# Tariq Aftab Khalid Rehman Hakeem Editors

# Plant Growth Regulators Signalling under Stress Conditions



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Signalling Under Stress Conditions



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(1908–1999)

Hakim Abdul Hameed was a great philanthropist, thinker, visionary, an Indian physician of the traditional medicine system of Unani, founder-chancellor of Jamia Hamdard, and a former chancellor of Aligarh Muslim University, India. He was honored by the Government of India in 1965, with the award of Padma Shri, the fourth highest Indian civilian award, and in 1992, the government awarded him the third highest Indian honor of Padma Bhushan.

## Preface

Agriculture faces many challenges to fulfil the growing demand for sustainable food production and ensure high-quality nutrition for a rapidly growing population. To guarantee adequate food production, it is necessary to increase the yield per area of arable land. A method for achieving this goal has been the application of growth regulators to modulate plant growth. Plant growth regulators (PGRs) are substances in specific formulations which, when applied to plants or seeds, have the capacity to promote, inhibit, or modify physiological traits, development, and/or stress responses. They maintain proper balance between source and sink for enhancing crop yield. PGRs are used to maximize productivity and quality, improve consistency in production, and overcome genetic and abiotic limitations to plant productivity. The use of PGRs in mainstream agriculture has steadily increased within the last 20 years as their benefits have become better understood by growers. Unfortunately, the growth of the PGR market may be constrained by lack of innovation at times when increase in demand for new products requires steady innovation and discovery of novel, cost-competitive, specific, and effective PGRs. It is expected that the need to raise agricultural production will lead to the increased use of plant growth regulators. They may make it possible to grow crops, changing the crop's time pattern so that it can mature and be harvested before adverse conditions. The effects of PGRs on plant functions such as root induction, control of flowering, sex expression, maturation, and aging have been documented, with many horticultural examples.

Apart from well-known PGRs, which are mostly plant hormones, there are a number of substances/molecules such as nitric oxide, hydrogen sulfide, seaweed extracts, melatonin, plant growth promoting rhizobacteria, etc., which act as PGRs. These novel PGRs, or biostimulants, have been reported to play important roles in stress responses and adaptation. They can protect plants against various stresses, including water deficit, chilling and high temperatures, salinity, and flooding.

The present book covers a wide range of topics, discussing the role and signalling of traditional as well as novel PGRs in challenging environments. Moreover, this will be a unique reference book on topics discussing the use of PGRs with latest biotechnological and omics approaches. In this volume, we highlight the working solutions as well as open problems and future challenges in PGR research. We believe that this book will initiate and introduce readers to state-of-the-art developments and trends in this field of study.

The book comprises 21 chapters, most of them being review articles written by experts, highlighting a wide range of topics, discussing the role and regulation of PGRs in plants under stressful conditions. We are hopeful that this volume furnishes the need of all researchers working or are interested in this particular field. Undoubtedly, this book will be a helpful general source of reference for research students, teachers, and those who have interest in PGRs.

We are immensely grateful to all our contributors for accepting our invitation for not only sharing their knowledge and research, but for venerably integrating their expertise in dispersed information from diverse fields in composing the chapters and enduring editorial suggestions to finally produce this venture. We also thank the Springer Nature team for their generous cooperation at every stage of the book production.

Lastly, thanks to well-wishers, research students, and authors' families for their moral support, blessings, and inspiration in the compilation of this book.

Aligarh, India Jeddah, Saudi Arabia Tariq Aftab Khalid Rehman Hakeem

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So far, Dr. Hakeem has authored and edited more than 50 books with international publishers, including Springer Nature, Academic Press (Elsevier), and CRC Press. He also has to his credit more than 110 research publications in peer-reviewed international journals and 60 book chapters in edited volumes with international publishers.

At present, Dr. Hakeem serves as an editorial board member and reviewer of several high-impact international scientific journals from Elsevier, Springer Nature, Taylor & Francis Group, Cambridge, and John Wiley Publishers. He is included on the advisory board of Cambridge Scholars Publishing, UK. He is also a fellow of Plantae group of the American Society of Plant Biologists, member of the World Academy of Sciences, member of the International Society for Development and Sustainability, Japan, and member of Asian Federation of Biotechnology, Korea. Dr. Hakeem has been listed in Marquis *Who's Who in the World* since 2014. Currently, Dr. Hakeem is engaged in studying the plant processes at eco-physiological as well as molecular levels.

