Stress in Plants

Stress in Plants:

The Hidden Half

Edited by

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PREFACE

Plants are aware of various stresses in their environment. They perceive changes in these factors as they scan the environment and assess what response they need to make. Based on the information they gather, they can alter their behaviour, morphology, biochemistry, and physiology in response to a stress in their surroundings. However, few of us are aware of the fascinating details of how they respond to such stress conditions. Nature has equipped plants with defence mechanisms, including those involving enzymatic and non-enzymatic antioxidants. Upregulation and downregulation of these antioxidants help plants tolerate stress. The biological mechanisms behind the adaptability of plants to diverse stress conditions are also very beautiful and interesting subjects of study.

This book presents detailed information about various types of hidden stresses that affect plants and their response mechanisms. It is aimed at young graduates, students, teachers, and researchers. The book also addresses the responses of plants to stressful situations in terms of adaptation and tolerance during their life cycle. This compilation paints a broad picture and uses a systems approach wherein most aspects of stress are examined. The chief objective of the book is to present important information for the development of strategies to combat plant or crop stress. I trust that the information covered in this book will clarify the mechanistic aspects of different hidden stresses in plants that lead them to adapt to the natural environment.

The book is organized into 16 chapters. Chapter 1 describes the origin and evolution of stress in plants. Chapter 2 discusses different hidden adaptation mechanisms, highlighting other stress situations plants face in the natural environment. Chapters 3 and 4 discuss the adaptation of plant roots to stress conditions and the role of plant pigments during stress responses. Chapters 5 and 6 deal with nanotechnology and the role of stomata under stress. Chapters 7 and 8 deal with flooding or submergence and aluminium toxicity and tolerance in plants. The ninth chapter of this book covers magnetic stress and its consequences in plants: it discusses interactive and adaptative effects under the influence of magnetic fields. The tenth chapter of the book discusses phytoremediation and contamination in relation to plant growth and development. In chapter 11, an attempt has been made to highlight important facts about trace metallic elements and metal nanoparticles inducing phytohormesis during stress in plants. Chapter 12 discusses cold shock tolerance in plants and describes adaptation mechanisms. Chapter 13 elaborates the responses of plants to different biotic environments. Chapter 14 relays information about the role of plant growth-promoting rhizobacteria in stress tolerance and adaptation. Chapter 15 elaborates the effects of salt and drought stress in plants and their consequences. And finally, in chapter 16, the discussion revolves around the effects of abiotic factors on the metabolic activities of plants, with particular reference to aquatic plants.

This book uses several figures and tables to simplify the understanding of the presented material. This book also includes a complete index and a list of acronyms to further increase the accessibility of the information explained. Each topic has been fully discussed to its full potential to ensure that readers receive complete information about it. A list of literatures cited is also provided for further reading in each chapter.

The collaboration and patience of the contributors during the preparation of this book cannot be forgotten. I would also like to thank Rebecca Gladders, Helen Edwards, Jamie George and other team members of Cambridge Scholars Publishing for their help, suggestions, and timely publication of this book. I thank all contributors for bringing together this valuable collection of ingredients for all of us who are studying, working, or doing research on plants and their environment related subjects.

Thank you.

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CHAPTER ONE

THE ORIGINS AND EVOLUTION OF STRESS IN PLANTS: STRESS TRIGGERS "DESCENT WITH MODIFICATION" IN PLANTS

A NAIR, AS RAO, K HARDI, V DIVYA, SANJANA R AND AISHWARYA G

All life forms adapt to locally stressful environmental conditions and plants are no exception. Plants are easily stressed and, being sessile organisms (immobile), they cannot escape the sources of their stress. Extremes of light, humidity, drought, salinity, and cold (abiotic stress), etc., are all triggers; if this were not enough, plants also have to fight against the activities of all kinds of pathogens and attacks by grazers (biotic stress). Plants are masters of survival, exhibiting multiple and varied strategies, including protein and metabolite production, gene activation and expression, and signalling cascade/transduction pathways, to combat stress. Many aspects of plant evolution remain enigmatic. The existence of plants was, and continues to be, fiercely challenged by their environment. A long-standing assumption is that the streptophyte algal progenitors of plants must have possessed exaptations that allowed them to deal with environmental stresses, as discussed further in this chapter. Stress is perceived by plants through a so-called "perceptron", being a complex regulatory network that receives input from phytohormones. Comparative RNA-sequencing of stress-treated ancestors of the plant kingdom has shown a particularly tight genetic interaction between the nucleus and plastid. The survival of plants across different eras may have enabled epigenetic or cellular stress memory, leading to the adaption of useful traits from previous failures in current generations. The significance of the contents of this chapter is that it is imperative that crops are equipped with multiple stress tolerances to meet growing population demands. Furthermore, with the impact of climate change, plants need to evolve and adapt to continue successfully on this planet. This is a multi-disciplinary endeavour combining plant systematics—physiology, phylogenomics, and ecology—to decipher the underlying stress mechanisms.

Subsistence in all sentient beings is dependent on maintaining constant internal vital conditions in a changing environment. Cannon (1929) termed this “homeostasis”. Selye (1956) defined “stress” as the effect of anything that critically threatens homeostasis. The actual or perceived threat to an organism is known as a “stressor” and a response to stressor is called a “stress response”. It is believed that stress responses evolved as adaptive processes. For example, as humans, we are provided with the benefit of the “fight or flight” response triggered by our sympathetic nervous system. Humans or animals have the advantage of being able to run away or seek shelter in grave situations, but plants are sessile and do not have such options. So, how exactly do they escape or face stressful situations? And what are these stress-creating conditions?

Stress: A Primary Driver of Evolution

Starting from the single-celled organisms that evolved into complex species, every organism on this planet has undergone its own journey towards achieving successful existence. Evolutionary forces, in conjunction with environmental insults, have shaped all lifeforms one earth, forcing them to adapt and reproduce. Stress is one of the major components that has shaped evolution on this planet. Plants represent one of the best examples for appreciating the impact of stress on evolution. For example, stomatal development in plants is a major characteristic that evolved as a product of environment-gene interaction (Agurla et al., 2018). The plant perceptron connects the environment to development and there are many instances of this. A number of phytohormones are considered to regulate the plant perceptron (Scheres et al., 2017). There are a number of signal transduction pathways that have dveloped in response to stress, like the ABA signalling pathway, which is present in *Zygnema* algae, but is now conserved across land plants. This was traced using RNA sequencing technologies, which showed conserved orthologues between the algae and land plants like *Arabidopsis.* Another common mechanism, plastid-nucleus communication, is observed in streptophyte algae and land plants. Plastids actively respond to stress by communicating with the nucleus through retrograde signalling and the genes in the nucleus directly control the expression of plastids. This helps the plant to sense and respond to stress (Vries et al., 2018). Cells respond to the external environment, deciding the fate of the cell. Signalling pathways determine the cell response and these pathways are governed by the activation and inactivation of transcription factors. Epigenetic mechanisms also play an important role in modifying these signalling pathways and thus affect transcription. These epigenetic mechanisms ultimately regulate the expression of genes in response to stress (Zhao et al., 2020).

