improve NUE. Improving the photosynthetic NUE by changing the leaf area index and leaf specific N content can improve the overall NUE. Regulation of physiological parameters that regulate nitrate or ammonium metabolism can also increase the NUE. The photosynthetic NUE also depends on the saturation point of Rubisco carboxylation, and therefore, optimizing the activity of Rubisco can improve the photosynthetic NUE, especially in C_3 species (Ullah et al. 2019).

18.4 Radiation Use Efficiency (RUE)

Radiation use efficiency is defined as the dry matter produced per absorbed radiation. The RUE can also be calculated by linear regression of accumulated dry matter against cumulative photosynthetically active radiation (PAR), where the slope of the regression line is considered the RUE (Tesfaye et al. 2006). Under favorable soil conditions and the availability of water and nutrients, plants can use the maximum available radiation. Variation in the efficiency of using radiation is generally caused by soil variability, climatic conditions, crop management practices, and various abiotic and biotic stress factors (Rouphael and Colla 2005).

Stressful conditions, such as drought and high temperature lead to stomatal closure and decrease CO_2 entry to the leaf, which increases photorespiration and reduces the efficiency of photosynthesis. On the other hand, high light intensities along with stomatal closure provide conditions of light saturation and photoinhibition, and finally, oxidative stress. Therefore, in this situation, receiving less light by the canopy can help to increase production efficiency. Under high temperatures, sunlight, and evapotranspiration, the soil water is not able to compensate for the evaporated water. Therefore, plants must close their stomata to minimize water loss, which reduces CO_2 absorption and increases leaf temperature (Galmés et al. 2007). These physiological changes are also reflected in plant morphology under stressful conditions, and the leaf surface, which is the main factor determining PAR absorption, is decreased and therefore, reduces the RUE.

Some physiological approaches can be used to increase biomass production and the RUE of crops. Some of the approaches are included reducing the respiration and photorespiration losses, prolonging the duration of photosynthesis, manipulating hormonal responses, increasing the nutrients absorption capacity and use, improving the conversion efficiency of photosynthetic radiation, and improving the physiological sinks strength and carbon allocation. Genetic manipulation can also be considered to improve the RUE. In the changing climate where the CO_2 level is expected to increase, plants will likely face the limited conditions required for optimal photosynthesis at different time intervals. To deal with such conditions, plants need the ability to regulate the flow of carbon and they should have the ability to remobilize carbon during the grain-filling stage.

Photorespiration is a process that limits the efficiency of photosynthesis, which occurs mostly under drought stress and high temperature. Minimizing photorespiration losses can significantly increase the RUE. It seems that under the conditions of climate change when plants will face drought and high-temperature stresses, the conditions will be provided for more photorespiration. For this purpose, the simultaneous overexpression of three photosynthetic enzymes in the leaves of C_3 plants to reduce carbon and nitrogen losses caused by photorespiration might be an effective approach (Sun et al. 2009; Parry et al. 2011). The quantum efficiency of photosystem II is linearly related to gross photosynthesis and is used as the RUE index. Plants with similar photosynthetic radiant energy conversion efficiency can have different performances based on the canopy greenness longevity and leaf area index. For example, two C_4 plants, silver grass and corn, have similar photosynthetic RUE, but due to longer canopy greenness and higher leaf area index, silver grass can produce ~50% more biomass than corn (Heaton et al. 2008).

In general, C_4 plants have higher RUE than C_3 plants, which is related to the difference in the photosynthetic system and some anatomical features. The stomata of C_4 plants have a lower degree of aperture compared with C_3 plants. Since C_4 plants have evolved in tropical regions with high temperatures and radiation intensity, they have a higher optimal photosynthetic temperature and do not suffer from light saturation and photoinhibition, like what happens in C_3 plants. But the maximum photosynthetic efficiency and the growth rate of C_3 plants are obtained at light intensities lower than the light saturation point. Therefore, the angle of the leaves is of special importance in C_3 plants. One of the approaches that can be considered for increasing the RUE, in addition to improving the photosynthetic efficiency and increasing the optimal temperature of photosynthesis, is reducing the angle of the leaves with the stem. The vertical leaves on the top of the plant help reduce light saturation and lead to light penetration to the depth of the canopy, resulting in the participation of the lower leaves in photosynthesis and dry matter production. Therefore, a canopy with a lower extinction coefficient can help to increase the density without increasing respiration and negative effect on plant production (Ullah et al. 2019).

Studies have shown that the high rate of leaf photosynthesis increases the RUE (Sinclair and Horie 1989). The photosynthetic capacity of leaves can be improved by increasing the investment in some photosynthetic enzymes to reduce photorespiration enzymes (Sun et al. 2009). Another method is the engineering of C_3 plants with a C_4-like photosynthetic system (Parry et al. 2011). The C_4 photosynthetic system is an efficient process, especially in stressful conditions. These plants use an oxygen-sensitive enzyme called phosphoenol-pyruvate carboxylase (PEP carboxylase) as the primary CO_2 fixation enzyme, which reduces the possibility of photorespiration. The leaves of these plants have Cranz anatomy, which consists of bundle sheath and mesophyll cells. It is possible to express C_4 genes in C_3 plants (Mitchell and Sheehy 2006), but it is difficult to produce Kranz-type anatomy in C_3 plants. Some terrestrial C_3 plants, such as Hydrilla and *Chenopodiaceae*, have a C_4-like photosynthetic system in one cell (there is no spatial separation like that seen in C_4 plants), which can be a better model for this purpose. But the rate of photosynthesis may still be slow and limiting (Parry et al. 2011).

18.5 Root Structure and Improvement of Harvest Index

Increasing plant tolerance to stressful conditions under climate change by improving the ability of crops to extract water from deep layers of the soil through a more optimal root structure, along with reducing water demand (improvement of WUE) can be considered a potentially sustainable approach to reduce the risk of crop production loss. Less attention has been paid to the genetic improvement of the root system structure to achieve a plant species with a more efficient production capacity. The root system structure is an integral part of plants in the absorption of nutrients and water and crop yield, and the changes in the structure of the root system can be related to an increase in the productivity of plants (Smith and De Smet 2012; Zhu et al. 2019).

Breeding for the root system can lead to the second green revolution, and increasing the absorption of resources can enhance yield and reduce the need for inputs such as fertilizers (Lynch 2007). One of the dwarf wheat cultivars that greatly contributed to the Green Revolution was Pitic62, which had an exceptionally large root system (MacKey 1973). Roots are the bases of plants, but compared to the rest of the plant, they have remained relatively unknown, and plant breeders have largely neglected the direct selection of root traits. This is partly due to the lack of easy access to the roots, their phenotypic flexibility, and the impossibility of selecting high-yielding phenotypes (Manschadi et al. 2006).

Research showed that increasing the concentration of CO_2 stimulated root growth and increased dry matter allocation to tubers and increased potato tuber yield (Ahmadi Lahijani et al. 2019). The results of this research showed that an increase in root growth can increase yield by improving water absorption, WUE, and dry matter allocation to the economic parts of the plant. In addition, the increase in the concentration of CO_2, which is one of the consequences of future climate change, can stimulate the growth of the roots, so that the plant can explore the soil more deeply and can benefit from higher absorption of water, nutrients, and increasing production.

A developed root system that penetrates the deep layers of the soil can increase the absorption of nutrients. Water shortage in the reproduction stage significantly reduces the harvest index, and therefore, strategies to reduce water consumption are necessary to supply the water needed for the next stages of growth, such as the reproduction stage. Phenotypic and field-based selection methods, considering the characteristics of the root structure in stressful conditions and high resource efficiency use should be given special attention.

18.6 Conclusion

The need to meet food security (and safety) and prepare to face climate change has become increasingly important, and efforts should be made to introduce a plant suitable for a biomass-oriented agricultural system and compliance with stressful conditions. Domestication has focused on yield-related traits and not on stress tolerance or disease resistance traits, which fails when concurring stressful conditions. Plant species should be continuously evolved to meet changing demands and increase production. Physiological approaches have a huge potential in the development of next-generation agriculture. Physiological traits, such as stay-green trait, CTD, cell membrane thermostability, RUE, NUE, chlorophyll fluorescence, relative water content, and stomatal conductance and structure are especially important in developing high-yielding stress-tolerant species. Plant species optimized for future climatic conditions can provide a road map for selecting target traits and their optimal combination to improve production and genetic compatibility for researchers and plant breeders to increase yield potential. It is essential to integrate crop physiology, genomics, and breeding approaches to understand complex stress tolerance traits, and the molecular basis of drought tolerance, and develop the next-generation crops for our changing climate.

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Chapter 19
Redesigning Root Architecture for Improved Performance of Plants Under Stress

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Abstract Plants respond to abiotic stress condition by alterations to their root system architecture, including morphology, topology and distribution patterns. Favourable root-to-shoot ratio, branching angle, root proliferation, topsoil foraging and development of root hairs or specialized structures like cluster roots are commonly observed under abiotic stress conditions. Drought stress and phosphorus (P) deficiency reduced primary root growth but increased length and density of lateral roots and root hairs. Species belonging to the Proteaceae family (like white lupin) develop specialized cluster root structures with dense lateral roots, covered with abundant root hairs. Hence, root system architecture plays an essential role in improving abiotic stress such as nutrient acquisition efficiency. Spatial arrangement, branching, size, density

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_19

and length of roots profoundly influence nutrient acquisition. Root system architecture responds positively elevated [CO_2] as reported in several crops. Elevated [CO_2] stimulates lateral root branching, especially in the surface horizons. Elevated [CO_2] increased carbon allocation to below-ground processes like root growth, respiration and efflux of organic compounds. Signals from greater carbohydrate availability in plants grown under elevated [CO_2] might help stimulate lateral root branching, ultimately leading to shallow and highly branched root architecture. A change in the rhizosphere microenvironment due to nutrient deficiency or altered [CO_2] enhances root density and produces more lateral roots.

Keywords Abiotic stress · Root system architecture · Lateral root branching · Elevated [CO_2] · Nutrient acquisition efficiency

19.1 Introduction

Plants are essential for sustaining life on Earth, providing us with food, fiber, medicine, and ecological services. However, their growth and productivity are frequently hindered by various environmental stresses, including drought, salinity, nutrient deficiency, and pathogen attack. These stresses can lead to reduced crop yields, economic losses, and compromised food security. As the global population continues to rise, the need to develop innovative strategies to enhance plant performance under stress conditions becomes increasingly urgent (Sharma et al. 2023a, b; Wang et al. 2023). One promising avenue of research is the redesign of root architecture to improve plant resilience and productivity. Roots play a crucial role in a plant's ability to cope with stress by facilitating the uptake of water, nutrients, and minerals from the soil. Traditional root systems typically exhibit a shallow and extensive lateral spread, which may not be efficient for acquiring limited resources or accessing deeper water sources (Saqib et al. 2023; Devi et al. 2023). In contrast, plants with deep and well-branched root systems have been observed to exhibit enhanced stress tolerance due to their ability to explore a larger volume of soil and tap into untapped nutrient and water reservoirs (Dash et al. 2017; Gobu et al. 2022). Over the past few decades, significant progress has been made in understanding the genetic and molecular mechanisms governing root development and stress responses (Yadav et al. 2023; Mandal et al. 2023a). The emerging knowledge in this field has presented exciting possibilities for enhancing plant performance under stress conditions through targeted manipulation of root architecture.

Researchers have successfully utilized genetic engineering and molecular breeding techniques to modulate key genes involved in root development and stress signaling pathways. For instance, the gene DRO1 (Deeper Rooting 1) has been identified as a significant quantitative trait locus (QTL) linked to deep rooting in rice (Oryza sativa) under upland field conditions (Uga et al. 2011). Overexpression of *DRO1* has demonstrated the ability to promote the development of deeper and denser root systems, effectively enhancing the plant's resilience to drought stress.

Similarly, the transcription factor *LBD29* (Lateral Organ Boundaries Domain 29) has been found to play a pivotal role in lateral root development. By manipulating *LBD29* expression, researchers have successfully generated plants with increased lateral root branching, resulting in improved nutrient acquisition efficiency and overall stress tolerance (Guan et al. 2023). These breakthroughs offer promising prospects for tailoring root traits and, in turn, improving crop resilience in challenging environments.

Advances in imaging technologies have also revolutionized the study of root architecture. Three-dimensional root phenotyping and high-resolution microscopy techniques enable researchers to visualize and quantify root traits under different stress conditions, such as root length, angle, and branching patterns (Rather et al. 2022; More et al. 2023; Jaiswal et al. 2023a, b; Thakur et al. 2023a, b). These tools provide valuable insights into the responses of roots to stress and help identify specific root traits associated with stress tolerance that can be targeted for improvement. The research of root-to-shoot communication and resource allocation mechanisms has further advanced our understanding of plant responses to stress. Long-distance signaling between a plant's roots and aerial parts has emerged as a crucial mechanism for coordinating adaptive responses in the face of stressful conditions. With the aid of molecular markers and advanced bioinformatics tools, researchers have made significant strides in identifying genes responsible for this long-distance signaling and resource allocation (Mangal et al. 2023; Tiwari et al. 2023; Sharma et al. 2023a, b). These findings have uncovered potential mechanisms that can be precisely targeted to optimize root architecture, offering promising avenues for enhancing plant performance and resilience under stress (Jia et al. 2023). This exciting progress holds great potential for the development of innovative strategies to improve crop productivity and sustainability in challenging environments.