# **Chapter 1 Prospective Role of Plant Growth Regulators for Tolerance to Abiotic Stresses**



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#### Abbreviations

ABA	Abscisic	acid
ADA	AUSCISIC	aciu

- ACC Aminocyclopropane carboxylic acid
- ARFs Auxin response factors
- AXs Auxins
- BRs Brassinosteroids
- CGR Crop growth rate
- CKs Cytokinins
- EPS Exopolysaccharides

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ET	Ethylene
GAs	Gibberellins
ISR	Induced systematic resistance
JAs	Jasmonates
LAI	Leaf area index
NAR	Net assimilation rate
PGRs	Plant growth regulators
RNA	Ribonucleic Acid
ROS	Reactive oxygen species
SA	Salicylic acid
SLs	Strigolactones
VOCs	Volatile organic compounds

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#### 1.1 Introduction

Several climate models predict a sharp decline in crop productivity owing to changing climate across the globe which may jeopardize the food security of increasing population (Battisti and Naylor 2009; IPCC 2014). The arid and semi-arid regions are expected to confront increasing desertification due to global warming and fluctuation of rainfall distribution leading to a decrease in the area under plow (Agbola and Ojeleye 2007). Another manifestation of climate change is a severe intensity and more frequent incidence of abiotic stresses especially drought, salinity, heat, and heavy metals toxicities, which are projected to drastically plummet staple crops' productivity. Heat stress alters the constancy of numerous proteins, RNA species, and construction of cytoskeleton along with reducing the effectiveness of several enzymatic activities which results in unbalancing of metabolic activity. The net result of heat stress is cell death especially at the reproductive growth stage which leads to complete crop failure. Similar to heat stress, drought negatively affects and even halts vital molecular, biochemical, physiological, and morphological processes in plants. Moreover, salinity is equally harmful to crops as it leads to osmotic stress and salt-induced ion toxicity (Munns 2005). These types of stresses are linked to unwarranted Cl<sup>-</sup> and Na<sup>+</sup> toxicity, leading to the deficiency of Ca<sup>2+</sup> and K<sup>+</sup> along with other macro- and micronutrients (Marschner 1995). The ROS-mediated ion toxicity leads to chlorosis and necrosis which hamper photosynthesis by accumulating Na<sup>+</sup> and ultimately inhibits numerous physio-biochemical activities in plants (Munns 2002; Kundu et al. 2018).

Plant growth regulators (PGRs) have become commercialized in some countries to improve the productivity of crops (Jahan et al. 2019; Iqbal et al. 2015). These PGRs play essential functions in modulating growth and development of plant by inducing morphological, physiological, and molecular adaptations under stressful environment (Iqbal et al. 2018; Afzal et al. 2015). Previous studies showed that PGRs bolster plant defense system (Iqbal 2015; EL Sabagh et al. 2019a, b, c) against plant pathogenic bacteria, which need alive cells to finish their life cycle (Bari and Jones 2009). Wani et al. (2016) studied that plant growth hormone is a signaling molecule of natural origin, recognized to play a vital and complex role in regulating boom, physiology, development, morphology, and response to abiotic stress. Plant growth regulator acts as a sign of transduction agent in a very complicated way (Iqbal 2014), keeping plant life sustainably optimal during growth and development, and is consequently considered to be the principal thing in plant reaction to abiotic and biotic stresses (Bücker-Neto et al. 2017; Pál et al. 2018a, b). Therefore, several hormonal signaling pathways are integrated to modulate different stress responses, in turn triggering stress tolerance mechanisms under changing climate; it will play a key role in environmental security.

