Phytohormones in Abiotic Stress

Edited by
Dhandapani Raju, R Ambika Rajendran,
Ayyagari Ramlal, and Virendra Pal Singh

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Plants are continuously exposed to different environmental stresses that negatively impact their physiology and morphology, resulting in production reduction. As a result of constant pressure, plants evolve different mechanisms for sustenance and survival. Hormones play a major role in defences against the stresses and stimulate regulatory mechanisms. One of the ways through which they mitigate stress is via the production of hormones like auxins, ethylene, jasmonic acid, etc. The phytohormones help in signaling and enhance the chances of their survival. Plant hormones play many vital roles from integrating developmental events, physiological and biochemical processes to mediating both abiotic and biotic stresses. This book aims to highlight these issues and provide scope for the development of tolerance in crops against abiotic stresses to maximize yield for the growing population. There is an urgent need for the development of strategies, methods and tools for the broad-spectrum tolerance in plants supporting sustainable crop production under hostile environmental conditions.

The salient features are as follows:

- It includes both traditional and non-traditional phytohormones and focuses on the latest progress emphasizing the roles of different hormones under abiotic stresses.
- It provides a scope of the best plausible and suitable options for overcoming these stresses and puts forward the methods for crop improvement.
- It is an amalgamation of the biosynthesis of phytohormones and also provides molecular intricacies and signalling mechanisms in different abiotic stresses.
- This book serves as a reference book for scientific investigators from recent graduates, academicians and researchers working on phytohormones and abiotic stresses.

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Foreword

In an ever-changing world, where environmental uncertainties are bound, the remarkable tenacity of plant life takes the central stage. Plants, as the silent sentinels of nature, continually confront various challenges that test their growth and productivity. They stand as nature, unwavering soldiers, facing adversities head-on. Unlike mobile creatures, plants are sessile. They cannot escape harsh climatic conditions or environmental stresses. Instead, they have evolved ingenious strategies to withstand these challenges. Yet, these stresses, which encompass waterlogging, searing heatwaves, relentless droughts, cold and salt-riddled soils, continue to thwart their full potential. Abiotic stresses remain among the leading causes of global crop losses. Amid these trials, plants deploy a remarkable defence mechanism – phytohormones. These natural chemical messengers, including auxins, ethylene, gibberellins, cytokinins and jasmonic acid, emerge as the plants' allies. Phytohormones serve as signals of distress and hope, enhancing the plant's chances of survival.

Phytohormones play pivotal roles in the intricate tapestry of plant life. They integrate developmental events, orchestrate physiological processes and steer biochemical reactions. Moreover, they serve as mediators in the face of both abiotic and biotic stresses, offering a multi-faceted defence mechanism. As our world grapples with the urgent need for sustainable agriculture, the quest for strategies, methods and tools to bolster broad-spectrum resistance in plants becomes paramount. Crop failures loom large and the demand for increased food production to meet the needs of a growing global population continues to surge. It is a race against time, exacerbated by the diverse abiotic stresses triggered by a fluctuating climate, often driven by human activities. Studies have unveiled the pivotal roles of various plant hormones, such as brassinosteroids, strigolactones and jasmonates, in orchestrating responses to environmental stimuli. These hormones act as the plant's vigilant guardians, ready to trigger adaptive measures when adversity strikes.

In this context, *Phytohormones in Abiotic Stress* takes root. This book seeks to provide an extensive exploration into the world of phytohormones and their utility in bolstering plant tolerance to abiotic stresses. Tailored for agriculturalists and plant physiologists, it navigates the latest discoveries and insights into the roles of hormones in mediating responses to environmental challenges. In addition to unravelling the discoveries, this book offers a spotlight on the most promising approaches to combat the challenges that lie ahead. It serves as a beacon of knowledge in an era where resilience in agriculture is non-negotiable. The book will provide a wide coverage of phytohormones and their utility in the development of abiotic stress tolerance in plants in light of the current knowledge on the subject for agriculturalists and plant physiologists. The book deals with recent and cutting-edge updates about the discoveries and information about the role of hormones in mediating environmental stresses. It will also highlight and provide updated information on the most plausible approaches to combat the challenges.