Redesigning root architecture improves stress tolerance and enhances nutrient and water uptake efficiency. Efficient nutrient acquisition is particularly crucial in nutrient-deficient soils, where the availability of essential minerals is limited. Root modifications that increase the surface area for nutrient absorption or alter the expression of transporters involved in nutrient uptake can significantly enhance plant performance under nutrient-stress conditions (Jaiswal et al. 2022; Kumar et al. 2023a; Mandal et al. 2023b; Buttar et al. 2023). Moreover, optimizing root architecture has the potential to improve water use efficiency in drought-prone regions. Deep-rooted plants can access deeper soil layers with higher water availability, reducing their dependence on surface water sources. Root traits such as root hair density, diameter, and distribution play a critical role in water uptake efficiency, making them prime targets for manipulation in the development of drought-tolerant plants capable of thriving in water-limited environments. The strategic redesign of root architecture offers a promising avenue to enhance plant performance under stressful conditions. With the integration of genetic engineering, molecular breeding, and cutting-edge imaging techniques, researchers have made significant progress in unraveling the genetic and molecular mechanisms governing root development and stress responses (Singh et al. 2023; Jia et al. 2023; Watpade et al. 2023; Raza et al. 2023b). Through precise manipulation of specific genes and traits associated with root architecture, scientists can create plants with improved stress tolerance, enhanced nutrient and water uptake efficiency, and ultimately, increased productivity. This groundbreaking research has immense potential to address the pressing challenges of global food security and sustainability amid mounting environmental stresses. By equipping crops with robust root systems optimized for resilience, we can cultivate more resilient and productive agricultural systems, ensuring food availability for a growing world population while promoting resource-efficient and sustainable agricultural practices.

19.2 Effect of Abiotic Stress Condition on Root Growth and Development

Climate change has become a big issue for agriculture, aggravating abiotic and biotic stresses. Abiotic variables significantly impact the growth and development of plants in this drastically changing climate. The Abiotic stresses like salinity, nutrient deficits, drought, fluctuating temperature, flood and heavy metal toxicity negatively affect plant growth, development, productivity and quality (Altaf et al. 2023; Zhao et al. 2023; Lin et al. 2023). In general, roots experience higher abiotic stress than shoots and are affected more than the above-ground parts. Due to the restricted number of opportunities for root observations, the impact of abiotic stressors on root structure and development has received much less research attention than that of the above-ground sections of plants. Roots serve a variety of functions for the growth and development of plants, including establishing a connection between the plant and its surroundings, absorbing nutrients and water and transporting them to the plant's above-ground organs, secreting particular hormones, and guaranteeing the efficacy of nutrients in the nutrient solution (Mangal et al. 2022; Lal et al. 2023b; Li et al. 2023). During stress conditions, such as salinity, nutrient deficits, drought, fluctuating temperature, flood, and heavy metal toxicity around the root zone produces, certain signals or hormones communicate with the other parts of the plants that will able to adapt in adverse climatic condition (Kul et al. 2020).

A wide range of abiotic factors can also influence how roots develop. The osmotic potential of plant root cells is also impacted by high salt conditions in the root zone, which causes exosmosises in plant root cells (Pattnaik et al. 2021). Root respiration rates are reduced by waterlogging conditions, which also produce methane, a major greenhouse gas that contributes to climate change. However, plants have created a number of physiological and cellular adaptations in their life mechanisms to combat the impacts of abiotic stress (Khan et al. 2016a, b; Goswami and Deka 2020).

Due to the complexities and challenges of studying root traits, most research efforts have focused on improving shoot performance (Comas et al. 2013). As a result, there is a significant lack of knowledge regarding roots' critical role in plant processes. To address this gap, researchers increasingly turn to sophisticated and artificial phenotyping platforms to thoroughly examine root system architecture (RSA) responses to various abiotic stresses in Arabidopsis and different crop species. By uncovering the crucial molecular and cellular mechanisms underlying RSA responses to stress, they aim to gain valuable insights for crop selection with improved stress tolerance (Koevoets et al. 2016). Obtaining practical evidence on the role of root plasticity will be instrumental in supporting breeders as they strive to incorporate root properties into their current selection pipeline for abiotic stress tolerance, ultimately enhancing the resilience of crops. The components that make up root morphology, such as primary root length, secondary roots, tertiary root growth, root hairs, and root thickness, exhibit considerable variation both geographically and in diverse environments (Kul et al. 2020). Understanding these variations will be crucial for developing crops with better adaptability to challenging conditions, contributing to the advancement of sustainable agriculture and food security (Lal et al. 2023a; Thakur et al. 2023a, b; Verma et al. 2023; Jaiswal et al. 2023a, b).

The current understanding of how various abiotic stress situations affect roots' molecular and physiological responses is also important in order to understand how they respond to these situations. In this way, the omics and phenotyping methodologies that were used as part of the investigation of these responses will be discussed in more detail. As a result, plant cells are able to detect and activate adaptive responses due to the signals released by the roots in response to environmental stress (Singh et al. 2022; Mandal et al. 2023b; Buttar et al. 2023; Jeevalatha et al. 2023). The interaction between hormonal regulatory pathways, changes in gene expression across the board, and changes in protein homeostasis are some of the key regulatory processes influencing root adaptation to stress situations. In addition, all these signals are analyzed to see how the root system utilizes them all to produce a variety of physiological responses, such as morphological changes, long-range signaling, and root exudation (Vives-Peris et al. 2020).

A plant's response to stress begins with perception of harmful conditions. Roots are affected mainly by abiotic stress, especially drought, although most studies on abiotic stress resistance mechanisms focus on aerial organs, due to the difficulty of studying roots in their natural environment. As has been pointed out (Prince et al. 2013; Calleja-Cabrera et al. 2020a, b), aboveground and belowground organs respond differently to stress, and physiological and molecular mechanisms leading to stress tolerance differ but are complementary (Zhang and Shi 2013). Accordingly, a number of novel strategies are emerging for the development of crops to be more resistant to abiotic stress conditions, which involves targeting specific tissues or organs rather than the whole plant as a whole, instead of targeting the entire plant as a whole (Zhang 2015). In many plant species, abiotic stresses induce transcriptional changes in the roots of the plants. In spite of this, it has been noted that aboveground and belowground organs will respond differently to stress in different ways.

The goal of this study was to determine whether it can be achieved by targeting certain tissues or organs rather than the entire plant as a whole in order to create crops that have increased tolerance to abiotic stress conditions. Many plant species undergo transcriptional alterations when they are exposed to stress conditions (Zhang et al. 2021). During times of abiotic stress, roots are induced to produce various phytometabolites, such as osmoprotectants, antioxidants, etc., in order to cope with the adverse conditions that they are faced with (Arbona et al. 2016). In the roots of maize plants under water stress conditions, there is an upregulation of antioxidant enzymes (Sandhya et al. 2010). In addition, an intricate network of plant hormones such as abscisic acid (ABA), jasmonates (JA), salicylic acid (SA), or ethylene (ET) that modulate stress responses are also responsible for controlling root activity during stress (Lorenzo and Solano 2005). The auxin proteins are responsible for controlling root hair elongation and root branching under abiotic stress and have also been shown to play a role in the positive regulation of drought stress tolerance through the arrangement of root architecture (Karlova et al. 2021). The role of roots in these processes is, however, much less well known. During various abiotic stress conditions, roots undergo a variety of changes in biochemistry, physiology, and gene expression, which will be important to develop breeding programs in a more targeted way in the future (Vives-Peris et al. 2020).

19.3 Physiological and Biochemical Response of Root Under Abiotic Stress Condition

It is well known that plants are subjected to various abiotic stresses, such as drought, salinity, extreme temperatures, and heavy metal toxicity, which can severely affect their growth (Altaf et al. 2023; Raza et al. 2023a; Zhao et al. 2023; Kumar et al. 2023c) and development. Under such adverse conditions, the root system plays a crucial role in the plant's survival by absorbing water and nutrients from the soil and utilizing them for the plant's growth. For the development of stress-tolerant crops and the improvement of agricultural practices, it is essential to understand the physiological and biochemical responses of roots to abiotic stress. There are many physiological and biochemical responses that roots exhibit in response to conditions of (Jia et al. 2023; Aggarwal et al. 2023; Saqib et al. 2023; Watpade et al. 2023) abiotic stress, which we will explore in this discussion. It is one of the primary functions of roots to absorb and transport water from the soil to the surface of the plant, which is one of the primary functions of roots. As a result of drought conditions, plants experience a deficit of water, which as a consequence results in a reduction in soil water availability. The roots, in response, exhibit a number of adaptive mechanisms in order to maximize their water uptake and minimize their water loss. Under drought stress, plants can adjust root morphology by extending their roots, branching out, and increasing their root hair density, which boosts the root surface area for enhanced water absorption by increasing their root length, branching out, and root hair density (Dash et al. 2022); Comas et al. 2013). Furthermore, roots have the ability to modulate their hydraulic conductivity in a way that regulates water transport and minimizes water loss through transpiration (Tardieu et al. 2018).

Drought and salinity affect plant cells' osmotic potential, disrupting their cellular processes. Roots adjust to osmotic stress by accumulating compatible solutes, such as proline, sugars, and amino acids, in their cytoplasm. By increasing the osmotic potential of cells, these solutes allow roots to maintain water uptake even under water shortages (Jaiswal et al. 2022; Singh et al. 2023; Devi et al. 2023). Dehydration also damages cellular structures and enzymes as a result of osmotic adjustment (Munns and Tester 2008). In plants, abiotic stress conditions like salinity and heavy metal toxicity can disrupt ion homeostasis. Toxic ions, such as sodium (Na^+) or heavy metals, can accumulate in roots and impair their normal function. In response to these stresses, roots regulate ion uptake, transport, and sequestration. It has specialized transporters that actively remove toxic ions from the cytoplasm and accumulate essential ions, such as potassium (K^+), in order to maintain ion homeostasis (Munns and Tester 2008). Plant cells can be damaged by oxidative stress caused by reactive oxygen species (ROS) produced by abiotic stress. Antioxidant defense mechanisms are activated by the roots to scavenge ROS and protect the plant against oxidative stress by scavenging ROS. In order to neutralize ROS, enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), and ascorbate peroxidase (APX) play a critical role (Rather et al. 2022; Thakur et al. 2023a, b; Sharma et al. 2023a, b; Kumar et al. 2023b). In the root cells, these enzymes catalyze the breakdown of reactive oxygen species (ROS) and maintain a balanced redox environment. Non-enzymatic antioxidants, such as ascorbic acid (vitamin C) and glutathione, also contribute to the antioxidant defense system in roots (Mittler et al. 2017). Plant hormones are key regulators of plant growth and development, including the response to abiotic stress. Roots produce and respond to various hormones, such as abscisic acid (ABA), ethylene (ET), and jasmonic acid (JA), which play vital roles in stress signaling and adaptation. ABA, for example, is known for its involvement in stomatal closure, thereby reducing water loss. It also regulates root growth and promotes the accumulation of osmoprotectants under drought stress (Sah et al. 2016). ET and JA, on the other hand, are involved in root growth inhibition and modulation of root architecture in response to various stresses. Under abiotic stress conditions, roots modulate gene expression and signaling pathways to adapt to the challenging environment.

Transcription factors, such as DREB (dehydration-responsive element-binding protein) and MYB (myeloblastosis), regulate the expression of stress-responsive genes involved in osmotic adjustment, ion transport, antioxidant defense, and other adaptive processes (Geda et al. 2019; Watpade et al. 2023; Mangal et al. 2023; Saqib et al. 2023; Kumar et al. 2021). These transcription factors bind to specific regulatory regions in the DNA and activate the expression of stress-responsive genes (Gupta et al. 2021a, b). Additionally, various signaling molecules, such as calcium ions (Ca2+), reactive oxygen species (ROS), and hormones, participate in stress signaling pathways in roots (Huda et al. 2013). Abiotic stress conditions can lead to metabolic alterations in roots. Metabolomic studies have revealed changes in the levels of various metabolites, including sugars, organic acids, amino acids, and secondary metabolites (Mukherjee et al. 2023; Gu et al. 2023; Rahman et al. 2023; Wang et al. 2023). These metabolic adjustments help plants maintain energy production, osmotic balance, and stress tolerance. For instance, under drought stress, roots may accumulate sugars as osmoprotectants and energy sources. Amino acids, such as proline, can also accumulate in roots to act as osmoprotectants and participate in redox regulation (Obata and Fernie 2012).

19.4 Role of Reactive Oxygen Species and Reactive Nitrogen Species on Root Morphology

Reactive oxygen species (ROS) and reactive nitrogen species (RNS) are highly reactive molecules involved in numerous cellular processes, including root development and morphology.

ROS, such as superoxide radicals ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), and hydroxyl radicals (•OH), are generated during normal metabolic processes as byproducts of respiration, photosynthesis, and enzymatic reactions. Similarly, RNS, including nitric oxide (NO) and peroxynitrite (NO−), are produced from the oxidation of nitric oxide and the reaction between superoxide and nitric oxide, respectively. Environmental stresses, such as high light intensity, temperature extremes, heavy metals, and pathogens, can also induce ROS and RNS production in roots. ROS and RNS play dual roles in regulating root growth and elongation (Altaf et al. 2021; Lal et al. 2021b, 2022). Low concentrations of ROS and RNS function as signaling molecules, promoting cell elongation and root growth. Conversely, excessive ROS and RNS levels can lead to oxidative and nitrosative stress, resulting in root growth inhibition and damage. ROS and RNS signaling pathways are also involved in the regulation of lateral root development. ROS, particularly hydrogen peroxide, act as positive regulators, promoting lateral root initiation and primordium development. Nitric oxide has also been shown to modulate lateral root formation by interacting with auxin signaling pathways.

It also influence root hair formation, a crucial adaptation for nutrient acquisition and stress response. Hydrogen peroxide, as a key ROS, plays a vital role in root hair tip growth and the establishment of a polar growth axis. Nitric oxide is also involved in root hair development, acting as a mediator of auxin-induced root hair initiation. Both ROS and RNS contribute to the regulation of root architecture by modulating the balance between primary and lateral root growth, as well as the control of root branching (Lal et al. 2021a; Raigond et al. 2021; Devi et al. 2022). ROS and RNS signaling interact with hormone signaling pathways, including auxin, cytokinin, and abscisic acid, to shape the overall root system architecture.

ROS and RNS act as important mediators of plant responses to various environmental stimuli. Abiotic stresses, such as drought, salinity, and heavy metal exposure, trigger ROS and RNS accumulation in roots. These reactive species, in turn, activate signaling cascades and defense mechanisms that enhance stress tolerance. Additionally, ROS and RNS are involved in the crosstalk between roots and beneficial microbes, influencing symbiotic interactions and nutrient acquisition (Fig. 19.1).