The Array of Stressors that Impact Plant Growth

In general, stressors are factors that affect typical biology by causing anatomical and physiological effects. Broadly, stressors can be classified into abiotic and biotic factors (**figures 1 and 2**).

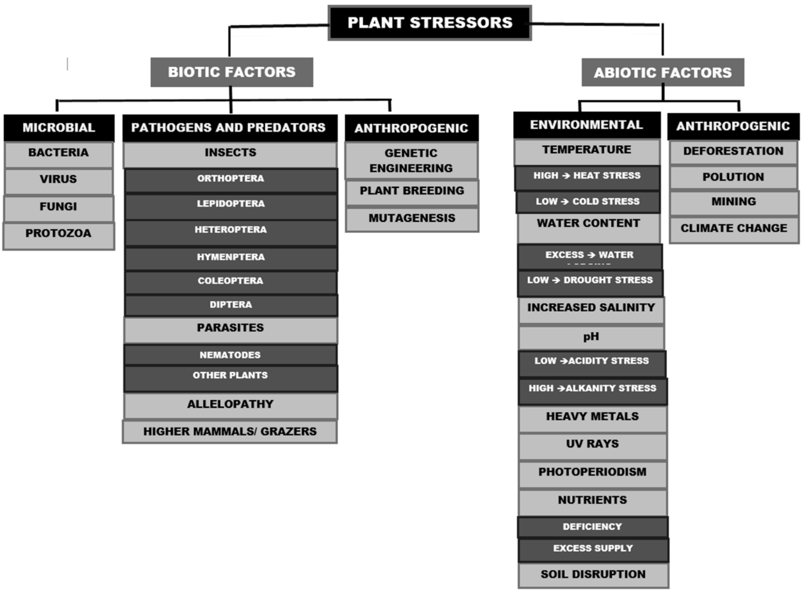

Figure 1. Systematic flowchart demonstrating array of stressors adversely affecting plant growth and survival.

The Effect of Biotic Stressors on Plants

Of all the biological factors that induce stress, microorganisms represent the predominant one. Many **bacterial** species cause plant diseases, including blights, cankers, wilts, and rots, etc. Most of these bacteria are mesophilic in origin and require high humidity to cause infection. For example, *Clavibacter michiganensis* pv., found at moderate temperatures and high humidity, causes wilting in tomato and chilli plants (Abo-Elyousr et al., 2019), while *Erwinia* spp. cause soft rot in a wide range of vegetables, including lettuce, brassica, cucurbit, tomato, capsicum, potato, carrot, and various herbs, etc. (Zhao, 2012). There are many **viral** stressors, including tobacco mosaic virus (TMV), gemini virus, *African cassava mosaic virus* (ACMV), and plum pox potyvirus (PPV), etc. (Garcia and Cambra, 2007). Infection can result in discoloured rings, spots, vein clearing, mosaics, and stunted growth, etc., in a wide range of plants. **Fungi,** like *Alternaria*, *Phytophthora*, *Cercospora*, *Claviceps*, *Rhizoctonia*, *Fusarium*, and *Ralstonia*, etc., cause diseases like damping off, leaf spots, root rot, canker, and fruit rot, etc. Finally, **protozoa** cause necrosis, wilt, and rot etc.

Pathogens and **parasites** are usually insects and other organisms (plants and animals) that interfere with plant survival, causing immense stress. Chewing insects injure plants by consuming the foliar parts, while root chewing insects subsist entirely on plant tissue for development, such as root weevils and root maggots. Sucking insects remove the cell contents (e.g., thrips) or sap (e.g., aphids, leafhoppers, and scales, etc.), weakening the plant, sometimes injecting salivary fluids: (1) killing the plant, as evidenced by armoured scale feeding; (2) causing galls to form, as with gall aphids; and (3) kill off portions of leaves, as seen in leafhopper "burn". The transmission of pathogens is an adverse effect caused by the insertion of sucking mouthparts into plants. For example, leafhoppers transfect plants with mycoplasma-like organisms causing peach X-disease and aster yellows (portal.ct.gov/CAES).

Insects of diverse classes can be stressors. Locusts (orthoptera) are highly mobile and their periodic swarming can destroy hundreds of acres of crops through extensive feeding. Among the **Lepidoptera** (butterflies and moths), potential pests include the diamondback moth (*Plutella xylostella*), which damages cabbage plants; pod-boring moths that feed on chilli plants (*Spodoptera litura*); and shoot and fruit borers, which feed on brinjal and okra (*Earias fabia*). Major damage is caused by the chewing mandibles, substantially reducing the plant's photosynthetic ability and therefore carbohydrate production. In contrast, heteroptera (plant bugs, chinch bugs, lace bugs, and stinkbugs) damage both wild and domestic plants by sucking sap or injecting tissue-killing fluids into plant tissue, harming the protective layers and allowing bacterial infection (Sanjay, 2019). The larvae of the cherry leech **hymenopteran** (*Caliroa limacina*) are predators. They damage the upper epidermis of leaves thinning them and over time these leaves become reddish brown and fall, exposing the plant's extremities to stress.

In addition, invasive ant species disrupt growth and photosynthesis by nesting in plant roots. *Pheidole megacephala*, known as the "big-headed ant", is a major pest. The formation of tunnel networks around the roots of trees causes higher baseline water stress, reducing photosynthesis by more than half and limiting carbohydrate availability. The largest insect order, **Coleoptera**, accounts for more than 360,000 species of insect. Of these, beetles cause considerable damage by transmitting plant pathogens, for example, plant viruses transmitted by the *Chrysomelidae*, *Coccinellidae*, *Curculionidae*, and *Meloidae* families (Fereres and Raccah, 2015; Wielkopolan et al., 2021). The **Diptera** include the Hessian fly (*Mayetiola destructor*), which is a major pest of wheat (*Triticum* spp. L.). Stress is caused by reduced yields resulting from larval feeding on seedlings. This leads to stunted growth, failure to produce seed heads, a reduction in the number of seeds per spike, and a reduction in seed weight (Schwarting, 2016; Abid et al., 2018).