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Preface

Plants are continuously facing and exposed to different environmental stresses. Plants, being sessile, need to develop strategies to overcome these harsh climatic conditions and stresses such as waterlogging, heat, drought, cold and salinity are some of the primary causes of crop losses globally. One of the ways through which they mitigate stress is via the production of hormones like auxins, ethylene, gibberellins, cytokinins, jasmonic acid and others. The phytohormones help in signalling and their production enhances their chances of survival. Apart from that, these hormones play many vital roles from integrating developmental events and physiological and biochemical processes to mediating both abiotic and biotic stresses. There is an urgent need for the development of strategies, methods and tools for the broad-spectrum resistance in plants supporting sustainable crop production under hostile environmental conditions.

Keeping the above objective, this book has been designed to provide wide coverage on phytohormones and their utility in the development of abiotic stress tolerance in plants. The efforts are made to include the sheer breadth of plant physiology with special reference to hormones and abiotic stress and the rapidly increasing knowledge in the field makes it impossible to include all of the relevant material in an entry-level text. Consequently, in light of the current knowledge on the subject, the broad scope of the field, ranging from molecular, environmental physiology, agronomy and genetics, makes it useful for agriculturalists and plant physiologists.

This edition is comprised of three units: *Introduction*, *traditional phytohormones* and *non-traditional phytohormones*. All efforts are made to retain the readability and overall approach.

Dhandapani Raju
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Editors

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Dr Dhandapani Raju is a senior scientist of plant physiology in the Division of Physiology, Indian Agricultural Research Institute (ICAR-IARI), Delhi, India. He is a post-doctoral fellow at the agricultural laboratory, College of Agriculture, Food and Natural Resources, University of Missouri. He completed his undergraduate in agriculture from Tamil Nadu Agricultural University (TNAU), Tamil Nadu, India. He pursued his post-graduate in agriculture with a specialization in plant physiology from C. S. Azad University of Agriculture and Technology, Uttar Pradesh, India. He completed his doctoral degree in plant physiology from the Indian Agricultural Research Institute. He has been awarded "young scientist" by the Indian Society of Plant Physiology, New Delhi, India, for his outstanding work on phenotyping banana fruits and identifying vitamin A enrichment gene (phytoene synthase gene) for the first time in bananas. His academic achievements are evident from possessing various awards, scholarships and merit medals (book prizes, ICAR-JRF, IARI-SRF and ICAR-ARS) at the national level during post-graduate education. He is the recipient of several best poster and oral presentation awards at the national level. Through agricultural research and development, he has invented five technologies, registered three international patents and published more than 15 peer-reviewed articles in both international and national journals of repute. He has currently been working on high throughput phenotyping of rice plants for drought tolerance for the last four years. He has hands-on experience in the phenotyping of whole-plant transpiration and developed the software for automatic and near real-time estimation of WUE in rice. He has hands-on experience in both structural and functional genomics techniques for nucleic acid isolation, quality testing and gene expression analysis. He is also involved in teaching and guiding students at the post-graduation level. He has guided nine MSc students to date. He has conducted three national-level trainings for professionals at state and central levels. Currently, he is working on a national-level multi-institutional project on plant phenomics to develop rice and wheat varieties with improved water use efficiency and nitrogen use efficiency.

Dr R Ambika Rajendran is a senior scientist of plant breeding in the Division of Genetics, Indian Agricultural Research Institute (ICAR-IARI), Delhi, India. She earned her bachelor's from Tamil Nadu Agricultural University (TNAU), Tamil Nadu, India in 2003, her master's from Kerala Agricultural University (KAU), Kerala, India in 2005 and obtained her doctorate in 2010 from Tamil Nadu Agricultural University (TNAU). She joined the Directorate of Maize Research (DMR), New Delhi (currently referred to as Indian Institute of Maize Research IIMR, Punjab, India) in 2009 till 2016; later, she joined the Division of Genetics, IARI as a scientist in a senior scale in 2016. She has over 15 years of research experience. She currently works in abiotic stress tolerance and doubled haploidy in soybeans. She worked in maize breeding for high oil along with baby corn. Her significant research includes heterotic grouping and patterning of quality protein maize using molecular markers, in vitro mutagenesis in rice and identification of sources of high oil post-*Fusarium* stalk rot resistance genetic stocks in maize and identification of tolerant sources for pre-germination anaerobic stress tolerance in soybean. She has edited two books, *Genetics and Breeding in Pulses* and *Handbook of Cereals*, and also served as an editor for a book on *Soybean*. She has many peer-reviewed research articles published in journals of international and national repute and book chapters to her credit. She is also serving as a reviewer in various national and international journals.