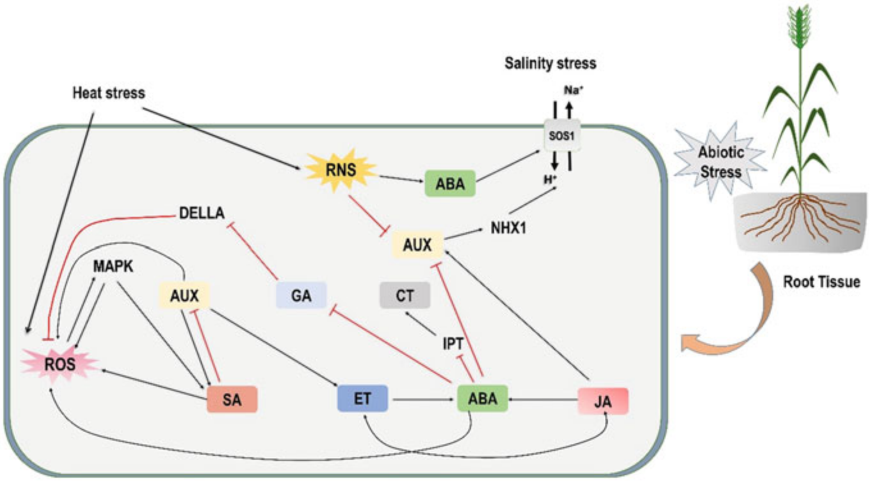

Fig. 19.1 The illustrative model suggesting the role of crosstalk of phytohormones and reactive species under abiotic stress conditions. Abbreviation: ROS: Reactive oxygen species; AUX: auxin; SA: salicylic acid; GA: gibberellic acid; ET: Ethylene; CT: cytokinin; ABA: abscisic acid; JA: jasmonic acid; RNS: reactive nitrogen species

19.5 Phytohormone Cross-Talk in Root Tissue

This organ possesses exceptional capacity for continuous tissue production and indeterminate growth of roots, making it a highly dynamic structure capable of rapid responses to external environmental stimuli. Following this initial response, precise formative cycles must be finely regulated, with hormonal cross-talk playing a crucial role in root development. At the apex of the meristem lies a pool of stem cells within a niche that continuously produces self-renewing cells for tissue formation (Kumar et al. 2021; Tiwari et al. 2021, 2022). The meristem's final size is achieved within the first few days after germination due to a delicate balance between cell division and differentiation. The coordinated interactions between various hormonal pathways contribute to these developmental processes, with recent efforts focusing on defining the molecular components of these networks through molecular and computational methods. The study by Cai et al. (2014b, a) delves into the molecular mechanisms responsible for hormone cross-talk and its impact on determining root meristem size (Cai et al. 2014b, a).

Developmental biology has significant challenges in figuring out how genes and hormones work together to control plant growth in response to environmental changes. Auxin concentration cannot alter independently of several interdependent hormones and genes, despite a localised auxin concentration maximum in the root tip being crucial for root growth. Review the interactions between auxin and other hormones for root growth under osmotic stress and without, as well as the involvement of the Arabidopsis POLARIS peptide in root growth and hormonal crosstalk.

Additionally, we go through the experimental data demonstrating that, during root growth, a network formed by relevant genes regulating relevant hormone activities and hormones regulating gene expression. An investigation of hormonal crosstalk that combines modelling and experimentation is crucial for future breeding purpose (Vanstraelen and Benkov 2012).

A recent study of several elements of hormonal crosstalk in root formation (Depuydt and Hardtke 2011a, b; Bishopp et al. 2011; Vanstraelen and Benkov 2012; Hwang et al. 2012; Garay-Arroyo et al. 2012). These researches are focused on particular interactions between a few hormones or a multitude of hormones. Consider the Garay-Arroyo et al (2012) research, which covers brassinosteroids, abscisic acid, ethylene, cytokinin, gibberellins, and auxin. The study by Hwang et al. (2012) focuses on the interaction of cytokinin and auxin in great detail. The study of hormonal crosstalk in root growth takes a combination experimental and modelling approach.

19.6 Hormonal Crosstalk Under Osmotic Stress

Plants adapt their root architecture to cope with osmotic stress by reducing lateral root initiation and changing root development rates (Van Der Weele et al. 2000; Deak and Malamy 2005). It has been shown that root development is promoted at low to moderate levels of osmotic stress and reduced at higher levels (Van Der Weele et al. 2000; Xu et al. 2013). As with other abiotic stressors, osmotic stress leads to an increase in abscisic acid levels, which integrates stress responses with developmental regulation. In root caps, abscisic acid levels are more significant than those in aerial tissues, but they are necessary for proper development under osmotic stress (Van Der Weele et al. 2000; Deak and Malamy 2005; Xu et al. 2013). In moderate osmotic stress, root growth rate is increased by ABA (Van Der Weele et al. 2000; Xu et al. 2013). PIN2 and AUX1 levels are elevated by osmotically induced ABA, which increases root elongation, H+-ATPase activity, and basipetal auxin transport. The application of ABA prompts the articulation of ARF2, a negative regulator of auxin reactions, and arf2 freaks exhibit altered auxin transport and limited roots under ABA application. As a result of osmotic pressure, plants alter their root design, preventing horizontal root beginning and altering root development rates (Van der Weele et al. 2000).

In low to moderate osmotic stress, root growth increases, but in high osmotic stress, it decreases (Van Der Weele et al. 2000). An increase in abscisic acid levels characterizes abiotic stress. Hormone crosstalk integrates stress responses and developmental control. Despite being less noticeable in aerial tissues than in root caps, abscisic acid increases are necessary for normal growth under osmotic stress (Deak and Malamy 2005; Xu et al. 2013). Under moderate osmotic tension, root advancement rate is extended in a way that is ABA-dependent (Van Der Weele et al. 2000). Through increased levels of PIN2 and AUX1, ABA induces basipetal auxin transport, H+-ATPase activity, and root elongation (Xu et al. 2013). Arf2, a negative controller of auxin reactions, is also initiated to be communicated at undeniable levels when

ABA is applied, and arf2 freaks display modified auxin transport and more limited roots when ABA is applied (Dash et al. 2020; Wang et al. 2020). In addition to osmotic stress responses, cytokinin is thought to be involved in dehydration stress responses. During dehydration stress, mature plants alter their gene expression of cytokinin metabolism and biosynthesis, resulting in lower levels of cytokinin synthesis and metabolism. ABA and osmotic stress-responsive genes are negatively regulated by the AHK2 and AHK3 cytokinin receptor kinases, and mutants deficient in cytokinins have increased survival rates (Tran et al. 2007; Nishiyama et al. 2011). The presence of a positive feedback on ABA suggests that cytokinin-deficient mutants exhibit lower levels of ABA (Nishiyama et al. 2011).

Like ABA, ethylene can inhibit root growth as a result of osmotic stress (Sharp 2002; Joo et al. 2013; Cheng et al. 2013; Liu et al. 2014). ABA restrains ethylene biosynthesis by decidingly managing ERF11 through HY5 to prevent articulation of ACS5, the rate-restricting catalyst in ethylene biosynthesis (Vogel et al. 1998; Liu et al. 2014). (Ghassemian et al. 2000; Chiwocha et al. 2005; Cheng et al. 2013) have shown that ethylene can also inhibit ABA biosynthesis as evidenced by the hyper-accumulation of ABA in ethylene-insensitive mutants and the increased expression of ABA biosynthetic genes. When exposed to severe osmotic stress, plants that lack ethylene signaling are not affected by ABA's inhibition of root growth, but they have shorter roots (Ghassemian et al. 2000). Plants are more likely to experience root shortening when ethylene biosynthesis is restricted pharmacologically, while plants are less likely to suffer root shortening when ethylene perception is restricted (Ghassemian et al. 2000). Under osmotic stress, root growth requires both hormones, but the antagonistic regulation of their biosynthesis does not explain why root growth responses are inhibited. According to mutation analysis (Cheng et al. 2013), there is little interaction between the two signal transduction pathways. It is possible that stress rather than ABA mediates ethylene signaling, as EIN2 is less expressed during osmotic stress than it is when treated with ABA. In a series of intricate interactions that cannot adequately explain root growth on their own, hormone levels are clearly impacted by osmotic stress. Plant roots are interconnected with hormones and regulatory and target genes that control hormone activities and hormones control gene expression through a network of relevant genes and hormones. A crucial question to answer is: How do the regulatory and target genes control the levels of the proteins encoded by them and the flux of plant hormones? In order to answer this question, mathematical modeling is becoming increasingly useful for analyzing hormonal crosstalk.

19.7 Mathematical Modeling as a Valuable Tool for Studying Hormonal Crosstalk

An example of a hormonal crosstalk network is a network that includes metabolic conversions, signal transduction, and gene expression. It is possible to analyze plant biological networks on a variety of levels using different mathematical tools (Liu et al. 2014). In particular, kinetic modeling can be used to quantitatively analyze hormonal crosstalk networks (Beauvoit et al. 2018). The crosstalk between auxin and cytokinin signaling has also been studied in the context of Arabidopsis root architecture using kinetic modeling (Parmar et al. 2013). The axis of auxin and cytokinin, which are the molecules that interact together, has led to the discovery that tissue-specific gene expression oscillations can be understood through a variety of studies (Parmar et al. 2013). In spite of the fact that other mechanisms can also cause oscillations in gene expression, these findings suggest that hormonal crosstalk can be a mechanism for describing time-dependent dynamics like oscillations (Bujdoso and Davis 2013; Rué and Garcia-Ojalvo 2013).

19.8 Conclusion

Root architecture plays a crucial role in plant performance, especially under stress conditions. The ability of plants to efficiently acquire water and nutrients from the soil and their capacity to withstand various environmental stresses heavily depends on their root system. Redesigning root architecture holds great potential for improving plant performance and enhancing stress tolerance. Understanding the complex molecular and physiological mechanisms underlying root development and its response to stress is essential for effective root architecture redesign. Advances in plant genetics, molecular biology, and biotechnology have provided valuable insights into the regulatory networks involved in root development. These insights can be leveraged to engineer plants with optimized root systems that exhibit enhanced performance under stress. One approach to redesigning root architecture involves altering the expression or activity of genes and transcription factors involved in root development. By manipulating these genetic factors, it is possible to modify traits such as root length, root branching, and root hair density. For instance, increasing lateral root formation and root hair density can enhance nutrient uptake efficiency and improve plant adaptation to nutrient-limiting conditions. Additionally, harnessing the potential of beneficial plant–microbe interactions can significantly impact root architecture and stress tolerance. Certain microbes, such as mycorrhizal fungi and rhizobacteria, establish symbiotic relationships with plants, promoting root growth, nutrient acquisition, and stress tolerance. By modulating the interactions between plants and beneficial microbes, it is possible to engineer root systems that are more resilient to stress conditions.

Furthermore, integrating knowledge from various disciplines such as plant physiology, soil science, and computational modeling can provide a holistic understanding of root-soil interactions and aid in the design of root systems that are optimized for specific environments and stress conditions. Redesigning root architecture represents a promising avenue for improving plant performance and stress tolerance. By manipulating genetic factors, leveraging beneficial plant–microbe interactions, and employing advanced imaging and phenotyping technologies, it is possible to engineer plants with enhanced root systems that are better equipped to cope with environmental stresses (Dash et al. 2021; Guru et al. 2021). Such advancements in root architecture redesign have the potential to revolutionize agriculture, enabling the cultivation of crops with improved productivity, resource-use efficiency, and resilience in the face of a changing climate.

19.9 Future Thrust

Continued advancements in genetic engineering techniques, such as genome editing technologies (e.g., CRISPR-Cas9), will enable precise manipulation of genes and regulatory elements involved in root development. This will allow for the targeted modification of specific root traits and the optimization of root architecture for stress tolerance. Integrating systems biology approaches, including transcriptomics, proteomics, and metabolomics, can provide a comprehensive understanding of the molecular networks and signaling pathways involved in root development and stress response. This knowledge can be leveraged to identify key genes, proteins, and metabolites that can be targeted for root architecture redesign. Developing computational models and simulations that capture the complex interactions between root architecture, soil properties, and environmental factors will aid in predicting and optimizing root performance under stress conditions. These models can be valuable tools for guiding root architecture redesign strategies and selecting the most effective traits for specific environments. Advancements in phenotyping technologies will enable high-throughput screening of large populations of plants for root architecture traits. Non-destructive imaging techniques, such as 3D root imaging and X-ray tomography, coupled with automated data analysis algorithms, will allow for efficient identification and characterization of desirable root traits. This will facilitate the selection and breeding of plants with improved root architectures. Further exploring the interactions between plants and beneficial microbes holds great promise for optimizing root architecture. By understanding the mechanisms underlying these interactions, it will be possible to engineer root systems that establish more efficient and resilient symbiotic relationships, leading to improved stress tolerance and nutrient acquisition. Redesigning root systems to incorporate traits such as deep rooting, adventitious root formation, and enhanced lateral root proliferation can enhance plant access to water and nutrients in drought-prone or nutrient-deficient soils. Engineering root systems that balance resource allocation between shoot and root can also optimize plant performance under stress conditions. Translating laboratory findings into real-world agricultural practices will be crucial for the widespread adoption of redesigned root architectures. Field trials and long-term studies will be necessary to validate the performance and productivity of plants with optimized root systems under diverse environmental conditions and stress scenarios. Integrating root architecture redesign efforts with studies at different scales, from molecular and cellular levels to whole-plant and ecosystem levels, will provide a comprehensive understanding of the functional implications of altered root architectures. This multi-scale approach will enable researchers to assess the ecological and agronomic impacts of root redesign and ensure the sustainability of agricultural systems. In summary, future prospects for redesigning root architecture to improve plant performance under stress involve advancements in genetic engineering, systems biology approaches, computational modeling, phenomics, and the harnessing of microbial interactions. Field validation, multi-scale integration, and consideration of ecological implications are also essential for the successful implementation of redesigned root architectures in real-world agricultural settings. By pursuing these avenues, we can unlock the full potential of root architecture redesign to address the challenges of global food security and sustainable agriculture.

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Chapter 20
Plant–Microbe Interaction in Developing Climate-Resilient Crop Species

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Abstract Climate change is one of the most pressing challenges facing agriculture today, with its adverse effects on crop productivity and global food security. To combat the impacts of climate change, the development of climate-resilient crop species is crucial. Plant–microbe interactions play a significant role in enhancing plant resilience to various stressors, including drought, heat, salinity, and pathogen attacks. This chapter explores the intricate relationship between plants and microbes and their potential role in developing climate-resilient crop species. It delves into the various mechanisms involved, highlighting the importance of harnessing these interactions for sustainable agriculture in the face of a changing climate.