Parasites dwell upon host plants, which suffer stress caused by these unwanted intruders. Roots, like carrot, beet, parsnip, and potato, are damaged by **root-knot nematodes** (*Meloidogyne* spp.) and cyst nematodes (*Heterodera ciceri*), which possess straw-like mouth parts that inject a mixture of enzymes (cellulolytic and pectolytic enzymes). These break down roots leading to water stress and nutrient deficiency (Pandey et al., 2021). In **cyst nematodes**, larvae migrate intercellularly upwards in the vascular cylinder, mobilizing photosynthetic products from the shoots to the roots. *M. incognita* secretes calreticulin to suppress host defence responses by preventing calcium ion flux through the sequestration of free calcium (Zwart et al., 2019). **Parasitic plants** use a structure called a haustorium to penetrate the host plant and drain it of nutrition. *Cuscuta*, commonly known as dodder, is an obligate parasite and cannot survive without a host. It has no roots or leaves and its peculiar and easily identifiable yellow/orange stems have a stringy, hair-like appearance and drain all the nutrients from a plant until it dies. The Australian Christmas tree (*Nuytsia floribunda*) is another parasitic plant. It can photosynthesise, but steals water from neighbouring plants by severing the host's xylem vessels with guillotine-like structures in its haustoria (Zwart et al., 2019).

Competition is foundational to success in the biosphere. **Plant allelopathy** refers to chemical warfare between plants wherein one releases chemical to supress others. This causes competitive stress between plants for sunlight, nutrients, water, and space, etc., which impacts their survival. As a result, seed germination, seedling vigour, growth, and photosynthesis, etc., are all affected. Interestingly, gaseous toxins and noxious chemicals from dropped leaves can inhibit other species and is an adaptive mechanism to induce stress in an ecosystem. For example, black walnut (*Juglans nigra*) is an allelopathic plant known to secrete a respiration-inhibiting substance called "juglone" into soil.

Overgrazing is another important biological stress factor leading to desertification by reducing plant cover. Small mammals, like rabbits and deer, graze extentively, affecting sapling growth and jeopardizing their chances of survival to adulthood. Large herbivores, like goats, cows, and elephants are natural biotic stressors, affecting the spatial variation of plant growth and survival (Croft, 2002). **Anthropogenic** activities such as the addition of new genetic material through genetic engineering can activate inactive pathways, or, in some cases, increase the levels of toxic substances. The manipulation and overuse of plants to cater to human needs is also taking a toll. In this process, strategies of in-breeding and selective breeding lead to molecular stress in plants as they attempt to maintain genomic integrity and this can lead to mutagenesis.

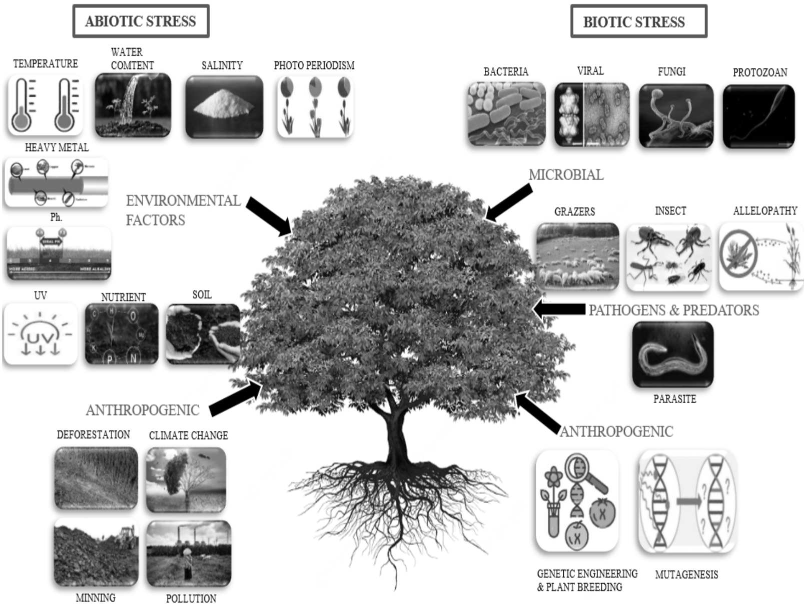

Figure 2. Major stressors adversely affecting plant growth and survival.

The Effect of Abiotic Stressors on Plants

Abiotic stresses constitute a major group of stressors that reduce crop production across the world. Multiple abiotic factors can cause stress simultaneously, resulting in unfavourable conditions and triggering the disruption of many essential pathways. Plant water status is intermittent under changing temperatures. **Heat Stress** causes dehydration and water potential and relative water content decrease. Altered levels of soluble sugars and proteins negatively affect the osmotic pressure within cells and maintaining homeostasis becomes challenging (Ding et al., 2020; Li et al., 2021).

Plant **chilling injury** refers to injury caused by a temperature drop to below 10 to 15 °C, but above freezing. Crops like maize, common bean (*Phaseolus*), rice, tomato, cucumber, sweet potato, and cotton are chill-sensitive. The most common site implicated in chilling injury is the plasma membrane, changes to which may lead to cell leakage or disruption, electrolyte leakage and plasmolysis, altered metabolism-cracking, splitting and dieback of stems, and vascular browning. **Freezing stress** occurs at temperatures below 0 °C, primarily by ice crystal formation, which deprives the plant of water due to the fluids within it freezing (Vicente et al., 2022).

The soil and crop environment are adversely affected by **excess water** due to the depletion of oxygen, which leads to reduced root respiration and other vital plant processes, including the production and accumulation of phytotoxic compounds (ethylene) in plant roots and soil. The redox potential of the soil changes in a way that favours loss of nitrogen and the production of toxic ions (Jia et al., 2021). On occasion, **drought stress** is accompanied by other detrimental effects, like salinity, heat stress, and pathogenic attacks, triggering plants to undergo modifications with reduced rates of transpiration and photosynthesis, osmotic adjustments, modified stress signalling pathways, and senescence. These forced modifications can cause permanent injury in plants (Ojasvini et al., 2021; Wahab et al., 2022).

Two kinds of plants exist: halophytes and glycophytes. Halophytes are salinity-tolerant plants. They are adapted to high salinity and some even benefit from high salt concentrations (Jing et al., 2019; Nazish et al., 2020). In contrast, glycophytes are **salinity-sensitive plants** for which high concentrations of sodium ions in saline soil limit water uptake and the absorption of nutrients (Volkov et al., 2017). Major crops tend to be glycophytes for which salt stress hinders seed germination, flowering, and fruiting (Yuanchun et al., 2019). **Acidic stress** with the action of protons (H+) leads to rhizotoxicity, arrested root growth, reduced nutrient availability, disrupted plasma membranes, and ATPase activity through the production of reactive oxygen species (ROS) (Borhannuddin et al., 2019). **Alkaline stress** greatly reduces seedling survival rate and shoot and root growth, characterized by the development of clusters of short, highly branched roots. High pH has a nuanced effect on root oxidative status (Zhang et al., 2017). Plants experience **oxidative stress** when exposed to **heavy metals**, leading to cellular damage by the accumulation of metal ions that disturb cellular ionic homeostasis. Heavy metals, like cadmium, copper, lead, chromium, and mercury, are significant environmental pollutants. Predominantly, heavy metal toxicity is the excessive accumulation of reactive oxygen species (ROS) and methylglyoxal (MG), causing the peroxidation of lipids, oxidation of protein, inactivation of enzymes, and DNA damage (Zhang et al., 2017).