Mr Ayyagari Ramlal is a doctoral scholar at the Plant Biotechnology Laboratory, School of Biological Science, Universiti Sains Malaysia, Malaysia. He completed his bachelor's and master's in botany from the University of Delhi, Delhi, India in 2017 and 2020, respectively. He has worked as a junior research fellow at the Division of Genetics, Indian Agricultural Research Institute

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Dr Virendra Pal Singh completed his PhD in plant physiology and has over 35 years of research and 27 years of teaching experience. His areas of specialization include post-harvest and seed physiology, abiotic stress and climate change. He is a fellow at the Indian Society for Plant Physiology and served as the editor of the *Indian Journal of Plant Physiology* for nine years and national consulting editor for the *Advances in Plant Physiology* series (ten volumes). He is a gold medallist in MSc in botany with a specialisation in plant physiology. He was awarded a Council of Scientific and Industrial Research (CSIR) fellowship for PhD and post-doctoral. He was awarded the Emeritus Professorship by the Indian Council of Agricultural Research (ICAR), Delhi, India. He worked on an Indo-U.S. project on tropical climate and he has supervised nine PhD and three MSc students and trained many agricultural research service (ARS) scientists. He served as an advisor in various committees of Agricultural Universities and Institutes and Staff Selection Commission, India. He has more than a hundred publications to his credit.

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Unit I

Introduction

1 Introduction to Phytohormones

Ayyagari Ramlal, Ambika Rajendran, Dhandapani Raju, and Virendra Pal Singh

1.1 INTRODUCTION

A hormone is described as “a chemical which, being created in any one area of the organism, is transported to another portion and there regulates a specific physiological process“ by Went and Thimann in 1937. These chemical messengers work in coordination through which the activity of specific organs is coordinated with that of other organs (Went & Thimann, 1937; Ghorbel & Brini, 2021). The term “hormone” and its concept came into existence based on the observation made by Sachs 1880–1893. He stated, “Morphological differences between plant organs are due to differences in their material composition” (Sachs, 1893; Went & Thimann, 1937; Davies, 2010). The majority of plant cells seem to be able to create most hormones with varied transport routes, and they can impact both the cell from where they originated and distant cells. The term “hormone“ has become widely accepted to describe these molecules in plants because there are significant similarities between the roles of hormones in animals and plants, including that they are active in very small quantities and serve as chemical signals (as opposed to having nutritional or catalytic functions). According to Went and Thimann (1937), “To prevent any potential misunderstanding with animal systems, the word phytohormones has been created for similar compounds in plants” (Weyers & Paterson, 2001). The prefix, however, may be dropped as this book will exclusively cover the plant kingdom. The five traditional plant hormones that were discovered at the start of the mid-20th century are widely mentioned, namely ethylene (1901 by D. Neljubow (Abeles & Heggestad, 1973), auxins (discovered in 1926 by Fr. Went (Moore & Moore, 1979)), gibberellins (1926 by E. Kurosawa (Armstrong, 1958)), cytokinins (discovered in the 1950s by F. Skoog (Skoog et al., 1966)) and abscisic acid (ABA; 1950s, T. Bennett-Clark and N. Kefford (Sacher, 1980)). Other substances that fit the definition of hormones have been discovered over the past 50 years. Brassinosteroids (BRs) (Fujioka & Sakurai, 1997; Fujioka & Yokota, 2003), jasmonates (JAs) (Howe, 2004), salicylic acid (SA) (Raskin, 1992), oxylipins (Blee, 2002), strigolactones (SLs) (Xie et al., 2010), karrikins (Nelson et al., 2009), indolamines (IAs) (Dowling & Ehinger, 1978), nitric oxide (NO) (Herbette et al., 2003) and peptide hormone (PH) (Gancheva et al., 2019) are some of the most recently discovered non-traditional phytohormones. Phytohormones serve a variety of purposes, including cell division, elongation, differentiation, and overall growth; additionally, they impact seed germination, root and shoot development, flowering, fruiting and stress responses, and they all have a significant impact on growth and development. From seed to seed, hormones have an impact on the life cycle of plants and how they react and interplay with the biotic and abiotic factors. Unraveling the roles of phytohormones has been challenging due to their pleiotropic effects, and it is still one of the most active areas of plant biology study. The study of plant hormones and the genes that govern their synthesis, transport and after-effects has discovered several new tools for agricultural advancements because of their core functions as integrators and regulators. This chapter briefly discusses the biosynthesis, evolution and purposes of both conventional and non-traditional plant hormones. Their functions and roles will also be discussed. The molecular mechanisms and proteins that underlie the