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Environmental Science and Engineering, https://doi.org/10.1007/978-3-031-43729-8_20

Keywords Climate change · Plant–microbe interactions · Climate-resilient crops

20.1 Introduction

In various regions, climate change is causing a rise in global temperatures and an increase in the frequency and severity of droughts. The escalating challenges of climate change have sparked the need for innovative agricultural practices that focus on enhancing plant resilience to adverse environmental conditions. As climate change continues to unfold, it poses escalating challenges for agriculture worldwide (Abegunde et al. 2019). The challenges faced by agriculture have created a need for innovative techniques that can improve plant resilience in harsh environmental conditions. Rising temperatures and frequent heat waves affect plants, reducing crop yields and quality as well as affect plant microbiome (Fig. 20.1). Extreme temperatures cause heat stress, disrupts flowering and reduces pollination (Raza et al. 2019). A recent study suggested, for example, that the global production of 10 major crops, including barley, cassava, maize, oil palm, rapeseed, rice, sorghum, soybean, sugarcane, and wheat, has already been affected by climate change, and although variability among crops and regions occur, overall consumable food calories of these 10 crops has been reduced by about 1% (Ray et al. 2019).

Changing precipitation patterns, including more intense and prolonged droughts, significantly impact water availability for agriculture. Drought stress affects plant growth and leads to crop failures (Shahzad et al. 2021). Moreover, climate change has been associated with more frequent and severe weather events, such as hurricanes, storms, and floods, which cause significant damage to crops and farmland (Lamichhane et al. 2015). Warmer temperatures and altered climatic conditions influence the distribution and behavior of pests and diseases, leading to new and more challenging outbreaks for crops. Climate change also exacerbates soil erosion, nutrient depletion, and degradation, affecting crop productivity and reducing the overall suitability of land for agriculture (Wang et al. 2022).

Additionally, climate change disrupts ecosystems and threatens biodiversity, including beneficial soil biota essential for maintaining healthy soils and supporting pollination. Changes in temperature and precipitation patterns disrupt traditional growing seasons, impacting planting schedules and crop choices (Nguyen et al. 2023). To address these challenges, innovative agricultural practices have emerged to enhance plant resilience, including (1) climate-resilient crop breeding, (2) precision agriculture, (3) drought- and heat-tolerant crop varieties, (4) agroforestry and intercropping, (5) water management strategies, (6) soil conservation and regeneration, and (7) climate information services. Developing and promoting crop varieties that are more tolerant to temperature extremes, water scarcity, and pests improve resilience and adaptability. Utilizing smart agricultural technologies such as remote sensing, drones, and data analytics helps farmers optimize resource use, manage irrigation more efficiently, and improve crop productivity (Neupane et al. 2022). Introducing genetically modified or selectively bred crops that are better adapted

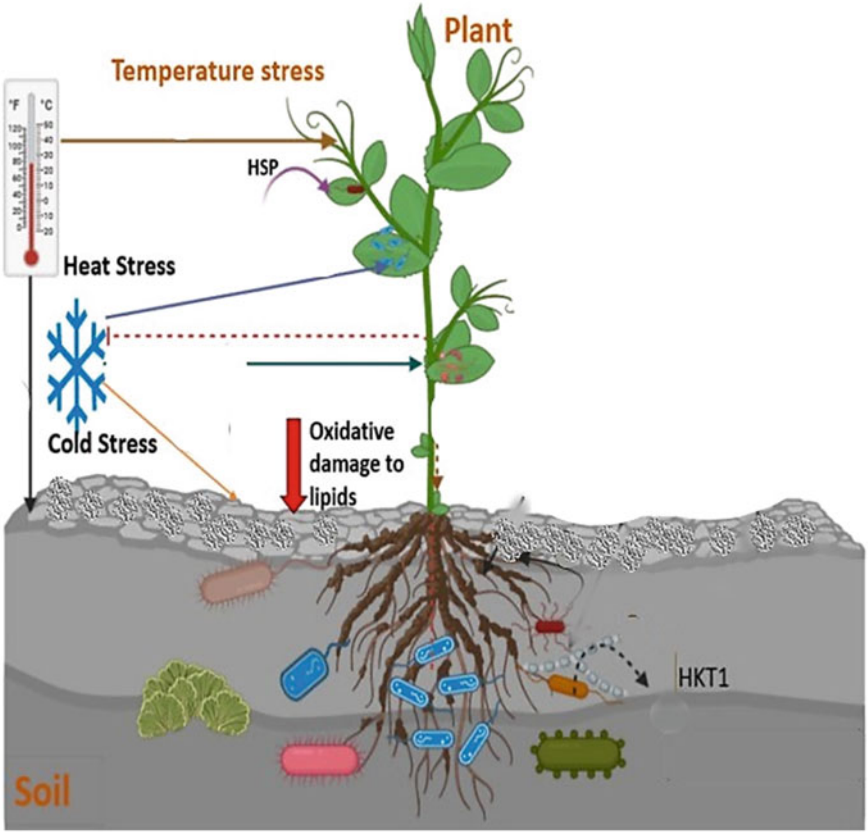

Fig. 20.1 Temperature effects on plant-microbiome interactions

to drought and heat stress helps ensure higher yields in challenging conditions. However, planting trees and integrating diverse crops in the same area provides better microclimates, prevents soil erosion, and creates a more resilient and productive agricultural system (Fahad et al. 2022).

Furthermore, implementing water-saving irrigation techniques, such as drip irrigation or rainwater harvesting, helps mitigate water scarcity issues and improve water use efficiency. Likewise, promoting agricultural practices such as cover cropping, no-till farming, and organic farming may help restore soil health and improve its ability to withstand adverse climate conditions (Jacobs et al. 2022). Providing farmers with real-time climate information and weather forecasts enables them to make more informed decisions about planting, harvesting, and resource management. Integrating these innovative practices can help ensure food security and sustainability in the face of escalating climate challenges while fostering a more resilient and adaptive agricultural sector (Azadi et al. 2021).

The plant associated-microbiome plays a significant role in influencing how biotic and abiotic stressors affect the overall health and well-being of the plant. Nonetheless, changes in plant microbiomes caused by climate change can impact the functions of the host plant. Plant–microbe interactions (PMIs) have emerged as a promising avenue to improve crop performance and mitigate the negative impacts of climate change (Pattnaik et al. 2020). These interactions involve a wide range of beneficial relationships between plants and microorganisms such as bacteria, fungi, and viruses) that profoundly influence plant health and productivity (Schlossarek et al. 2023). Several important methods utilize PMI for agricultural and climate change mitigation purposes: (1) enhanced nutrient acquisition, (2) disease suppression, (3) drought and heat tolerance, (4) carbon sequestration, (5) climate-resilient crops, (6) reduced environmental impact, and (7) sustainable agriculture. Certain microorganisms, such as mycorrhizal fungi (MF) and nitrogen (N_2)-fixing bacteria, form symbiotic relationships with plants, improving nutrient uptake. MF extends the plant's root system, increasing the absorption of water and nutrients such as phosphorus and zinc. N_2-fixing bacteria convert atmospheric N_2 into a form that plants can use, reducing the need for synthetic N_2 fertilizers, which are energy-intensive to produce and contribute to greenhouse gas emissions (Yan et al. 2022). Some beneficial microorganisms have the ability to suppress plant pathogens, including fungi, bacteria, and viruses. Farmers can reduce their reliance on chemical pesticides, which are harmful to the environment and non-target species, by introducing or promoting the growth of beneficial microbes (Mehla 2023). This may also help mitigate the effects of plant diseases that become more prevalent in changing climates.

Microorganisms help plants cope with abiotic stresses such as drought and heat. However, plant growth can be improved by increasing water efficiency and nutrient uptake. Additionally, certain compounds are produced by microbes to help protect the plant from damage caused by stress. This is particularly crucial in the face of climate change, which is expected to bring about more frequent and severe droughts and heat waves. Additionally, plant–microbe interactions influence soil carbon storage and facilitate the decomposition of plant residues, contributing to soil organic matter formation. Meanwhile, increased soil carbon storage helps sequester atmospheric carbon dioxide, a major greenhouse gas responsible for climate change. Harnessing plant–microbe interactions offer a promising approach to developing climate-resilient crop varieties. Researchers can select or engineer plants with specific beneficial microbial associations that improve their adaptation to changing environmental conditions.

Beneficial microbes reduce the need for synthetic agrochemicals, decreasing the environmental impact of agriculture. This includes lowering greenhouse gas emissions associated with producing and applying chemical fertilizers and pesticides. The integration of plant–microbe interactions into agricultural practices aligns with sustainable agriculture principles. It fosters soil health, reduces reliance on external inputs, and promotes long-term productivity. Ongoing research and application in the field of plant–microbe interactions will lead to more innovative approaches in optimizing crop performance and mitigating the negative impacts of climate change on agriculture. It is crucial to note that the successful implementation of these approaches requires careful consideration of local environmental and agronomic factors. This will ensure their effectiveness and sustainability in various agricultural systems and regions.

Unraveling the complexities of plant responses to stress combinations could therefore facilitate the development of climate-resilient crops, improving global food production and securing our future food supply. This chapter aims to explain how microbes play vital roles in enhancing stress tolerance to combat climate change and promote sustainable crop production.

20.2 The Microbiome: An Untapped Resource for Climate-Resilient Crops

20.2.1 Microbial Diversity in the Rhizosphere

Microorganisms form diverse and organized communities that are closely associated with plants. These communities, known as plant microbiota, comprise of bacteria, fungi, protists, nematodes, and viruses that occupy all accessible plant tissues, as noted by Trivedi et al. (2020). The rhizosphere, a hotspot for microbial activity, is the soil region surrounding plant roots. In the rhizosphere, there are several types of microorganisms, including mycorrhizal fungi (MF), Rhizobium bacteria, plant growth-promoting rhizobacteria (PGPR), actinomycetes, Trichoderma, arbuscular mycorrhizal fungi (AMF), and Pseudomonas spp. These microorganisms have the potential to improve crop health and resilience (Chamkhi et al. 2022). The interactions between plants and the rhizosphere microbiome are complex and symbiotic, benefiting both the plants and the microorganisms. Plants release various organic compounds (via their roots into the soil), such as sugars, amino acids, organic acids, and vitamins, collectively known as "root exudates" (Hakim et al. 2021). Root exudates serve as a food source for many microorganisms, stimulating their growth and activity in the rhizosphere. The rhizosphere contains nutrients from root exudates, decaying organic matter, and minerals released during root growth and turnover (Nwachukwu and Babalola 2021. This nutrient-rich environment provides an abundant food source for microbial communities, encouraging their proliferation. In addition, plant roots actively release oxygen during respiration. As a result, the rhizosphere is generally an aerated zone with higher oxygen levels compared to the bulk soil. Aerobic microorganisms thrive in this oxygen-rich environment, contributing to increased microbial activity Pathan et al. 2020). Plant roots and their associated fungal networks (mycorrhizae) create a complex physical structure in the rhizosphere. These structures provide niches and protected microsites for microorganisms to colonize and establish themselves (Zvinavashe et al. 2021).

The root surfaces also offer attachment sites for various bacteria and fungi. The activity of roots and the release of root exudates can alter the pH of the rhizosphere. Different microorganisms thrive under specific pH conditions, leading to a diverse microbial community with varying metabolic capabilities. Apart from root exudates, plants release other organic materials into the rhizosphere, known as rhizodeposits (Sharma et al. 2022). These include sloughed-off root cells and mucilage. These materials further support microbial growth and activity. Certain microorganisms establish beneficial relationships with plants, such as mycorrhizal fungi, that assist in nutrient uptake, thereby promoting plant growth (Nanjundappa et al. 2019). In turn, plants influence the types of microorganisms that thrive in their rhizosphere through specific chemical cues and interactions. These factors combined create a microenvironment in the rhizosphere that fosters a higher density and diversity of microorganisms compared to the surrounding bulk soil. This increased microbial activity in the rhizosphere contributes to various essential ecological functions, including nutrient cycling, soil structure formation, and plant health (Bickford et al. 2020).

20.2.2 Beneficial Microbes: Plant Growth-Promoting Rhizobacteria and Mycorrhizal Fungi

Plant growth-promoting rhizobacteria and MF are beneficial microbes that significantly impact plant growth and climate resilience. Their interactions with plant roots enhance nutrient uptake, hormone production, and disease resistance as well as improve the plant's ability to withstand environmental stressors, ultimately resulting in healthier and more tolerant plants (Azizi et al. 2021). PGPRs are a diverse group of bacteria living in the rhizosphere that benefit plants through various mechanisms, such as nutrient mobilization, production of phytohormones (auxins, cytokinins, and gibberellins), biocontrol via antimicrobial activities, induced systemic resistance (ISR) against pathogenicity, and enhanced abiotic stress tolerance (Meena et al. 2020). On the other hand, MFs are widespread in natural ecosystems, forming a mutualistic symbiotic relationship with the roots of most plants and significantly influencing plant growth and health. The most common types of mycorrhizae are arbuscular mycorrhizae (AM) and ectomycorrhizae (ECM) (Song et al. 2022). The interactions between plants and mycorrhizal fungi offer several benefits, including enhanced nutrient uptake and photosynthesis, hormone production, protection against soil-borne pathogens, drought tolerance and soil structure improvement. Therefore, beneficial PGPR and MF microbes play a significant role in sustainable agriculture and climate change resilience, reducing the need for chemical fertilizers and pesticides and improving overall crop productivity (Das et al. 2022).