Light stress induced by **UV rays** includes DNA damage and the generation of reactive oxygen species. These promote metabolic disturbances including DNA damage, impairment of pathogen resistance, and the generation of ROS, resulting in morphological changes such as decreased rosette diameter, reduced epidermal cell expansion, and shortened inflorescence stem (Akram et al., 2019; Borhannuddin et al., 2019). Sudden changes in the photoperiod, particularly its prolongation, cause **photoperiod stress** in short-day-adapted plants. During the night, the stress hormones JA and SA increase, coinciding with a strong decrease in the ascorbic acid (ASC) redox state and peroxide accumulation, which is fatal (Iqbal et al., 2021; Roeber et al., 2022). In this scenario, plants cannot get rid of **excess nutrients** resulting in root and leaf damage. Leaf damage or burn leads to reduced photosynthesis with less surface area available, reducing glucose production. This is not optimal for growth. All mineral nutrients enter the plant in ionic form and play a key role in osmotic regulation and cellular permeability to maintain cell-ion homeostasis. If the supply of a particular nutrient increases, the availability of other nutrients is reduced (a limitation of the genetic potential of crops), resulting in no increase or even a decrease in yield. For example, excess nickel (Ni) displaces magnesium (Mg^{2+}) ions from the RuBisCo pathway (Pandey et al., 2021).

Stress imparted due to **soil compaction** and high salinity or heavy metal levels in the soil can hinder plant growth and development. In addition, the water-holding capacity of the soil is affected reducing the availability of nutrients to the growing plant. An optimal soil pH is important for normal development. Many **anthropogenic activities** also have an impact—rising temperatures and changes in precipitation patterns as a result of climate change are making it difficult for many plants to survive in their natural habitats (e.g, due to deforestation). "Invisible damage" covers such aspects as a decrease in size and yield due to heavy metal pollution. If the plant's defence systems are insufficient, irreversible damage appears (cell death, leaf necrosis, etc.), which is referred to as "visible damage", due to air pollution. Air pollution often results in an increase in concentrations of amino acids (proline), soluble proteins, and sugars in leaves, increasing the risk of attack by pathogens. Some tree roots are diverted from the deeper soil layers in order to avoid soils that have been mined and they therefore lack anchorage within the deep soil layers and are at greater risk of uprooting in strong winds.

Diverse Plant Adaptations to Stress

Plants have developed varied mechanisms to cope with stress. Each adaptation allows the plant to not only successfully withstand environmental insults, but they can also be passed on to subsequent generations. These adaptations start at the molecular or cellular level and are later translated to changes in morphology (**figure 3**).

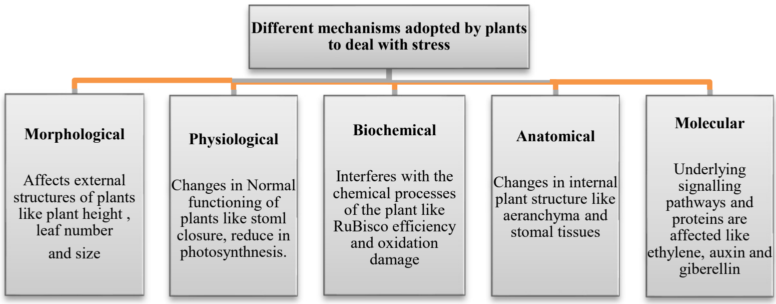

Figure 3. Representative flowchart of well understood plant response mechanisms classified on basis of reaction produced by plant under vivid stimuli

Plant Adaptations to Biotic Stress

Biotic stress usually involves attack by pathogens like bacteria, fungi, and viruses. Plants lack immune systems, but they have developed defensive mechanisms. For instance, the accumulation of nitric oxide and active oxygen species leads to hypersensitive reactions, resulting in the death of infected tissue around the pathogen-invaded site. This localises the infection and prevents its spread to unaffected regions. By fortifying the cell wall, consisting of lignin and callose, etc., plants create an initial deterrent to invading pathogens (Liu et al., 2018). Plants have been shown to produce a battery of antimicrobial compounds, such as phytoalexins. The aforesaid mechanisms for resisting biotic stress are seen in variety of plant families, including the *Leguminosae*, *Solanaceae*, *Amaryllidaceae*, *Euphorbiaceous*, and *Orchidaceae* (**figure 4**).

Plant Adaptations to Abiotic Stress

The development of cuticles and hair, and an upright arrangement of leaves can protect plants from high temperature fluctuations. This is seen in the case of plant species such as bromeliads. A high wax content in the cuticle helps the plant handle low temperature stress, as observed in the high wax mutant *Dianthus spiculifolius* (Xin et al., 2022). Additionally, during low temperature conditions, the photochemical efficiency and electron transfer rate has been found to increase in *Angelica sinensis* seedlings (Zhang et al., 2019).

By controlling carnal functions, such as stomatal closure (in plants such cacti) during the daytime and nighttime, the plant can prevent excessive loss of water via transpiration (Serna et al., 2022). Plants like cabbage (*Brassicaceae* spp.) produce an array of secondary metabolites such as isothiocyanates and glucosinolates, or reactive oxygen species (ROS). These compounds have the capacity to scavenge free radicals, allowing plants to battle the devastating effects of oxidative stress, include modulating the size of the xylem vessel under changing temperature conditions. In plants like *Fagus sylvatica* L., phytohormones such as brassinosteroids act as growth regulators (in *Brassica napus* and *Alnus glutinosa pollens*) to increase antioxidant activity and heat resistance (Peres et al., 2019). Plants like *Arabidopsis thaliana* can withstand lower temperatures by altering their lipid metabolism (Ding et al., 2020).