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production, activity and interactions between each of the key hormones will be covered in greater detail in the following chapters of the book, with special reference to abiotic stress factors.

1.2 TRADITIONAL PHYTOHORMONES

1.2.1 Auxins

Auxins were the first essential plant hormone identified. Auxins are a class of plant hormones (or plant growth regulators) and they possess distinct morphogenetic characteristics that contribute significantly to various aspects of plant development (George et al., 2008). Darwin (1880), initially made his observations about the presence of some chemical entity that led to the bending of grass coleoptile (Darwin, 1880). Dutch biologist Frits Warmolt Went initially described auxins and their role in plant growth in the 1920s and isolated auxin based on the decapitated coleoptile and named it *Wuchsstoff* (and later changed to auxin from auxien meaning to grow) (Davies, 2010; Jiang et al., 2017). Went isolated for the first time one of these phytohormones and determined their chemical structure as indole-3-acetic acid (IAA). Auxin occurs in all parts of a plant but at varying concentrations and is closely linked through metabolism and transport (Simon et al., 2011). Auxins play a crucial role in coordinating growth and behavioral processes in plant life cycles and are essential for the development of the plant body. The distribution pattern of auxin in the plant is a critical factor for the plant's growth, its reaction to the environment and, in particular, the development of the plant organs. All auxins are made of an aromatic ring and a carboxylic acid group at the molecular level (Taiz & Zeiger et al., 1998). The most prominent member of the auxin family, indole-3-acetic acid (IAA), causes most of the auxin effects in intact plants. It is the most potent native auxin (Benková et al., 2003) and synthesized from the precursor, tryptophan (Trp) via the Shikimate pathway.

1.2.2 Gibberellic Acid

Gibberellic acid (also gibberellins A3, GA and GA3) is a hormone found in plants and fungi (Silva et al., 2013). GA promotes elongation and germination of stems and, in some plants, flowering and development of fruits. Manipulating the GA levels through genetic variation or chemical application of synthetic GA or GA inhibitors are standard farming practices to optimize plant growth and yield. The development of semi-dwarf cereal varieties with an attenuated response to stem elongation was the most important achievement of agricultural practices of the 20th century. It significantly increased the yield of global crops (Claeys et al., 2014). The characteristic response to GA-induced stem lengthening was first investigated in rice plants infected by the fungus *Gibberella fujikuroi*, which produces GA. Subsequently, the compound responsible for stem elongation was purified and characterized, and shortly thereafter, GAs were found in non-infected plant extracts. The ability of purified GAs to restore wild-like growth in dwarf pea mutants and corn mutants was essential to their recognition as endogenously produced plant hormones. These mutations and radioactive tracers have been used to gradually identify the biosynthetic pathway for GA production (Hedden et al., 2012). This process converts trans-geranylgeranyl diphosphate into bioactive GA (GGDP). Terpene synthases (TPSs), cytochrome P450 monooxygenases (P450s) and 2-oxoglutarate-dependent dioxygenases are employed in the MEP route to produce GA from GGDP (2ODDs). Gibberellins play a role in germination, including the natural breaking of dormancy. The GA produced in the scutellum diffuses to the aleurone cells, where it stimulates the secretion of alpha-amylase, as shown by the model for the gibberellin-induced synthesis of alpha-amylase. When a plant is subjected to low temperatures, a larger quantity of gibberellins is produced. They encourage germination, fruit ripening without seeds, breaking and blossoming and cell elongation (Yamaguchi et al., 2008). It produces an enzyme to promote growth in the embryo when its hormone interacts with a receptor, calcium activates the protein calmodulin and the complex binds to DNA.