20.3 Mechanisms of Microbial-Mediated Stress Tolerance

20.3.1 Induced Systemic Resistance (ISR)

With rising global temperatures, a significant number of plant pathogens are expected to increase, and unfortunately, many common methods of disease control are ineffective at high temperatures. Additionally, these pathogens may develop new strategies for invading plants by altering their virulence, which can potentially compromise plant resistance mechanisms mediated by *R*-genes. Furthermore, both high temperatures and drought can weaken the plant's immune system, making it more susceptible to disease in many plant pathosystems. Certain members of the plant microbiome have traits that alleviate the effects of abiotic stresses on plants (Trivedi et al. 2020, 2021). Induced systemic resistance (ISR) is a plant defense mechanism triggered by beneficial microbes. It involves the activation of systemic defense responses that protect plants from a wide range of pathogens and pests. Additionally, ISR is considered an environmentally friendly and sustainable approach to plant protection because it relies on natural interactions between plants and beneficial microorganisms (Kamle et al. 2020). Certain beneficial microbes, such as PGPR and MF, establish a symbiotic relationship with the plant's roots. These microbes colonize the root surface or penetrate the root tissues. Upon recognizing the presence of beneficial microbes, the plant initiates a series of signal transduction pathways that activate its immune responses. This recognition is often mediated by specific molecular patterns or signals released by microbes. Plants produce signaling molecules, such as salicylic acid (SA), jasmonic acid (JA), ethylene (ET), and reactive oxygen species (ROS), among others (Abdul Malik et al. 2020). These signaling molecules act as messengers to communicate the presence of beneficial microbes and trigger systemic defense responses throughout the plant. Signaling molecules, particularly SA and JA, play a crucial role in priming the plant's immune system (Bukhat et al. 2020). The term "priming" refers to the process by which the plant's defense mechanisms are sensitized and prepared for a more rapid and robust response upon subsequent pathogen attacks. The primed plant is now better equipped to defend itself against potential pathogens. When the plant is later exposed to pathogenic attacks, it can mount a quicker and more effective defense response, reducing disease symptoms and pathogen growth. The specific molecular mechanisms behind ISR vary depending on the beneficial microorganism and the pathogen involved. Researchers and agricultural practitioners have been exploring the potential of using these beneficial microorganisms to enhance crop protection and reduce reliance on chemical pesticides (Rastegari et al. 2020). By harnessing induced systemic resistance, it might be possible to improve plant health, increase crop yields, and promote more sustainable agriculture practices.

20.3.2 Priming

Microbial priming is another fascinating phenomenon where microbes “prime” plants for enhanced stress tolerance. Priming, in the context of agriculture, refers to the process of exposing plants or crop species to certain stimuli or conditions that enhance their ability to withstand and recover from environmental stresses, such as drought, extreme temperatures, and disease (Tiwari et al. 2022). Priming is a powerful tool for developing climate-resilient crop species, as it allows plants to build up their defense mechanisms and adapt to challenging environmental conditions. By priming the plant’s immune system, the plant becomes more prepared to respond quickly and effectively to subsequent stressors. The process of microbial priming typically involves a sequence of interactions between plants and beneficial microorganisms (Llorens et al. 2020). When a plant comes into contact with certain beneficial microbes, either in the soil or through other means, these microbes activate specific defense pathways in the plant. This activation prepares the plant to respond more effectively to future stressors, such as pathogens, pests, drought, extreme temperatures, or nutrient deficiencies. The underlying mechanisms of microbial priming are complex and vary depending on the specific plant–microbe interaction. However, some common mechanisms involved in microbial priming include ISR, enhanced antioxidant defense, improved nutrient uptake, hormonal cross-talk, and metabolic changes (Nephali et al. 2020). Applying these microorganisms to crop plants improves their stress tolerance, leading to more climate-resilient crops. In agricultural practices, the application of beneficial microbes as biofertilizers and biopesticides is being explored to harness microbial priming effects and improve overall crop health and resilience. Overall, microbial priming represents an exciting avenue for sustainable agriculture and ecosystem management, as it leverages the power of beneficial microbial communities to enhance the resilience and stress tolerance of plants in a changing environment (Tan et al. 2022).

20.4 Mitigation of Abiotic Stress Through Microbial Interactions

20.4.1 Drought Stress

Drought is a major consequence of climate change, posing severe threats to crop productivity and plant microbiome (Fig. 20.2). Climate change alters weather patterns, leading to changes in precipitation levels, increasing temperatures, and more frequent extreme weather events (Kogo et al. 2021). These changes directly impact water availability, soil moisture, and overall agricultural conditions, making it increasingly challenging for crops to thrive. Mitigating the impacts of drought on crop productivity requires a multifaceted approach. Microbial-assisted strategies hold great promise in developing drought-resistant crops (Hamann et al. 2021). Certain

Actinobacteria species, such as *Streptomyces*, can aid in the growth and development of plants that are facing drought conditions. Microbes enhance the drought tolerance of plants by improving water use efficiency and osmotic regulation. Some microbes influence stomatal regulation, allowing plants to balance conserving water and maintaining sufficient carbon dioxide intake for photosynthesis. In addition, beneficial microbes act as biocontrol agents, protecting plants from harmful pathogens and minimizing additional stress on the plant. Some microorganisms produce compounds that help plants combat drought stress. For instance, certain bacteria synthesize osmoprotectants, which accumulate in plant tissues and safeguard cellular structures from damage caused by dehydration (Phour et al. 2022). Microbial activities also improve soil structure and porosity, leading to better water infiltration and retention in the root zone. Improved soil structure ensures that plants have access to water for a more extended period during dry spells. All of these processes are referred to as "plant–microbe symbiosis" or "plant–microbe interactions." Research in this field is ongoing, and scientists are continually exploring new microbial strains and their interactions with plants to unlock their full potential in developing drought-resistant crops (Meurer et al. 2020).

20.4.2 Heat and Cold Stress

Microbes also help mitigate the impacts of extreme temperatures on crops. Some microbes produce heat-shock proteins (HSPs) that protect plants from heat stress, while others help improve tolerance to cold stress. HSPs are a group of proteins that are produced by cells in response to exposure to high temperatures (Hamann et al. 2021). For example, a certain type of bacteria called root endophytic bacterium *Enterobacter* sp. SA-87 can help plants withstand high temperatures. This is done through a unique method where a heat shock factor called HSFA2 is constantly expressed through the ethylene signalling pathway and a transcription factor called EIN3. This leads to the methylation of genes that improve the plant's ability to handle heat stress. This was discovered in a study by Shekhawat and colleagues in 2021. Additionally, some bacteria that promote plant growth can even help them deal with multiple types of stress. This was found in studies by Lata et al. (2018) and Bokhari et al. (2019). HSPs act as molecular chaperones, helping to protect other proteins from denaturation or damage caused by heat stress. On the other hand, microbes also promote the synthesis of certain compounds within the plant, such as antifreeze proteins, which help prevent ice crystal formation within plant cells during freezing temperatures (Meurer et al. 2020). This protection against cold stress helps the plant survive and resume normal growth once the cold period passes. In addition, microbes play a crucial role in agriculture, and they help mitigate extreme temperature impacts on crops through heat stress tolerance, improved nutrient uptake, water stress management, disease resistance, enhanced photosynthesis, biocontrol agents and improved soil health. To develop crops resilient to temperature extremes,

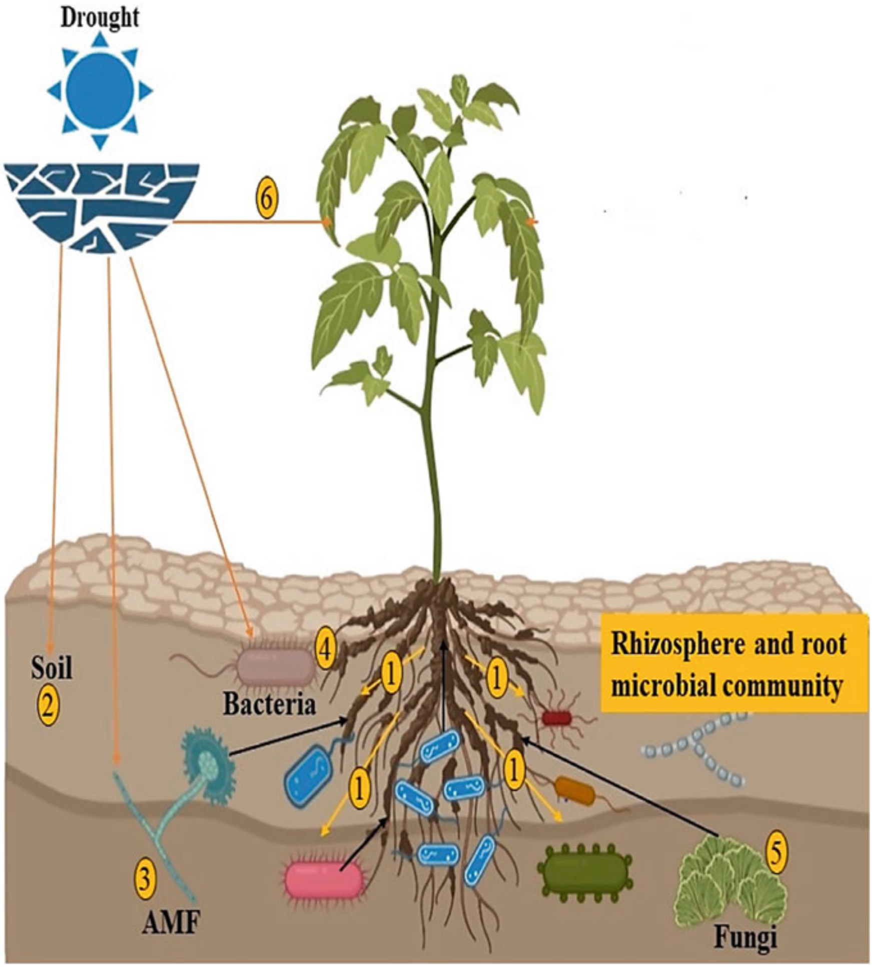

Fig. 20.2 Effect of drought stress on plant microbiome. AMF, Arbuscular mycorrhizal fungi; (1) plant to microbe, (2) Drought to soil interactions, (3) AMF to plant interactions, (4) drought to bacteria, (5) drought to fungi, and (6) drought to plant interactions

researchers are actively exploring the use of beneficial microbes in various agricultural practices, such as seed treatments, soil amendments, and biofertilizers (Khan et al. 2020). Integrating these microbial mechanisms into crop breeding and management strategies holds promise for enhancing crop resilience to heat and cold stress, ultimately contributing to food security and sustainable agriculture in the face of climate change. However, it is essential to carefully study the interactions between specific microbes and crops to ensure their safety and effectiveness in practical applications. Moreover, it is widely believed that plants perform better under stress due to multiple microbiome mechanisms that are activated at the same time. However, we still have a limited understanding of how these mechanisms interact with each other and with the plant itself when dealing with climate change.

20.5 Disease Management Through Microbial Interactions

20.5.1 Biotic Stress: Plant–Pathogen Interactions

Plant diseases often intensify under changing climate conditions, threatening crop yields. Changes in temperature, humidity, and precipitation patterns significantly impact the development and spread of plant diseases, which in turn threaten crop yields and food security (Lehmann et al. 2020). Changing climate conditions intensify plant diseases in several ways, such as extended growing seasons, altered distribution of pests and pathogens, increased overwintering survival, changes in host–pathogen interactions, stress on plants, and increased resistance to pesticides. However, some microbes act as biocontrol agents that suppress the growth and spread of pathogens. For instance, the bacterium *Bacillus thuringiensis* produces toxins that are lethal to certain insect pests, making it a valuable biopesticide used to protect crops from insect damage (Azizoglu et al. 2023). Similarly, some fungi, such as *Trichoderma* species, have been used as biofungicides to control plant diseases caused by soil-borne pathogens. Utilizing beneficial interactions to develop disease-resistant crop varieties is a promising approach in agricultural biotechnology. These interactions involve mutually beneficial relationships between plants and other organisms, such as beneficial microbes (e.g., bacteria and fungi), insects, and other plants. By harnessing these interactions, researchers aim to enhance the plant's natural defense mechanisms against various diseases, ultimately leading to more sustainable and resilient crop production (Kumar et al. 2021). Despite the potential benefits, utilizing beneficial interactions to develop disease-resistant crop varieties requires careful research, field trials, and consideration of potential risks and unintended consequences. Additionally, factors such as environmental conditions, crop species, and specific pathogens will influence the effectiveness of these strategies. Collaborative efforts among researchers, farmers, and policymakers are essential to implementing these approaches on a larger scale and realizing their full potential in sustainable agriculture (Phour et al. 2022).

20.6 Application and Challenges in Harnessing Plant–Microbe Interactions

20.6.1 Application in Crop Breeding

The knowledge gained from plant–microbe interactions can be leveraged in crop breeding programs to develop climate-resilient varieties. Integrating microbial interactions into modern breeding techniques presents both challenges and opportunities in the field of agriculture and plant breeding. This approach, known as "microbial-assisted breeding" or "microbial-based breeding," aims to influence the beneficial interactions between plants and microbes to enhance crop productivity, resilience, and sustainability (Varshney et al. 2021). However, certain challenges are associated with this integration, such as the complexity of microbial interactions, lack of understanding, host specificity, environmental variability, regulatory hurdles, and testing and validation. Despite the challenges, the integration of microbial interactions into modern breeding techniques holds significant promise for transforming agriculture into a more sustainable, resilient, and productive industry. Continued research, collaboration between biologists and breeders, and technological advances will be essential to unlocking the full potential of microbial-assisted breeding (Fahad et al. 2021).

20.6.2 Environmental and Societal Impacts

As with any agricultural intervention, the application of plant–microbe interactions raise environmental and societal concerns as follows.

20.6.2.1 Environmental Concerns

Introducing new microbes or altering existing plant–microbe interactions might have unintended consequences on local ecosystems. These changes may disrupt the natural balance, potentially leading to the proliferation of invasive species or the decline of native species. If not adequately managed, introduced microbes may spread beyond their intended target, affecting non-target species and habitats and leading to ecological imbalances and biodiversity loss. Some plant–microbe interactions may involve genetically modified organisms (GMOs) (Duke 2021). There is a risk of gene transfer from GMOs to wild relatives, potentially creating superweeds or promoting the spread of unwanted traits in nature (Llorens et al. 2020).