Longer root length and smaller root diameter increases root surface area so that plants can take up nutrients under salt stress (Zhao et al., 2021). Halophytes like mangroves have developed resistance to salt stress by increasing their osmotic potential and water levels in the stomata, thereby dampening the toxic effect of ions (Agurla et al., 2018; Jing et al., 2019). Increased accumulation of sugars to tolerate salt and osmotic stress has been observed in halophytes like common bean (*Phaseolus vulgaris* L.) (Hiz et al., 2014). Increasing the thickness of the cuticle and trichome density in the epidermal tissue layer lowers the transpiration rate, which, in turn, helps adapt to salinity stress (Srivastava et al., 2022). This has been observed in the family of amarantaceous flowering plants (Nazish et al., 2020). On the other hand, some plants have evolved to complete their growth cycle before the onset of seasonal drought (Wahab et al., 2022) (**figure 4**).

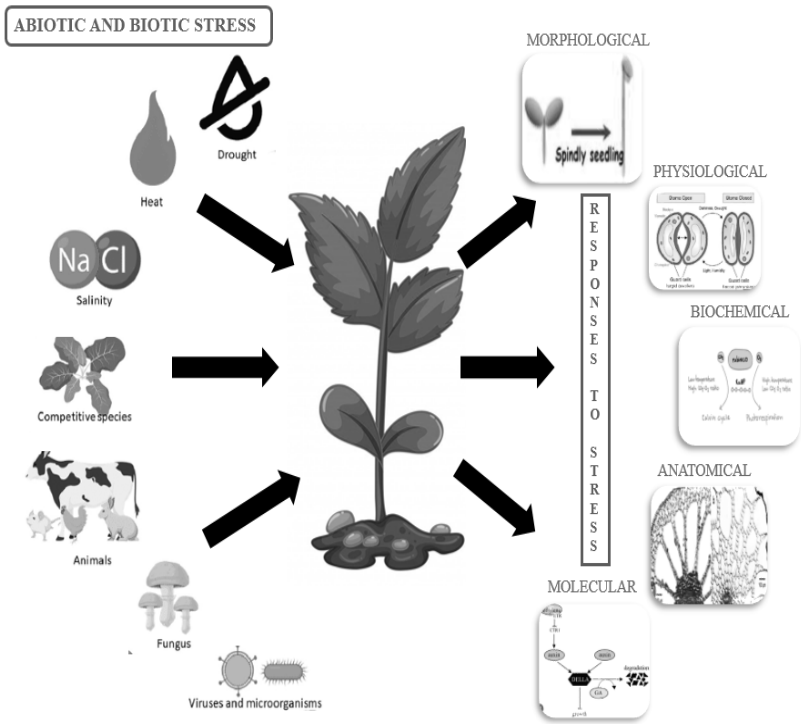

Figure 4. Vivid stress responses in correspondence to diverse abiotic and biotic stressors

Conclusion

Stress is pivotal to maintaining life and evolution. All creatures face threats to homeostasis and evolving adaptive responses is a natural consequence. The future of plant species depends on their ability to adapt to potent stressors. Acute stress responses in young, healthy plants may be adaptive and stereotypically do not impose a burden for survival. As a matter of fact, organisms possessing coping responses may benefit from such exposures (Garmezy, 1991; Glanz and Johnson, 1999).

Plant diversity, in general, is impacted by a multitude of factors. Such factors are both biotic and abiotic in nature. These factors predominantly act as stressors, impacting plant survivability. In response, plants have risen to this challenge by evolving new developmental and metabolic traits, allowing them to adapt to these environmental insults. However, the current rapid rate of climate change caused by human activity is bringing unparalleled challenges. Exceptional cutting-edge methods, such as synthetic biology and genome engineering, should be applied to mitigate the consequences of anthropogenesis. The amalgamation of all these interdisciplinary studies can help pave the way for the generation of stress resistance in plants, developing them from scratch and ensuring our "oxygen-mates" stand strong on earth.

Literature Cited

Abid, M., Ali, S., Qi, L. K., Zahoor, R., Tian, Z., Jiang, D., Snider, J. L., & Dai, T. 2018. "Physiological and biochemical changes during drought and recovery periods at tillering and jointing stages in wheat (*Triticum aestivum* L.)." *Scientific reports*, 8(1): 4615.

Abo-Elyousr, K.A.M., Khalil Bagy, H.M.M., Hashem, M. et al 2019. "Biological control of the tomato wilt caused by Clavibacter michiganensis subsp. michiganensis using formulated plant growth-promoting bacteria." *Egypt J Biol Pest Control*, 29:54.

Agurla S., Gahir S., et al., 2018. "Mechanism of Stomatal Closure in Plants Exposed to Drought and Cold Stress." *Adv Exp Med Biol*, 1081:215-232.

Akram, R., Fahad, S., Masood, N., Rasool, A., et al., 2019. "Advances in Rice Research for Abiotic Stress Tolerance: Plant Growth and Morphological Changes in Rice Under Abiotic Stress.", 69-85.

Borhannuddin Bhuyan, M.H.M. et al. 2019. "Plants Behavior Under Soil Acidity Stress: Insight into Morphophysiological, Biochemical, and

Molecular Responses.” *Plant Abiotic Stress Tolerance. Springer, Cham:*35-82.

C, Jing., E. C. Bo., N, Siria., R, Ute., 2019. “Morphological and metabolic responses to salt stress of rice (Oryza sativa L.) cultivars which differ in salinity tolerance.” *Plant Physiology and Biochemistry,* vol144: 427-235.

Ding Y., Shi Y., Yang S., 2020. “Molecular Regulation of Plant Responses to Environmental Temperatures.” *Mol Plant*, 13(4):544-564.

Hiz MC, Canher B, Niron H, Turet M., 2014. “Transcriptome analysis of salt tolerant common bean (Phaseolus vulgaris L.) under saline conditions.” *PLoS One,* 9(3): 925-98.

Iqbal Z., Iqbal MS., et al., 2021. “Plant Defense Responses to Biotic Stress and Its Interplay with Fluctuating Dark/Light Conditions.” *Front Plant Sci,* (12): 631-810.

J, Zhao., Z, Lu., L, Wang., B, Jin., 2020. “Plant Responses to Heat Stress: Physiology, Transcription, Noncoding RNAs, and Epigenetics.” *Int J Mol Sci,* 22(1):117.

Li Z., Howell SH., 2021. “Heat Stress Responses and Thermotolerance in Maize.” *Int J Mol Sci,* 22(2):948.

Liu Q., Luo L., Zheng L., 2018. “Lignins: Biosynthesis and Biological Functions in Plants.” *Int J Mol Sci*, 19(2):335.

M, Yuanchun., W, Li., W, Jiaoyang., Z, Yan., C. M. Zong 2019. “Isolation and expression analysis of Salt Overly Sensitive gene family in grapevine (Vitis vinifera) in response to salt and PEG stress.” *PLoS ONE,* 14(3): 212-666.