1.2.3 Cytokinins

A group of plant hormones known as cytokinins (CKs) encourages cytokinesis, or cell division, in the roots and shoots of plants (Aina et al., 2012). Expanding on Haberlandt's results, Jablonski and Skoog observed in 1954 that the chemical that triggered cell division in the pith cells was also present in the vascular tissue (Haberlandt, 1913; Jablonski & Skoog, 1954; Mok et al., 2000). Miller et al. (1955) extracted autoclaved herring fish sperm DNA in crystalline form and discovered and improved the cell division component. This active ingredient was named "Kinetin" and became the first cytokinin, due to its ability to promote cell division (Miller et al., 1955; Schaller et al., 2015). Eventually, 6-furfuryl-amino purine was found to be kinetin. Later, it was suggested to include kinetin and other substances with comparable properties under the umbrella word *kinin*. By simultaneously isolating and crystallizing zeatin from the milky endosperm of corn (*Zea mays* L.) in the 1960s, Miller and Lethum isolated the first naturally occurring cytokinin (Lethum, 1967; Miller, 1971; Großkinsky & Petrášek, 2019). In the production of isoprene cytokinins, the first reaction is catalyzed by the adenosine phosphate-isopentenyl transferase (IPT). As prenyl donors, it may utilize dimethylallyl pyrophosphate (DMAPP) or hydroxy methylbutenyl pyrophosphate (HMBPP) in addition to ATP, ADP, or AMP as substrates. The rate-limiting step in the production of cytokinin is this process. The methylerythritol phosphate route generates DMADP and HMBDP, which are necessary for cytokinin production (MEP). Recycled tRNAs can also be used by bacteria and plants to make cytokinins. tRNAs with anticodons that begin with uridine and carry prenylated adenosine close to the anticodon release when the adenosine is broken down as a cytokinin. These adenines are prenylated by tRNA-isopentenyl transferase (Koprna et al., 2016). CKs were later discovered to delay leaf senescence, which has been reported to improve plant drought tolerance.

1.2.4 Ethylene

Unique among plant hormones, ethylene (C_2H_4) is a simple two-carbon gaseous phytohormone. Being gaseous, ethylene can freely travel between cells and is often produced at the site of action. It can gather in specific places and spread out quickly (Wang et al., 2018). These gaseous qualities are believed to influence their roles in coordinating fruit ripening and reactions to injury, mechanical impedance and stress (Polko et al., 2019). Through complex positive and negative feedback networks, transcriptional and posttranscriptional mechanisms and response pathways, ethylene synthesis and levels are closely regulated. Working together, these regulatory systems allow for a rapid and precise ethylene response. These regulatory systems work together to make a very quick and accurate ethylene response (Pandey et al., 2021). By enhancing fruit ripening, postponing senescence and producing plants that are more tolerant to stress, understanding and controlling ethylene biosynthesis and actions can significantly affect agriculture and horticulture (Hartman et al., 2019).