20.6.2.2 Societal Concerns

The use of microbes in agriculture may raise concerns about food safety. If microbes are not adequately tested and controlled, there could be potential health risks from consuming crops with harmful microorganisms or toxins. Some microbes used in agricultural practices might have the potential to cause allergies or other health issues in humans or animals. Adopting plant–microbe interactions could have economic implications, affecting traditional farming practices and livelihoods, especially for farmers relying on conventional methods. The implementation of plant–microbe interactions could raise questions about access to these technologies, particularly for small-scale farmers in developing regions who may face challenges in adopting such interventions (Rastegari et al. 2020).

20.6.2.3 Regulatory and Ethical Considerations

Due to the potential risks and uncertainties associated with plant–microbe interactions, appropriate regulatory frameworks should be in place to assess and manage their use. There might be ethical considerations related to the use of genetically modified microbes or the potential exploitation of vulnerable communities (Sharma et al. 2022).

To address these concerns, it is essential to conduct thorough risk assessments, perform long-term monitoring of introduced microbes, and prioritize sustainable agricultural practices. Collaboration between scientists, policymakers, and stakeholders can help strike a balance between utilizing plant–microbe interactions for agricultural benefits and mitigating potential negative impacts on the environment and society. Public awareness and engagement are also crucial to ensure responsible and informed decision-making around these interventions.

20.7 Conclusion and Future Perspectives

Climate change is a significant threat to global food production, affecting crop yields and water availability and increasing the frequency of extreme weather events. Plant–microbe interactions hold immense promise for developing climate-resilient crop species. Research and application of plant–microbe interactions in agriculture are continuously evolving. As our understanding of these complex relationships deepens, their potential for developing climate-resilient crop species will only grow. By harnessing the power of these interactions, we can improve food security and sustainable agriculture in the face of a changing climate. Increasing plant productivity in the face of climate change is a top priority for national and international policy agencies. One way to achieve this is by manipulating the plant-soil microbiome, either through direct manipulation of the plant microbiome, functional management practices, or the use of probiotics. The role of emerging technologies, such as precision agriculture and gene editing, in optimizing agroecosystem interactions under climate change conditions requires further investigation. By using breeding, advanced genome-editing tools like CRISPR, and synthetic biology approaches, it may be possible to engineer plants that release exudates to promote beneficial plant–microbe interactions. The genetic diversity found in wild relatives of domesticated crops can also be tapped to identify traits that help plants adapt to climate change and support the assembly of distinct microbiomes.

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Chapter 21

Traditional and Emerging Climate-Resilient Agricultural Practices for Enhancing Food Production and Nutritional Quality

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Abstract Sustainable food production is one of the biggest challenges of the twenty-first century. This is because of global environmental problems like climate change, a growing population, and the loss of natural resources like soil and biodiversity. Climate change is one of the biggest problems that threaten agricultural systems. Even though the Green Revolution increased agricultural production by many times, it had a huge negative effect on the environment, including climate change. It threatened

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T. Aftab (ed.), *New Frontiers in Plant-Environment Interactions*,
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the ecological integrity of agroecosystems by using a lot of fossil fuels, natural resources, agrochemicals, and machinery. Because of how climate change affects farming, the future food security of billions of people in tropical and subtropical regions is uncertain. For obvious reasons, the above challenges are hard and scary. To solve them, we will need transdisciplinary research teams that work together on research ranging from genomics to agro-ecosystems. This will help us feel less uncertain about food production and security in the future. On the other hand, there seems to be less uncertainty about what will happen to food quality, which is likely to get worse with higher CO_2 and especially with warmer temperatures. For example, CO_2 enrichment has been shown to reduce the amount of protein in most crops. Even though a slightly lower food quality (in terms of proteins but not lipids and carbohydrates) may be partially offset by a slightly higher yield in a globally changed environment, agronomic and physiological strategies for minimising changes in food quality should be a priority area for further research, especially since they will become more and more linked to food security.

Keywords Sustainable food production · Climate change · Food security · Agroecosystems · Food quality

21.1 Introduction

Increasing demands for crop production are being exerted by an ever-expanding world population. It becomes more crucial to implement effective and sustainable solutions to address this challenge when estimates indicate that global agricultural production may need to double by 2050 (Tilman et al. 2011; Mall et al. 2017). However, global food security and food production are threatened by climate change. Changes in climate patterns have a profound impact on agricultural systems and food production, including warming temperatures, changing precipitation patterns, and increasing severity of extreme weather events (Thrane et al. 2017; Prasad et al. 2019; Habib-ur-Rahman et al. 2022; Tiwari et al. 2022a; Kumar et al. 2023). The United Nations Framework Convention on Climate Change (UNFCCC 2011) defines climate change as ‘the change in climate resulting from human activity that alters the composition of the global atmosphere’. Changes in temperature, precipitation, energy exchange, and drought and flood intensity and frequency are examples. Environmental challenges caused by human activity are a common topic of conversation, study, and research. Recent climate change has been unprecedented in the past 10,000 years and perhaps even farther back (Blois et al. 2013; Yadav and Lal 2018; Tiwari et al. 2021a; Thakur et al. 2023). Temperatures have increased by around 0.9 °C over the past century. Anthropogenic activities contribute primarily to this increase in greenhouse gases (GHGs) in the atmosphere. GHG emissions increase the greenhouse effect, causing temperatures to rise. Deforestation, energy production, industrial processes, transportation, and the burning of fossil fuels are the main contributors. In 2050, global average temperatures are predicted to rise by 1.5 °C or even more.

Increasing temperatures can have a profound impact on ecosystems and the environment, leading to a variety of outcomes, including a rise in sea levels, a rise in extreme weather events, a shift in precipitation patterns, and biodiversity losses (Singh and Singh 2017; Ahmed et al. 2019; Jeevalatha et al. 2021; Kumar et al. 2021b; Lal et al. 2022c). GHG emissions are being reduced, clean energy is being transitioned, sustainable practices are being promoted, and natural resources are being conserved to mitigate these effects. In order to nurture a sustainable farm, traditional agricultural practices have been developed and refined throughout history. In addition to maintaining soil fertility, controlling pests and diseases, and providing additional benefits like shade and income diversification, organic farming methods, crop rotation, intercropping, and agroforestry have proven to be effective. Crop production and productivity have been adversely affected by climate change by modifying temperature patterns, rainfall distributions, and extreme weather events (Adhikari et al. 2018; Arora 2019; Biswaranjan et al. 2022; Sharma et al. 2022; Mangal et al. 2023). Droughts, floods, heatwaves, and an increase in pest and disease outbreaks are all possible consequences of rising temperatures and changing precipitation patterns. Reduced crop production and compromised food security result from these changes in climate parameters. The carbohydrate, lipid, and protein macronutrients play an essential role in crop growth and development. Crops can accumulate these macronutrients in greater quantities as a result of climate change-induced changes in temperature and precipitation.

Crops may contain limited carbohydrates as a result of high temperatures because high temperatures speed up carbohydrate breakdown. Crop lipid content can also be affected by changes in moisture availability. Additionally, climate changes can affect protein synthesis and composition, which can affect crop nutrition. Crops can be deprived of essential micronutrients due to climate change, which can interfere with their availability and uptake (Blois et al. 2013; Asthir 2015; Kumar et al. 2019; Lal et al. 2022c). Plant bioavailability of micronutrients can be affected by unfavourable climatic conditions. The soil is depleted of essential micronutrients as a result of soil erosion and nutrient runoff caused by extreme weather events. A change in climate can also affect how antioxidant molecules are synthesized and accumulated in crops. It is beneficial for human health to consume antioxidants, since they protect plants from oxidative stress. The antioxidant capacity of crops may be affected by differences in climate conditions, resulting in a reduction in their nutritional value. Overall food and nutritional quality are affected by the impact of climate change on crop production, macronutrients, micronutrients, and antioxidant molecules. Food scarcity and imbalanced diets can be caused by reduced crop yields and compromised macronutrient content. An increase in the risk of various diseases is associated with changes in the availability of micronutrients and antioxidants. Moreover, alterations in crop nutritional composition can worsen existing malnutrition problems among vulnerable populations (Yadav and Lal 2018; Ahmed et al. 2019; Shah et al. 2020; Habib-ur-Rahman et al. 2022). Developing sustainable agricultural practices and ensuring food security depend on understanding and addressing these

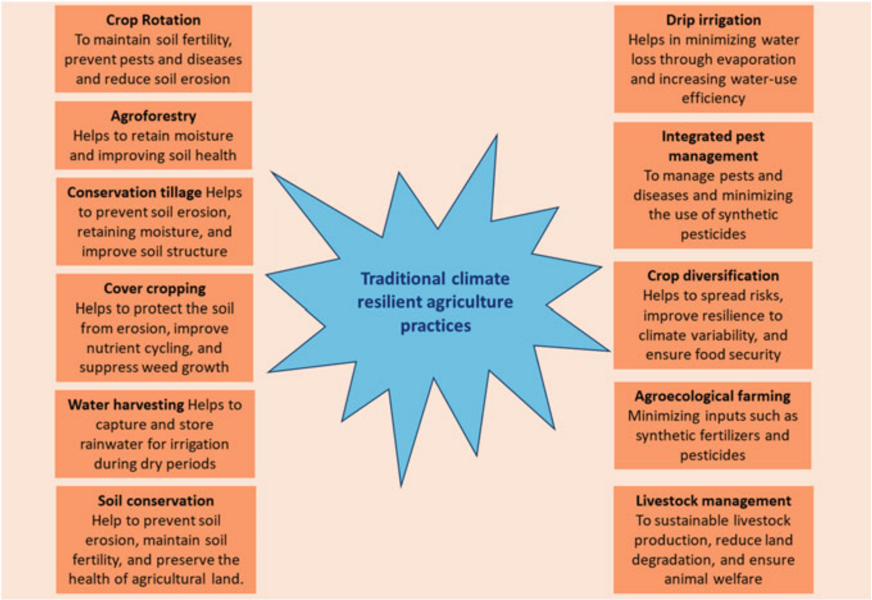


Fig. 21.1 Different traditional climate resilient agriculture practices

effects. In order to mitigate the adverse effects of climate change on crop production, protect nutritional quality, and secure a sustainable future for agriculture, adaptation and mitigation strategies, such as developing climate-resilient crop varieties, improving water management, and adopting sustainable farming techniques, can be implemented (Figs. 21.1 and 21.2).

A key role in enhancing climate resilience is also being played by emerging agricultural techniques. As an example, conservation agriculture emphasizes reduction of soil disturbance, maintenance of soil cover, and diversification of crop rotation (Figs. 21.1 and 21.2). Agricultural systems are more able to withstand droughts and floods when conservation agriculture minimizes soil erosion, conserves moisture, and improves nutrient cycling. Through precision agriculture, resources can be optimized and environmental impacts can be minimized. Real-time monitoring of soil moisture levels, crop health, and nutrient requirements can be achieved through remote sensing, GPS, and data analytics (Ahmed et al. 2019; Arora 2019; Ahsan et al. 2022; Biswaranjan et al. 2022). The use of this data-driven approach can lead to more efficient use of water, fertilizers, and pesticides by farmers. A number of initiatives are being taken to combat climate change, such as using climate-resilient crop varieties, reducing greenhouse gas emissions, using water-saving irrigation techniques, and managing soil sustainably.

A climate-resilient agricultural practice can be identified and promoted by investing in research and development. Providing financial and technical support to farmers and disseminating information are crucial to spreading adoption. To ensure

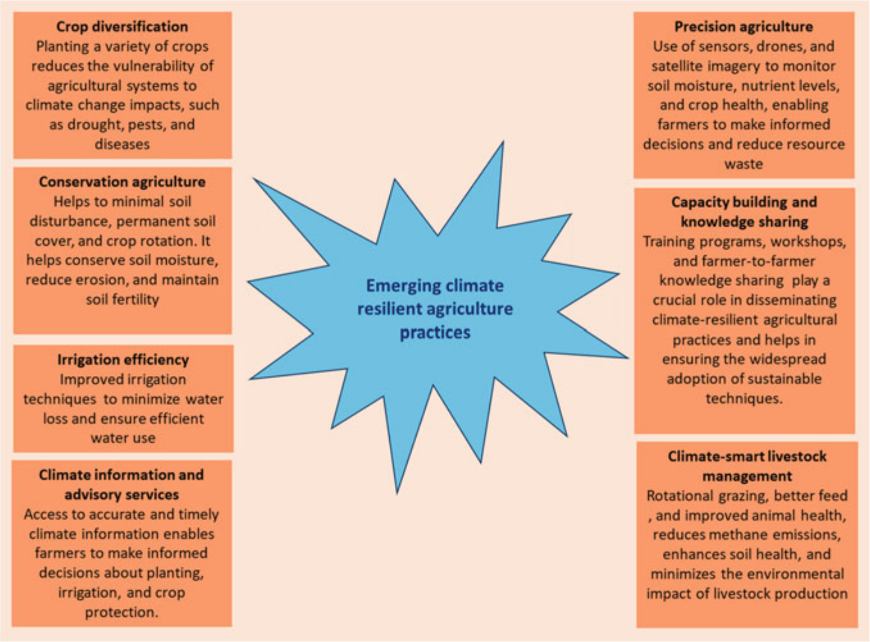


Fig. 21.2 Different emerging climate resilient agriculture practices

that farmers around the world have access to these practices, governments, organizations, and agricultural stakeholders must work together. The development of traditional and emerging climate-resilient agricultural practices is essential for ensuring food security in the future and increasing food production (Qi et al. 2018; Yadav and Lal 2018; Arora 2019; Altaf et al. 2022a; Lal et al. 2022b). Agricultural systems that are resilient to changing weather patterns and resilient to climate change can be built by combining traditional practices with innovative ones. We explore in this chapter the impact of climate change on the growth and productivity of crops, as well as its effect on the quality and quantity of various components of crops, such as carbohydrates, lipids, and proteins, that contribute to crop productivity and yield. In addition, we examine why climate change affects both the availability and uptake of micronutrients in crops, as well as how antioxidant molecules are produced as a result of climate change.