Nazish, M., Ahmad, M., et al., 2020. “Taxonomic implications of leaf epidermis in halophytes of Amaranthaceae from Salt Range of Punjab, Pakistan.” 79-90.

Ojasvini Ahluwalia, Poonam C. Singh, Ranjana Bhatia, (2021), A review on drought stress in plants: Implications, mitigation and the role of plant growth promoting rhizobacteria, Resources, Environment and Sustainability.” Volume 5: 100-032.

Pandey, R., Vengavasi, K. & Hawkesford, M.J. (2021), “Plant adaptation to nutrient stress.” *Plant Physiol. Rep,* 26:583–586.

Peres A.L.G.L., Soares JS., Tavares RG., 2019. “Brassinosteroids, the Sixth Class of Phytohormones: A Molecular View from the Discovery to Hormonal Interactions in Plant Development and Stress Adaptation.” *Int J Mol Sci,* 20(2):331.

Roeber, V. M., Schmülling, T., & Cortleven, A. 2022. “The Photoperiod: Handling and Causing Stress in Plants.” *Frontiers in plant science,* 12:781-988.

Scheres B., Van der Putten W.H., 2017. "The plant perceptron connects environment to development." *Nature,* 543(7645):337-345.

Serna L. 2022. "Maize stomatal responses against the climate change." *Frontiers in plant science*, *13*: 952-146.

Srivastava, S. 2022. "Morpho-Anatomical Adaptation against Salinity." In (Ed*.), Plant Defense Mechanisms.* IntechOpen.

Vicente E., Didion-Gency M., Morcillo L., et al., 2022. "Aridity and cold temperatures drive divergent adjustments of European beech xylem anatomy, hydraulics and leaf physiological traits." *Tree Physio,* 42(9):1720-1735.

Volkov V and Beilby MJ 2017 Editorial: "Salinity Tolerance in Plants: Mechanisms and Regulation of Ion Transport." *Front. Plant Sci*, 8:1795.

Vries J.D., Curtis B.A., et al.,2018. "Embryophyte stress signaling evolved in the algal progenitors of land plants". *Proceedings of the National Academy of Sciences of the United States of America,* 115(15): 3471-3480.

W, Jia., M Ma., J Chen., S, Wu., 2021. "Plant Morphological, Physiological and Anatomical Adaption to Flooding Stress and the Underlying Molecular Mechanisms." *Int J Mol Sci,* 22(3): 1-24.

Wahab., Abdul & Abdi., Gholamreza & Hamzah Saleem., et al., 2022. "Plants' Physio-Biochemical and Phyto-Hormonal Responses to Alleviate the Adverse Effects of Drought Stress: A Comprehensive Review." *Plants (Basel, Switzerland),* 11(13):1620.

Wielkopolan B, Jakubowska M and Obrepalska-Ste˛plowska A 2021. "Beetles as Plant Pathogen Vectors." *Front. Plant Sci,* 12:748-093.

Z, Xin., W, Jingang., F, Shuang., et al., 2022. "Morphological and physiological responses of Dianthus spiculifolius high wax mutant to low-temperature stress." *Journal of Plant Physiology*, vol 275:153-762.

Zhang, H., Liu, X. L., Zhang, R. X., Yuan, H. Y., Wang, M. M., Yang, H. Y., Ma, H. Y., Liu, D., Jiang, C. J., & Liang, Z. W. 2017. "Root Damage under Alkaline Stress Is Associated with Reactive Oxygen Species Accumulation in Rice (*Oryza sativa* L.)." *Frontiers in plant science,* 8:1580.

Zhao, S., Zhang, Q., Liu, M., Zhou, H., Ma, C., & Wang, P. 2021. "Regulation of Plant Responses to Salt Stress." *International journal of molecular sciences,* 22(9):4609.

Zwart RS, Thudi M, Channale S, Manchikatla PK, Varshney RK and Thompson JP 2019 "Resistance to Plant-Parasitic Nematodes in Chickpea: Current Status and Future Perspectives." *Front. Plant Sci,* 10:966.

CHAPTER TWO

PLANT STRESS AND HIDDEN ADAPTATION MECHANISMS

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Numerous biotic and abiotic stresses impact development, growth, and productivity in plants. In order to deal with all of these challenges, plants have to create effective coping mechanisms that allow them to adapt and defend themselves in stressful conditions, by either tolerating or avoiding stress. These adaptation techniques operate at the molecular, physiological, morphological, anatomical, and biochemical levels. Some of the modifications/mechanisms used by plants to adapt to and defend against environmental stress include molecular reactive oxygen species (ROS) signalling, the accumulation of plant hormones, changes in redox status and inorganic ion fluxes, R-gene resistance, and systemic acquired resistance (SAR).

Introduction

Stress can be defined as a stimulus or influence that is outside the normal range of homeostatic control in a given organism. If a plant is exposed to extreme stress conditions that are beyond its tolerance level, mechanisms are activated at the morphological, physiological, biochemical and molecular levels. Once the stress is reduced, a new physiological state is established and the plant may return to its original state, thereby reestablishing homeostasis (Fraire-Velazquez et al., 2011). Plants being sessile organisms face many environmental challenges from biotic and abiotic factors. In the course of evolution, plants have developed highly sophisticated and efficient strategies to cope with environmental stress imposed by nature. Even though plant species vary in their sensitivity and responses to various environmental stresses, they have developed numerous adaptation mechanisms to encode stress perception, signalling cascades, and gene transcription networks in response to environmental cues (Fu and Dong, 2013; Sanghera et al., 2011).

Major mechanisms underlying environmental stress adaptations and defences include: reactive oxygen species (ROS) signalling; accumulation of plant hormones, such as salicylic acid, ethylene, jasmonic acid, and abscisic acid (Wani and Kumar, 2015); changes in redox status and inorganic ion fluxes; molecular crosstalks; epigenetic modifications; and R-gene resistance and systemic acquired resistance (SAR), etc. (Kissoudis et al. 2014). Physical barriers, such as the cuticle, stomata, and cell walls, are also important for timely pathogen recognition and interception (Asselbergh et al. 2007).

This chapter has elaborated how morphological, anatomical, biochemical, and molecular adaptation strategies against different plant abiotic stresses occur. It also discussed molecular crosstalks and epigenetic modifications for stress responses and adaptations in plants.

Plant Responses to Water Stress

Drought: Physiological Responses

Mineral Nutrition

In agricultural fields, environmental conditions like drought may result in nutritional deficiencies, since each nutrient's capacity to be absorbed depends on the physicochemical makeup of the soil. The availability of nutrients in the soil declines with a fall in water availability, which lowers the nutrient concentrations in plant tissues. A shortage of water has a substantial effect on how nutrients are absorbed by the roots and transferred to the shoots. Drought stress has been shown to increase nitrogen (N) content and reduce phosphorus (P) content, while generally having little effect on potassium (K) content in plants. It has also been demonstrated that drought stress lowers calcium (Ca) levels in plants. The durability of membranes in the roots plays a crucial role in ensuring that plants receive the right amount of mineral nutrients. However, the first targets of many stresses, such as water stress, are cell membranes.