The enzyme methionine adenosyl transferase catalyzes the first reaction in the ethylene biosynthesis from the methionine to S-adenosyl-L-methionine (SAM). The enzyme 1-aminocyclopropane-1-carboxylic acid (ACC) synthase (ACS) then converts SAM to ACC and 5′-methylthioadenosine (MTA). The rate at which ethylene is produced depends on ACS activity. Therefore, controlling this enzyme is essential for the production of ethylene (Hartman et al., 2021; Pattyn et al., 2021). The penultimate stage involves the ACC-oxidase (ACO), formerly known as the ethylene-forming enzyme, and necessitates oxygen. Either endogenous or exogenous ethylene can stimulate the production of ethylene (Cho et al., 2022). High amounts of auxins, particularly IAA and CKs, promote ACC production. The majority of plants fight salinity through the hormone ethylene. Through a complicated signaling mechanism, ethylene controls plant growth and development and helps plants adapt to stressful situations (Maric et al., 2022).

1.2.5 Abscisic Acid

The primary hormone that regulates a plant's capacity for survival in a harsh, fluctuating environment is the abscisic acid (ABA). Plants create more ABA when under water stress, which causes them to respond by closing their stomata to stop sweating and expressing genes that make osmoprotectants (Zhang et al., 2021). ABA triggers similar genes in mature seeds, and it is assumed that these genes endow the developing embryo with desiccation tolerance (Jones et al., 2014). In addition, ABA controls seed dormancy and germination, assists in controlling development and takes part in biotic stress reactions (Wang et al., 2016). Since the 1980s, molecular genetics techniques in *Arabidopsis thaliana* and other plants have added to the ongoing efforts to elucidate the pathway for ABA production. At the beginning of the 21st century, after more than 40 years since ABA (abscisic acid) was first studied, scientists had completely figured out how it's made and used in plants. It's hard to highlight Jan Zeevart's exact role in understanding ABA because many scientists from around the world, working in different places, have contributed a lot to this knowledge (Waadt et al., 2014). ABA is an isoprenoid plant hormone that is made in the plastidial 2-C-methyl-D-erythritol-4-phosphate (MEP) pathway. In contrast to sesquiterpenes, which are structurally related but are made from the mevalonic acid-derived precursor farnesyl diphosphate (FDP), the C15 backbone of ABA is developed after cleavage of C40 carotenoids in MEP. Zeaxanthin is the first committed ABA precursor; subsequent oxidation of xanthoxin to ABA occurs as a result of a sequence of enzyme-catalyzed epoxidations and isomerizations via violaxanthin and final cleavage of the C40 carotenoid by a deoxygenation process through ABA (Bassaganya et al., 2011).

1.3 NON-TRADITIONAL PHYTOHORMONES

1.3.1 Jasmonates

Jasmonates (or jasmonic acid; JA) are oxylipins that are produced when a lipoxygenase oxidizes a polyunsaturated fatty acid (Caarls et al., 2015). The biological activity of the jasmonate family of chemicals, which are produced from JA, varies. Since JA itself has a very modest level of activity, the term "prohormone" has been used occasionally to describe it. Methyl jasmonate (MeJA) is the volatile methyl ester of JA (Acosta & Farmer, 2010). In 1962, MeJA was purified to describe jasmonate hormones for the first time. MeJA has a pleasant aroma and is volatile, like many mild esters. The jasmine blossom, *Jasminum grandiflorum* L., was used to extract and purify it (Demole et al., 1962; Sharma & Laxmi, 2016). Later, the metabolic process for the synthesis of jasmonates as well as the biological functions of jasmonates was discovered. Its function in plant defensive responses was discovered in the 1980s, and subsequently, the receptor protein and signal transduction pathway were discovered (Shitan et al., 2013). Plastid-localized lipases are necessary for JA production and to be quickly triggered by injury. Jasmonates are derived from a-linolenic acid, an octadecanoid fatty acid with three unsaturated double bonds, by the majority of higher plants; OPDA is converted to jasmonate in the peroxisome (Hsieh et al., 2014). JA controls a wide range of physiological functions in plants, but its impact on wound healing is best understood. After being mechanically injured or being eaten by a herbivore, JA biosynthesis is quickly stimulated, which causes the production of the necessary response genes. After playing a defense-related role, JAs have also been linked to cell death and leaf senescence (Schaller et al., 2009). JA can interact with a wide variety of kinases and transcriptional regulators linked to senescence. By causing the buildup of reactive oxygen species (ROS), JA can potentially cause mitochondrial apoptosis. These substances cause apoptosis, or programmed cell death, which compromises cells by damaging mitochondrial membranes (Reinbothe et al., 2009). The functions of JAs in these processes point to strategies by which the plant protects itself against biotic threats and restricts the spread of diseases.

