# 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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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

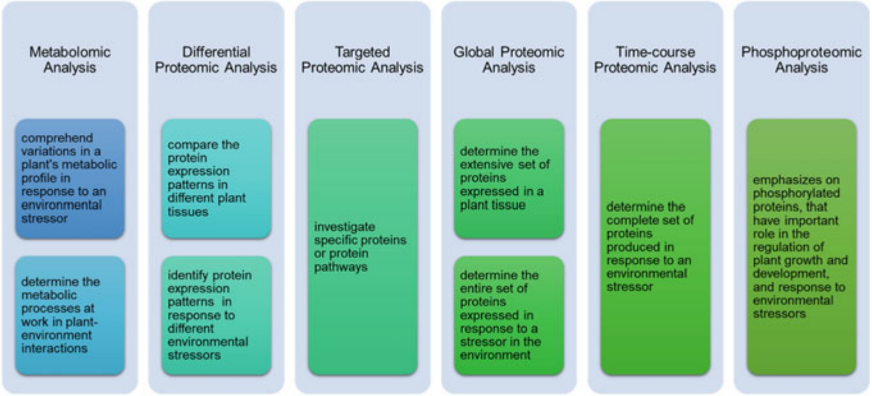

**Fig. 2.1** Proteomics studies implemented to understand plant-environment interaction

(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

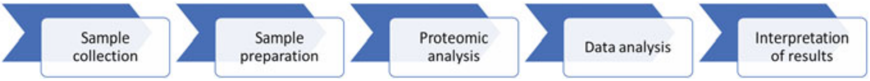

**Fig. 2.2** General steps to implement in a proteomics study

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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