As a result, maintenance of membrane stability is a crucial element of plant drought resistance. Under drought stress, damaged cell membranes are a major contributor to disordered ion balances in plants. Insufficient root functioning and sluggish water diffusion rates under drought stress render roots incapable of receiving nutrients from the soil. Stomatal closure, decreased transpiration, and limited transfer of nutrients from the roots to the top sections of plants are all consequences of water scarcity. As such, when there is a water shortage, there is less availability of soil nutrients and less uniformity in the way that nutrients are transported in plants. All of these factors have a severe impact on plant development, affecting a number of physiological processes.

Stomatal Movement

The closure of stomata is the chief physiological reaction of plants to water deficiency. By decreasing transpirational water losses, plants conserve cellular water levels. This conservation is generated by either hydropassive or hydroactive processes. Water deficit conditions can induce abscisic acid (ABA) generation, which leads to stomatal closure and stimulates the expression of drought stress-associated genes for the regulation of plant responses. The accumulation of ABA in plant cells leads to ROS production. Hydrogen peroxide (H_2O_2), an important ROS, participates in various plant metabolic reactions, stress responses, and apoptosis. Additionally, H_2O_2 takes part in the modulation of stomatal movement. The relationship between ABA and H_2O_2 plays an important role in responding to water deficient conditions. ABA stimulates H_2O_2 production in guard cells through the action of NADPH oxidase and H_2O_2 imparts ABA-generated closure of stomata.

Drought: Biochemical Reactions of Plants

Oxidative Stress and the Antioxidant System

Through the production of ROS, drought causes oxidation in plant cells (with superoxide radicals, hydrogen peroxide, hydroxyl radicals, and singlet oxygen). Several physiological and metabolic processes, including photosynthesis and the antioxidant defence system, are negatively impacted by ROS formation in plants. These processes include lipid peroxidation, chlorophyll disintegration, membrane destabilisation, and ion leakage. Under normal circumstances, a balance between ROS generation and scavenging results in a steady-state cellular ROS level. However, this equilibrium shifts under other strains, such as drought stress, where more ROS are produced than are scavenged leading to oxidative stress. Additionally, an early spike in ROS synthesis, prior to the point at which its production outpaces scavenging activity, can serve as a signalling mechanism for defensive measures.

In addition to being a negative impact of stress, ROS also contribute to growth and development. ROS, such as H_2O_2, have been shown to participate in root growth, root hair elongation, and radicle emergence during seed germination. They also play a part in pathogen defence during seed germination. H_2O_2 is a good candidate for signalling due to its relative stability versus other ROS and ability to permeate through cell membranes. For signalling, whether under stressful circumstances or in response to growth and development responses, the site and level of ROS production should be highly restricted.

The cell wall is one of the essential sites where defence responses through the action of ROS are engaged. In this compartment, the most exposed enzyme for the generation of ROS is NADPH oxidase, which produces $O_2^{\bullet -}$. Spontaneously or by the action of cell-wall located SOD, this is dismutated to H_2O_2. Apart from functioning as an ROS detoxifier, wall-bound peroxidases also play a role in ROS signalling with the production of ROS like $O_2^{\bullet -}$ and H_2O_2. The latter may also function as the substrate for lignin, which is essential for cell wall composition. Cellular ROS signalling peculiarities can be ascertained according to the site of their production, control, and transduction. Different plant cell compartments will have distinct impacts on the regulation of cellular redox signals under water deficit conditions. Downstream signalling of ROS or hydrogen peroxide occurs through calcium and reversible protein phosphorylation. Under environmental stress conditions, alterations in cytosolic free calcium ([Ca^{2+}] cyt) have been seen.

To enhance the influx of Ca^{2+}, ROS (including H_2O_2) can stimulate plasma membrane-localized hyperpolarization-activated calcium channels (HACCs). Intracellular Ca^{2+} can also establish a positive feedback loop by prompting NADPH oxidase to generate ROS in the apoplast. Reversible protein phosphorylation, on the other hand, has been revealed to be required in downstream signalling after the production of ROS, and a number of protein kinases have been shown to be induced by H_2O_2. However, such activation does not occur through the action of Ca^{2+}, and no Ca^{2+}-dependent kinase has been described under H_2O_2 regulation. Moreover, various studies have associated H_2O_2 with a mitogen-activated kinase (MAPK) signalling cascade, which regulates gene expression through the stimulation of transcription factors. Such modulated genes appear to play a role in cellular protection and repair processes because some of the gene products are known to play a role in desiccation tolerance and DNA damage repair. A cDNA microarray study in *Arabidopsis* revealed the upregulation of 113 genes and downregulation of 62 genes by the action of H_2O_2, suggesting that it has a key role in governing plant drought responses regulating Ca^{2+} signalling, MAPK cascades, and gene expression.

Plants that lack water, however, have developed a number of strategies to deal with shortages. Osmotic control and the antioxidant system are the two main defence mechanisms that give crops resistance to water stress conditions. Enzymatic antioxidants include catalase, peroxidase, superoxide dismutase, glutathione reductase, ascorbate peroxidase, and glutathione peroxidase; while non-enzymatic antioxidants include ascorbate, glutathione, and phenolic compounds. The balance between ROS formation and antioxidant system scavenging determines how much harm the ROS can do. In the presence of ROS, which results in the dismutation of O_2 radicals into H_2O_2, SOD serves as the first line of defence. H_2O_2 is detoxified by CAT and APX, which also prevent its accumulation.

Numerous non-enzymatic antioxidants, including flavonoids, tannins, and lignin precursors, actively contribute to the removal of ROS and hence reduce oxidative stress. Together, these antioxidants drive a variety of redox processes. Phenolic chemicals have also been found to be important for detoxifying the hydrogen peroxide cascade in plant cells. Total SOD and APX activities in rice (*Oryza sativa*) were reported to increase as water scarcity increased. Similarly, during drought stress, barley showed an increase in SOD, CAT, and APX activity. According to reports, drought stress raises SOD and POD activity in maize plants (*Zea mays*), and the accumulation of acetylsalicylic acid (ASA) further boosts enzyme activity.