1.3.2 Brassinosteroids

The sixth class of plant hormones has been identified as the brassinosteroids (BRs, or less frequently, BS), a subclass of polyhydroxysteroids (Khripach et al., 2000). They might be useful as an anticancer medication for malignancies that respond to endocrine hormones to trigger apoptosis and stop growth. Mitchell et al. (1970) observed that treating organic extracts of rapeseed pollen resulted in stem lengthening and cell proliferation, and sparked the first investigation into brassinosteroids. The biologically active molecule, called brassinolide, was discovered in 1979 when stem elongation and cell divisions were observed in rapeseed pollens (Grove et al., 1979; Karssen et al., 2012). All plant species contain brassinosteroids involved in disease resistance, vascular differentiation, development, light responses and growth. Brassinosteroids were initially discovered in 1979. Campesterol is used in the biosynthesis of BR. The BR biosynthesis mutants in *Arabidopsis*, tomatoes, and peas were studied to see whether the biosynthetic route that Japanese scientists had described was accurate. No experimental proof has been provided to back up the sites of BR synthesis in plants. The expression of BR biosynthetic and signal transduction genes in various plant organs lends credence to the idea that all tissues produce BRs. Additionally, this is supported by the hormones' short-range action (Lalarukh et al., 2022). The flow is from the base to the tips, and experiments have demonstrated that long-distance transfer is feasible (acropetal). If this movement is meaningful in terms of biology is yet unknown (Tossi et al., 2015). Under deficit irrigation system, BR effectively reduces drought stress and enhances wheat growth. Due to its crucial role in lowering oxidative stress indicators, it also exhibited additional favorable effects on raising plant development metrics. BRs may be found in plants like the bean using some bioassays.

1.3.3 Karrikins

A class of plant growth regulators known as karrikins is discovered in the smoke produced while burning plant matter (Flematti et al., 2015). Karrikins imitate strigolactone, a signaling hormone that aids in promoting seed germination and plant growth. Strigolactones are hormones that support the formation of symbiotic arbuscular mycorrhizal fungus in the soil, which in turn promotes plant growth and branching (Andreo-Jimenez et al., 2015). The heating or burning of carbohydrates, including sugars and polysaccharides, mostly cellulose, results in the formation of karrikins (Barickman et al., 2013). These sugars become karrikins when plant material burns. Karrikins' pyran moiety is most likely directly generated from pyranose sugar. Although karrikins are not known to naturally occur in plants, it has been hypothesized that karrikin-like compounds do exist in plants (Gutjahr et al., 2015). Karrikins are said to promote seedling vitality and stimulate seed germination. Karrikins affect the photomorphogenesis of seedlings in *Arabidopsis*, resulting in shorter hypocotyls and bigger cotyledons (Van Staden et al., 2006). Such reactions could be advantageous for seedlings when they emerge into the post-fire landscape. Since the KAI2 protein is also necessary for the formation of leaves, karrikins may impact several other aspects of plant development.

1.3.4 Oxylipins

A series of oxygenated natural products known as oxylipins are created from fatty acids by chemical reactions, including at least one stage of dioxygen-dependent oxidation (Wasternack et al., 2007). Plant growth and biotic/abiotic stress responses are known to be regulated by oxylipins (Wasternack & Feussner, 2018; Wasternack & Strnad, 2018). Polyunsaturated fatty acids (PUFAs) are converted into oxylipins by cyclooxygenases (COX), lipoxygenases (LOX) or cytochrome P450 epoxygenase (Barquissau et al., 2017). Numerous aerobic creatures, such as fungi, mammals and plants, produce oxylipins. Numerous oxylipins are important physiologically (Bolwell et al., 2002). Dioxygenases or monooxygenases initiate the biosynthesis of oxylipins. The