21.2 Impact of Climate Change on Production and Productivity of Crops

Agricultural sectors are among the most affected by climate change, which is a pressing global issue. For major crops to be produced and productive, the agricultural sector demands favourable climatic conditions. This sector faces significant challenges due to global warming and greenhouse gas emissions, resulting in adverse effects on crop yields, quality, and overall food security (Fig. 21.3). Our objective in this chapter is to discuss climate change's impact on crop production and identify potential ways to mitigate it. Agricultural production has been adversely affected by climate change due to changes in rainfall patterns. Climate change disrupts rainfall patterns, causing droughts, floods, and irregular growing seasons due to rising temperatures and changing precipitation levels (Kumar et al. 2020; Gomez-Zavaglia et al. 2020; Behra et al. 2022; Lal et al. 2023). The availability of water is a crucial factor in plant development, so these events directly impact crop growth and yield. In drought conditions, plants are under water stress, soil moisture is reduced, and nutrients cannot be absorbed, resulting in stunted growth and reduced yields (Fig. 21.3). A large amount of rain and flooding, on the other hand, can result in water logging, soil erosion, and crop damage, further reducing productivity. Agricultural production has also been affected by the escalation of extreme weather events. There has been an increase in the frequency and intensity of heat waves, hurricanes, cyclones, and storms, all of which pose a substantial risk to crop production (Kumar et al. 2008; Pandey et al. 2010, 2011; Tiwari et al. 2020a).

During high temperatures and heat waves, crop maturation will be accelerated, flowering will be reduced, pollination will be impaired, and yield will be reduced. Crop damage can also be caused by extreme weather events, such as lodging and breakage. Pests and diseases can expand their ranges and establish in new areas thanks to warmer temperatures and altered rainfall patterns (Kumar et al. 2021c; Tiwari et al. 2021b; Habib-ur-Rahman et al. 2022; Rahman et al. 2023). Invasive species and pests can greatly reduce yields and quality of crops. As a result, existing pests may become more resilient and difficult to control as temperature and humidity patterns change. Climate change poses a number of challenges for agriculture, which requires a multifaceted approach. A crucial part of promoting climate-smart agriculture is promoting practices that decrease greenhouse gas emissions. Precision agriculture practices enable water and fertilizer use to be optimized and resource efficiency to be increased by using remote sensing and satellite imagery. Conserving soil moisture, reducing erosion, and improving soil health can be achieved by implementing conservation agriculture practices (Figs. 21.3 and 21.4). It is also important to diversify crops and crops systems in order to be more resilient to climate change. It is important to encourage farmers to grow a variety of crops that are drought and heat tolerant to reduce risks associated with changing climatic conditions. It is also possible to improve soil fertility and resource utilization through crop rotation and intercropping techniques. Through conventional breeding and genetic engineering, climate-resilient crop varieties can be developed through investment in research and

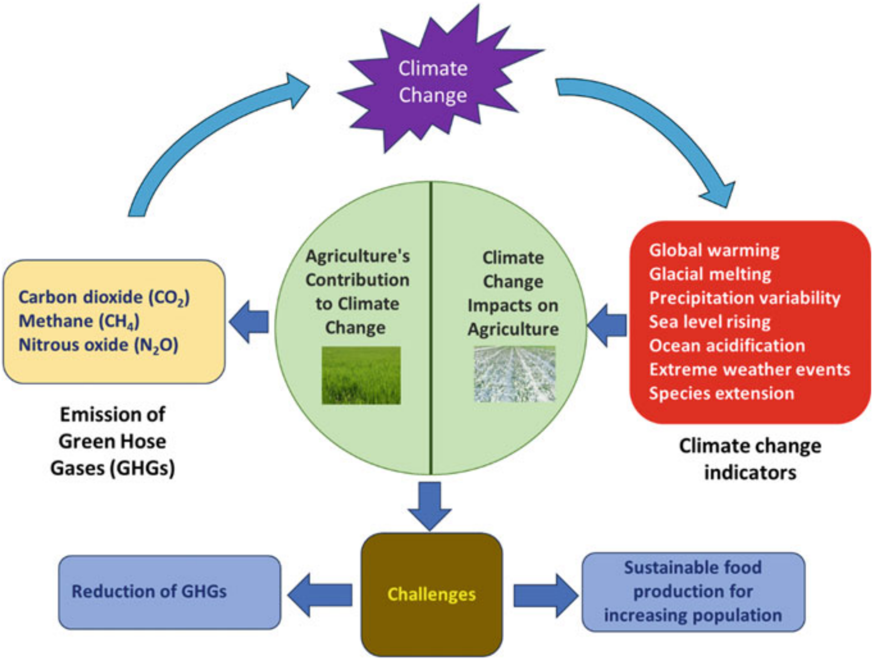
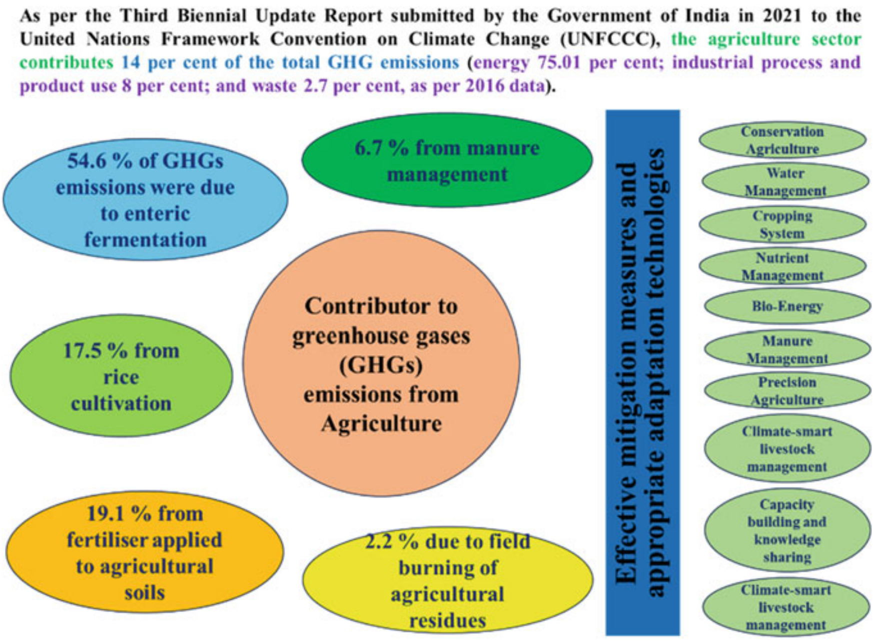


Fig. 21.3 The effect of climate change and the challenges that will be faced in the near future

development (Jeevalatha et al. 2015; Meena et al. 2017; Campos and Ortiz 2019; Naga et al. 2021; Kumar et al. 2022).

It is possible to safeguard productivity in the face of changing climate patterns by developing varieties that are drought-tolerant, heat-tolerant, and disease-resistant. The effect of climate change on crop production and productivity has been discussed in the following key points. The production of wheat in many countries is significantly impacted by climate change, particularly temperature extremes. With each degree Celsius rise in temperature, the crop yield may decrease by approximately 6%. The rise in temperature above 35 °C can disrupt Rubisco, the central enzyme of photosynthesis, leading to a halt in the photosynthetic process (Raza et al. 2019; El-Naby et al. 2020; Mishra et al. 2022). A negative influence of heat stress on antioxidant enzymes in Zea mays was observed. When examining the combined impact of heat and drought stresses on crop yield in sorghum, maize, and barley, it was found that the combined effect had more damaging outcomes compared to individual stress factors (Raza et al. 2019, 2022; Tiwari et al. 2020b).

The effect of temperature on crops: Increased heat stress can reduce yields, delay crop maturity, and decrease overall productivity. Heat waves can also lead to crop failures and reduced grain quality in cereal crops like wheat, rice, and maize (Escandón et al. 2018; Raigond et al. 2020; Tiwari et al. 2020a; Jahan et al. 2021; Ahsan et al. 2022). Crop production worldwide is affected by global warming and climate



As per the Third Biennial Update Report submitted by the Government of India in 2021 to the United Nations Framework Convention on Climate Change (UNFCCC), the agriculture sector contributes 14 per cent of the total GHG emissions (energy 75.01 per cent; industrial process and product use 8 per cent; and waste 2.7 per cent, as per 2016 data).

Fig. 21.4 Contribution of GHG from various sources

change. Various crops are at risk due to rising temperatures, including wheat, maize, rice, soybeans, and fruit trees. In addition to impacting food security and economic stability, these crops are highly sensitive to temperature changes. High temperatures are particularly damaging to wheat during its reproductive phase. Photosynthesis, pollen viability, and grain filling can all be compromised by heat stress, which can reduce grain yield. In consequence, food security may be compromised in many regions due to the decline of wheat production.

The growing temperatures are also threatening maize, another essential crop. In addition to reducing grain yield, modifying flowering patterns, and increasing water requirements, high temperatures can negatively affect maize growth and development. If pollination is exposed to high temperatures for an extended period of time, kernel set can be affected and grain quality will be reduced. Both food availability and animal feed supplies can be negatively affected by these challenges for maize production. Temperature changes have a direct impact on rice, one of the most important staple foods in the world. Different physiological processes can be disrupted by higher temperatures, resulting in lower rice yields. Spikelet sterility can cause a reduction in grain production when heat stress occurs during flowering. Rice cultivation can also be adversely affected by rising temperatures because pest and disease outbreaks are exacerbated (Oerke and Dehne 2004; Barnabás et al. 2008; Akter and Rafiqul Islam 2017; Raza et al. 2019; Tiwari et al. 2022b). During critical growth stages, soybeans, which are both food and industrial crops, are also sensitive to high temperatures. Flowering, pod formation, and seed development can be affected by heat stress, which can negatively impact soybean yield and quality. Pests and diseases may also increase with increasing temperatures, posing additional challenges to soybean production. There is a high degree of susceptibility to temperature fluctuations among fruit trees, including apples, citrus, and stone fruits. Pollination, fruit set, and fruit quality can be affected by temperature changes. In addition to temperatures rising, pests and diseases are more likely to infest fruit, potentially reducing the yield (Jeevalatha et al. 2018; Naga et al. 2019; Jahan et al. 2019).

It can affect the availability of fresh fruits for consumers and have severe economic implications for fruit growers. The development of strategies for mitigating these issues and ensuring global food security depends on understanding these impacts. Climate-resilient crop varieties and sustainable agricultural practices will also need further research and technological advancements to adapt to changing climates.

Changes in precipitation patterns: Due to climate change, frequent and intense droughts are likely to become more frequent and intense, while rainfall and flooding are likely to increase in certain regions. The production of crops can be harmed both by droughts and floods. Water logging, nutrient leaching, soil erosion, and increased disease incidence can result from insufficient rainfall, whereas excessive rainfall can cause water logging, nutrient leaching, and soil erosion. Certain regions may experience increased rainfall and flooding as a result of climate change (Akter and Rafiqul Islam 2017; Gomez-Zavaglia et al. 2020; Satognon et al. 2021; Altaf et al. 2023), which can change precipitation patterns and result in more frequent and intense droughts. There is a possibility that a drought, which is an abnormally low rainfall period, can negatively affect crops. Water scarcity caused by insufficient rainfall can cause plant stress. As a result, crop yields can be reduced, growth can be stunted, and even crop failure can occur. Wildfires can also damage agricultural land and crops due to drought conditions.

It is possible for soil to become saturated with water in the event of excessive rainfall, resulting in the stunting of root growth and a decrease in oxygen availability. A waterlogged environment can render nutrients unavailable to crops, preventing them from gaining nutrition. As rushing water can wash away valuable nutrients and topsoil, heavy rainfall can also lead to soil erosion. Several plant diseases can grow more quickly under standing water conditions during floods, in addition to increased incidences (Naga et al. 2021; Tiwari et al. 2022a; Watpade et al. 2023). A drought or a flood can pose challenges for crop production. Climate change will negatively affect precipitation patterns, and farming systems and farmers must adapt. Additionally, water conservation measures such as efficient irrigation systems may be necessary in addition to adopting crop varieties that are more water-resilient. A sustainable soil management program can also minimize erosion and nutrient leaching, keeping agricultural land healthy and productive over the long term.

Changes in water availability for crops: Changing rainfall patterns and glacier melting can impact freshwater availability for irrigation. Snow melt and rainfall are the main sources of water in regions affected by this situation. In summer, when irrigation demands are high, melting glaciers provide freshwater to many rivers and streams. The shrinking of glaciers may result in less melt water available for irrigation, as a result of global warming. Thus, agriculture productivity can suffer and water scarcity can result (Blois et al. 2013; Mall et al. 2017; Yadav and Lal 2018; Raza et al. 2019). Precipitation amounts, intensities, and timing may change in some regions. Water shortages and crop yields can be affected by unpredictable or reduced rainfall in areas that rely on rainfall for irrigation. Furthermore, flooding and soil erosion can occur in certain regions due to increased rainfall. Crops that require a lot of water for cultivation, like rice, can be particularly affected by water scarcity or reduced availability. It may be difficult for farmers to adequately irrigate their crops if irrigation water is limited, which may result in lower yields. Farmers who depend on irrigation for their crops can also suffer from water scarcity, which can affect food security and livelihoods. Sustainable water management practices are essential for mitigating the impacts of changing water availability. Water loss can be reduced by implementing efficient irrigation techniques, such as drip irrigation or precision irrigation. Water resources are also under pressure due to the adoption of drought-resistant crop varieties or the exploration of alternative sources of water, such as treated wastewater or rainwater harvesting. To mitigate long-term impacts of melting glaciers and shifting rainfall patterns, it is crucial to address climate change and reduce greenhouse gas emissions (Figs. 21.3 and 21.4). Water resources can be preserved and a stable environment can be maintained for agriculture and other sectors reliant on water if we limit global warming.

Shifts in growing seasons: As a result of climate change, growing seasons can shift, which can have profound effects on agricultural systems and crop yields. Because of global warming, the timing of seasons is changing, particularly spring's arrival. As a result, farmers and food producers will face a number of challenges in synchronizing crop growth stages with optimal environmental conditions. The problem arises when springs start early and then are followed by late frosts. Plants can begin flowering more quickly in the spring when temperatures are warmer. The blossoms may be damaged or destroyed by a subsequent frost event, resulting in lower yields. Flowering crops such as fruit trees, berries, and certain grains have a particularly sensitive response to weather conditions during flowering, as their reproductive processes are heavily dependent on these conditions. Additionally, crop growth can be affected by shifts in growing seasons. Crop development and maturity can be impacted by changes in temperature and precipitation patterns. In a short growing season or if their development extends beyond their usual harvest window, crops that require specific temperature ranges for optimal growth may face challenges. There can be significant economic and food security implications when seasons and growing periods are disrupted. Adapting planting schedules, using frost protection measures, or exploring new crop varieties with greater resilience to changing climate conditions are some ways farmers can adapt their practices. To minimize the negative impacts of climate change on agriculture and ensure future food production, these changes emphasize the importance of mitigation and adaptation strategies.