The Molecular Mechanism for Drought Responses in Plants

When exposed to drought, plants undergo a variety of molecular adaptations that alter the water content of the soil. In these circumstances, numerous genes are up and down-regulated at the transcriptional level, responding to stress, and the buildup of stress proteins works effectively for drought tolerance. Different dehydration-responsive element-binding genes have been shown to be involved in signalling pathways during abiotic stress, such as drought. The adverse impacts of drought stress on plants include ROS-mediated cell damage, increased cellular temperature and viscosity of cellular contents, and altered protein interaction, aggregation, and denaturation.

Plant biotechnologists have developed improved cultivars with high drought tolerance through the application of various molecular methods, including transcriptomics, proteomics, and metabolomics, in order to combat the damaging effects of drought stress on crops. According to several reports, plants alter the expression of a number of genes through a complex transcriptome network in response to water stress situations. Many physiological, cellular, and molecular processes, such as the up or downregulation of the expression of different genes responsible for osmolyte accumulation, increased content of enzymatic and enzymatic antioxidants, and decreased rates of transpiration, growth of shoots, and tillering, are responsible for the expansion of drought tolerance in plants. A higher concentration of abscisic acid (ABA) is crucial for closing stomata in response to water stress (**figure 5**). This regulates the expression of various stress-response genes. However, the expression of drought-receptive genes is also controlled by a system that is ABA-independent.

Numerous key protein-coding genes display drought-assisted expression and play a metabolic or regulatory role. For example, genes responsible for detoxification, the biosynthesis of osmolytes, water channels, ion transporters, heat shock proteins, and the proteolysis of cellular substrates and proteins are related to late embryogenesis. Furthermore, those genes having regulatory roles mainly comprise transcription factors (i.e., AREB, NAC, AP2/ERF, MYC, MYB, and bZIP); mitogen-activated protein kinases (MAPK); and those responsible for different cellular signalling pathways; protein kinases related to ribosomes, receptors, and the transcriptional regulated system and proteins responsible for synchronization of signal transduction (phosphatases). Various osmotic stress-response genes have been identified as playing a vital role in the expression of enzymes responsible for the induction of the ABA biosynthetic pathway and synthesis of different osmoprotectants like glycine betaine (GB), ectoine, mannitol, trehalose, and proline, thereby maintaining the correct osmotic balance under stressful conditions.

The signalling pathways of various abiotic stresses, including drought stress, involve some common key steps. Foremost is the perception of stress stimuli via sensors or receptors, which are localized in the plasma membrane or exist freely in the cytosol. The second is the transduction of signalling via secondary messengers. Once the perception of a stress stimulus occurs, secondary messengers are activated, like calcium ions, cyclic nucleotides (cAMP, cGMP), nitric oxide, sugars, and ROS, etc. Secondary messengers then activate the signalling pathway via modulation of the expression or repression of various genes that are responsive to different stresses. Protein kinases and phosphatases cause phosphorylation and de-phosphorylation, respectively, of the proteins involved in the signalling pathway (i.e., receptors, secondary messengers, and transcription factors). MAPKs and CDPKs are two protein kinases that play a vital role in the regulation of the drought stress-mediated signalling pathway.

Some transcription factors (TFs) synchronise the expression of a collection of downstream genes by directly interacting with the cis-acting regions present in the promoter regions of those genes. Additionally, a number of TFs are controlled by enhancers found in the gene's upstream region. The post-transcriptional modifications, ubiquitination, and sumoylation form a network of regulatory complexes that are crucial to controlling the stress-response genes in charge of numerous physiological and metabolic processes in plants. Numerous TFs, including AREB/ABF, AP2/ERF TFs, NAC TFs, and Bzip, have been discovered and characterised in many plants that exhibit up-regulation in response to drought stress.

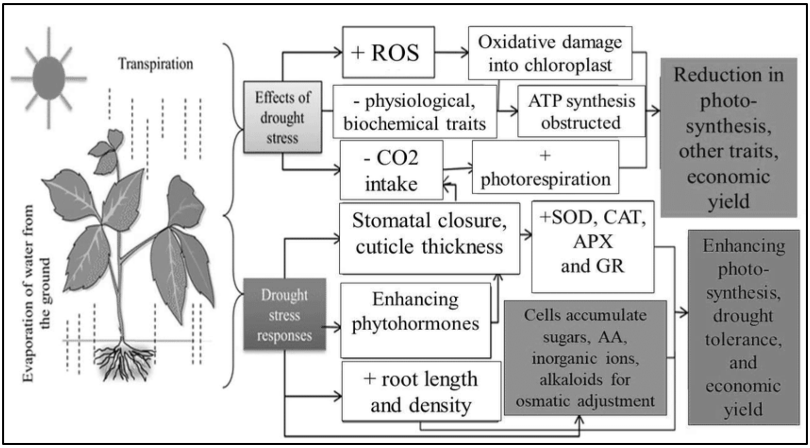

Figure 5. Adverse effects and adaptations of plants to drought stress

Plant Responses to Flooding Stress

Flooding is a natural occurrence that has adverse effects on plant growth and development. Many mechanisms of plant adaption to flooding stress have been discovered on the morphological, physiological, and anatomical scales.

The Morphology of Plants under Flooding Stress

Generally, flooding stress triggers adaptive changes in plant roots and shoots at the morphological scale, such as the formation of ARs, the growth of shoots being inhibited or accelerated. Previous studies have investigated plant responses to flooding stress in some important crops, including wheat, maize, rice, and soybean. For instance, wheat, as a dryland crop, is very sensitive to flooding stress. When exposed to waterlogging, the dry mass of wheat shoots and roots, as well as the ratio of roots to shoots was found to decline significantly compared to controls, indicating that root growth was inhibited more than shoot growth. Maize has been found to be intolerant of waterlogging stress with the trefoil stage being the most sensitive period. Waterlogging was found to inhibit growth in maize resulting in reduced plant height, ear height, dry weight, leaf area index, and grain characteristics (such as grain number per ear and 1,000-grain weight). Additionally, the amount of chlorophyll, soluble sugar, and starch in leaves, stems, and roots has also been found to decrease under waterlogging stress.

Many lowland cultivars of rice are susceptible to submergence stress and thus struggle to survive if heavy rain persists for a long period of time. However, several rice cultivars can experience flash-flooding conditions (complete submergence) for around two weeks by restricting shoot elongation, as well as carbohydrate consumption, and will recover once the flood waters recede. In contrast, deep water rice, which has adapted to submergence, is able to maintain its top leaves in the aerial environment to capture sufficient oxygen by rapidly elongating its internodes. The growth and yield of soybean is also affected by flooding. At the seedling stage, root growth in soybean has been found to be severely suppressed after prolonged submergence for 10 days. Different soybean genotypes utilize distinct mechanisms to resist waterlogging stress and proteins associated with energy metabolism are thought to operate in ensuring soybean tolerance to flooding stress.