Increased pests and diseases in agricultural crops: Due to climate change, crops are more susceptible to pests and diseases, which pose significant challenges for global agriculture (Kumar et al. 2012a, b; Shah et al. 2020; Lal et al. 2021; Kumar et al. 2021e). Agricultural productivity and food security are affected adversely by the rising global temperatures and changing precipitation patterns associated with climate change. Temperatures that are warmer allow pests to thrive and expand their range. It has been shown that many pests rely on specific temperatures in order to survive and reproduce, so when temperatures rise, they may move into previously unsuitable areas for survival and reproduction. Pests may be introduced to previously unaffected crops, causing significant crop damage and yield reductions as a result of this expansion.

Pests can also reproduce more rapidly at higher temperatures because their life cycles are accelerated. Multiple generations can be produced in a shorter period of time by pests that reproduce throughout a season. Infestations and crop damage may be more severe as a result of rapid multiplication of pest populations. Pest behavior and migration patterns can also be disrupted by climate change. Pests can alter their feeding habits or shift their ranges as a result of changes in temperature and precipitation (Haverkort et al. 2013; Pretty and Bharucha 2015; Bhatnagar et al. 2017). By changing their behavior, pests can invade previously pest-free areas and infest previously pest-free crops. The effects of climate change further weaken the natural defense mechanisms of crops, allowing pests and diseases to attack them more easily. In extreme weather events such as heatwaves or prolonged periods of high humidity, temperatures and humidity can fluctuate rapidly, which stresses plants and compromises their health. Pests are more easily able to overcome weak plants' defenses and cause substantial damage when they are infested by weak plants. Changes in climate also influence the spread and development of plant diseases (Skjoth et al. 2016; Yadav and Lal 2018; Raza et al. 2019; Merrick and Searle 2019). Pathogens multiply and grow more easily under higher temperatures and humid conditions, leading to increased disease incidence. Climate change can create an ideal environment for pathogens to thrive in warm and moist environments. In addition to causing significant yield losses and economic impacts, plant diseases can be catastrophic for crop health and productivity.

Minimizing the impact of pests and diseases requires the implementation of integrated pest management (IPM) strategies. The aim of integrated pest management (IPM) is to prevent pests by using planting rotation, habitat diversification, and pesticides when necessary. Pests can be effectively managed and environmental risks minimized by using IPM practices. A resilient crop variety must also be adopted. It's becoming increasingly common for plant breeders to develop cultivars that are more resistant to pests and diseases. With these varieties, crop productivity is enhanced in spite of changing weather conditions, since they are able to withstand pest attacks or recover quickly from disease infections. Moreover, sustainable agricultural practices can also minimize pest and disease impacts. Creating favorable conditions for beneficial organisms and natural pest control on farms can be achieved by maintaining healthy soils, improving irrigation efficiency, and enhancing biodiversity. The monitoring of pests and diseases can also be enhanced by early warning systems and surveillance networks. It is possible for farmers to minimize damages and losses caused by pests and diseases by adjusting planting dates or implementing targeted interventions based on timely and accurate information about pest populations and disease outbreaks. A major consequence of climate change for agriculture is that pests and diseases are more common and spread more rapidly. Plant diseases are prone to developing when conditions are warmer and precipitation patterns are altered. Agricultural sustainability and food security are significantly affected by these impacts. We can, however, mitigate the effects of pests and diseases and adapt to changing climate conditions by adopting integrated pest management strategies, resilient crop varieties, and sustainable agricultural practices, ensuring our agricultural systems are productive and resilient for many years to come.

Carbon dioxide fertilization effect: Photosynthesis, which is the process by which plants convert sunlight, water, and carbon dioxide into carbohydrates and oxygen, can take advantage of higher CO_2 concentrations when the amount of CO_2 in the air increases. Many plant species can benefit from increased CO_2 availability by enhancing their photosynthesis rate. While CO_2 fertilization can benefit all crops in all conditions, it is not universally beneficial. Wheat, rice, and soybeans, for example, are among the plants that respond more strongly to increased CO_2 levels than maize and sugarcane. Because of the highly responsive photosynthetic pathway of C_3 plants, they are more sensitive to CO_2 concentrations. Other factors essential to plant growth, such as the availability of nutrients, may also limit the effect of CO_2 fertilization. Photosynthesis can be enhanced by elevated CO_2, but the plant may also require additional nutrients, such as nitrogen. Elevated CO_2 may be detrimental if there are insufficient nutrients available to meet the increased demand. Another critical factor is the availability of water. While CO_2 levels can improve some plants' water-use efficiency, allowing them to conserve water, their overall productivity and growth depend on the crop and the water available. CO_2 fertilization may have a milder effect in environments with limited water resources (Larkin and Honeycutt 2006; Haverkort et al. 2014; Mall et al. 2017; Bagy et al. 2020). The CO_2 fertilization effect has been shown to improve crop growth and productivity under certain conditions, but it is not enough to counteract the negative effects of climate change on agriculture and ecosystems, such as increased temperatures and altered precipitation patterns. To predict and manage the impacts of climate change on agriculture and food security, it is essential to understand the complex interactions between elevated CO_2, crop productivity, and other environmental factors. Currently, this field is conducting research aimed at improving our understanding of these interactions and developing strategies for optimizing crop production under changing conditions.

21.3 Climate Change Affects Carbohydrate, Lipid and Protein of Crops

Crops can be adversely affected by climate change in terms of their lipid, protein, and carbohydrate content. Plant growth and development can be affected by climate change, precipitation patterns, and CO_2 levels. Plants produce carbohydrates mainly through the process of photosynthesis, which converts sunlight into energy. Accordingly, rising temperatures and changing rainfall patterns can influence carbohydrate production. As a result of increased temperatures, plants can produce more carbohydrates and respire faster, resulting in lower carbohydrate contents in crops. Plants may also experience stress due to drought conditions that limit water availability. Studies suggest that certain crops can produce more carbohydrates when CO_2 levels rise, which is linked to climate change. Plant growth, energy storage, and membrane integrity depend on lipids, including oils and fats. Increasing temperatures and changing rainfall patterns may affect lipid metabolism in crops as a result of climate change. The composition and accumulation of lipids in plants can be affected by warmer temperatures and longer growing seasons. Lipid synthesis and content can also be influenced by changes in water availability and drought stress. Some studies suggest that elevated CO_2 levels can increase the accumulation of lipids in certain crops, which can make lipid production more difficult. Crop protein content and composition can be affected by climate change (Xiao et al. 2011; Gilroy et al. 2011; Yousuf et al. 2017; Djanaguiraman et al. 2018). Crops' protein synthesis and amino acid composition can be negatively affected by high temperatures, especially during critical growth stages.

Plants can also lose protein content as a result of drought stress, which is often related to climate change. Protein quality and quantity can be affected by elevated CO_2 levels, potentially resulting in changes in protein synthesis and nitrogen metabolism. There is no doubt that climate change can have a wide range of impacts on crop composition, depending on species, geographic location, and magnitude and duration of stress factors. In addition, it is difficult to predict the exact outcome due to the complex interactions between multiple environmental factors. Crop composition and food security can be mitigated through agricultural practices, breeding strategies, and technological advancements.

21.4 Effect of Climate on Micronutrients and Antioxidant Molecules

Crop micronutrients and antioxidant molecules can also be affected by climate change. Antioxidants protect cells from free radical damage caused by micronutrients, such as vitamins and minerals. There are numerous climate-related factors that can affect micronutrient availability and uptake by crops, including increased CO_2 levels, altered rainfall patterns, and changes in soil conditions. CO_2 concentrations in the atmosphere can affect mineral concentrations in plants, as well as their bioavailability. In populations that rely heavily on crops like iron, zinc, and calcium, elevated CO_2 levels can lead to nutrient deficiencies due to the reduction of essential minerals in crops (Manna et al. 2017; Rna et al. 2017; El-Naby et al. 2020; Kumar et al. 2021a; Altaf et al. 2022b). The absorption of micronutrients from soil can also be negatively affected by changes in rainfall patterns, such as an increase in drought frequency. Antioxidants mitigate free radical damage caused by oxidative stress. There are multiple mechanisms by which climate change can influence antioxidant levels and activity in crops. Due to climate change, plants are exposed to higher temperatures and increased ultraviolet radiation, which increases oxidative stress. Antioxidant molecules are produced by plants in response to damage caused by ROS. Crops, however, can be more susceptible to oxidative damage if they are exposed to prolonged stressors such as heat and drought. Plant metabolism may also change due to climate change, potentially altering the antioxidant profile of crops by affecting synthesis and accumulation of certain antioxidants.

Crop productivity and production are affected by climate change differently in different regions and crops. The long-term trends indicate that negative effects outweigh potential positive effects, even when localized benefits occur under certain conditions. To mitigate adverse effects on crop yields and food security, agricultural practices must be adapted, climate-resistant crop varieties developed, and sustainable farming techniques adopted. There are several factors to consider, including changing weather patterns, shifting seasons, challenges with water availability, insect outbreaks, and soil degradation. Climate-smart approaches include the deployment of resilient crop varieties, the implementation of efficient irrigation systems, the promotion of sustainable land management, the enhancement of early warning systems, and the education of farmers. Depending on the crop species, environmental conditions, and antioxidant compounds involved, climate change can affect micronutrients and antioxidant molecules differently. Climate change has the potential to negatively impact crop quality and nutritional value. Therefore, agriculture practices, soil management techniques, and breeding strategies aimed at enhancing nutrient content and antioxidant activity can mitigate this.

21.5 Food and Nutritional Quality Affected by Climate Change

Increasing atmospheric CO_2 concentrations can affect food nutrient content and, as a consequence, human health. Various C_3 crops such as rice, wheat, barley, and potatoes have been shown to lose protein content when CO_2 levels are elevated. In the world, billions of people rely on these staple crops for dietary protein (Kumar et al. 2018; Lal et al. 2020, 2022a; Naga et al. 2021). Those who consume large quantities of these crops may overconsume carbohydrates and other nutrition due to the decrease in protein content. In addition to their important roles in immune function, cognitive development, and energy metabolism, iron and zinc are important micronutrients for human health. In crops such as cereals and legumes, iron and zinc concentrations decrease as CO_2 concentrations increase (Mall et al. 2017; Sharma et al. 2021; Kumar et al. 2023). There is an increased risk of anaemia, compromised cognitive development, and compromised immune function in regions where iron and zinc deficiency is already prevalent. People who already have trouble accessing nutritious food may be disproportionately affected by the negative effects of climate change on crop nutrient content. Low-income communities may have a limited range of diet diversity and quality for some populations, including children, pregnant women, and the elderly. Malnutrition can be further exacerbated by reduced nutritional content in staple crops. In these populations, nutrient deficiencies can result from reduced nutrient content of these crops due to elevated CO_2. Deficiencies in vitamins and minerals can impair growth, stunt cognitive development, and increase infectious disease susceptibility (Wale and Cattlin; Singh and Lal 2011; Chourasia et al. 2022). Farmers can also lose income and livelihoods as a result of changes in crop nutrients. They may lose their marketability if their nutrients are reduced. Farmers in regions dependent on specific crops can lose money as a result, especially in those regions where warming climates negatively affect specific crops. There may be a need for individuals and communities to make dietary adjustments as staple crops lose nutrient content. The result may be dietary changes and changes in food preferences, as people consume alternative foods or incorporate more nutrients into their diets. In addition to contributing to global health challenges related to malnutrition, the carbon nutrient penalty is projected to reduce nutrient availability. In addition to adding pressure to healthcare systems, it may lead to an increase in noncommunicable diseases, nutrient deficiencies, and diet-related health problems. Due to climate change, crop nutrient content has been reduced, which could have an adverse impact on human nutrition and health. As a result of climate change, addressing the impact of food nutrient content is crucial for safeguarding human health and ensuring food security in the face of changing climates, even though additional research is needed to fully understand these effects and develop effective mitigation strategies.

21.6 Conclusion and Future Impact

Agricultural systems are facing significant challenges due to climate change, including decreased productivity, yield, and nutrient content. With the rise in temperatures, altered precipitation patterns, and increased frequency of extreme weather events, crop yields have been reduced, with heat stress negatively affecting key growth stages. It is undeniable that climate change is a pressing issue that requires thorough investigation and understanding, and its potential impact on crop production is one of the most critical. Climate change has already been observed to affect agriculture and food security, as evidenced by rising temperatures and elevated CO_2 concentrations. A variety of crop growth simulation models have been developed to address this challenge. They have been calibrated and validated for various crops in different regions. Climate models are able to predict rainfall and extreme weather events in the future, but they have limitations and uncertainties associated with them as well. Despite the improvements in climate models, they still have a negative effect on predicting climate patterns, especially rainfall patterns. Climate change impacts on farmers can be difficult to incorporate into farm projects and agricultural systems because of these uncertainties. Although climate change has been linked to crop physiology, the evidence suggests that it poses a credible threat to the sustainability of global productivity growth. In light of this, it is crucial that more investment be made in crop improvement, with a special focus on addressing the impact of climate change. We can ensure food security by sustainably growing yields in the coming decades. Fishing catches and forestry yields have also declined due to climate change. Some crops have been found to have reduced nutrients as a result of elevated carbon dioxide levels.

Food production is further threatened by geographic shifts in agricultural areas and water scarcity. There have also been changes in the dynamics of pests and diseases. Sustainable agricultural practices, improved water management, and climate-resilient crop varieties are essential in addressing these challenges. We must act urgently to protect food security and livelihoods, especially in developing countries where vulnerable communities are concentrated. Detailed studies and analyses are required to fully understand the threats climate change may pose to agriculture. Several crucial aspects should be examined, including how climate change might affect rainfall patterns, groundwater and surface water availability for irrigation, and temperature variations across different agro-climatic regions.

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