This chapter synthesizes and critically evaluates the drastic impact of abiotic stresses especially heat, drought, and salinity on plant growth and development. In addition, PGRs' role in ameliorating the negative effects of abiotic stresses by imparting stress tolerance through morphological, physiological, and biochemical

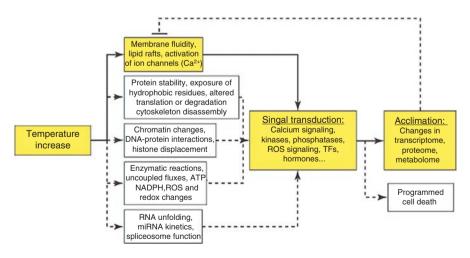
alterations has been objectively analyzed. An attempt through the synthesis of available literature has been made to develop PGRs as an effective and biologically viable tool to cope with abiotic stresses under changing climate leading to bolstering food and nutritional security of populace.

#### **1.2** Abiotic Stress Effects on Crops

#### **1.2.1** Temperature Fluctuations

Heat stress can have a hostile effect on almost all aspects of growth and development of plants (Mittler and Blumwald 2010; Lobell et al. 2011). For example, in the last three decades (1980–2008), wheat and maize yield were decreased by approximately 5.5 and 3.8% due to heat stress (Lobell et al. 2011). Generally, stage-specific, most of the plant is vulnerable to the temperature above or below its optimum levels; particularly the reproductive stage is more sensitive (Zinn et al. 2010). Heat stress alters the constancy of numerous proteins, RNA species, and construction of cytoskeleton, reduces the effectiveness of several enzymatic activities, and also unbalances metabolic activity (Ruelland and Zachowski 2010; Suzuki et al. 2011); ultimately cell death occurs as a result of excessive production of reactive oxygen species (ROS) (Mittler et al. 2012; Fig. 1.1). Although, a direct association exists between heat-induced ROS and plant survive to heat stress (Ruelland and Zachowski 2010; Suzuki et al. 2011).

Rising temperature results in cell death owing to water scarcity to plants (Radin et al. 1994; Grill and Zeigler 1998; Hetherington and Woodward 2003). For



**Fig. 1.1** A schematic model for temperature sensing in plants. Increases in ambient temperature affect many different processes (Modified, Mittler et al. 2012)

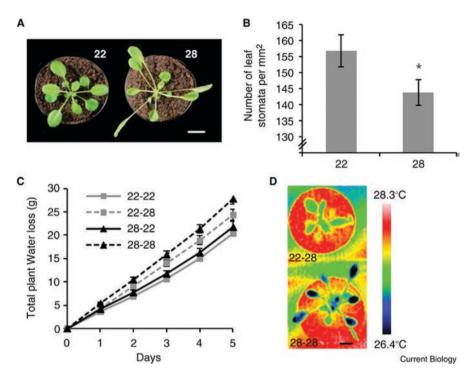


Fig. 1.2 The increasing temperature increased the transpiration and also enhanced the leaf cooling capacity of *Arabidopsis thaliana*. (Adapted from Crawford et al. 2012 with permission)

example, Crawford et al. (2012) observed the effect of heat stress-induced expansion on plant water usage approach in Fig. 1.2 (a–c). It has been observed that the growth of *Arabidopsis*, at heat stress (28 °C), results in improved water loss, conspicuous elongation of stems, improved leaf cooling capacity in these conditions, and enlarged leaf advancement from the soil surface, regardless of producing fewer leaf surface pores (stomata) (Crawford et al. 2012).

#### 1.2.2 Drought Stress

Similar to heat stress, drought is also a big threat in agriculture, particularly in arid or semi-arid regions where rainfall is scarce and available water is limited (Silva et al. 2011; Barutcular et al. 2016, 2017). It is the greatest devastating stress and could cause a reduction in crop productivity (Molla et al. 2019). Since drought has an unfavorable consequence on agricultural ecosystems, it leads to a thoughtful threat to sustainable crop production systems all over the world (Kogan et al. 2019).

Plants need available water and nutrition throughout the life cycle (Taiz and Zeiger 2006; Ajum et al. 2011), and their reduction consequently affects all molecular, biochemical, physiological, and morphological processes in plants (Sarker et al. 2005; Sircelj et al. 2005; Silva et al. 2009). It is documented that drought could cause nutrient deficiency, even in the fertile soil, due to the reduction of nutrient movement and absorbance from the soil solution to the root systems (Silva et al. 2011).

Drought induces the secondary stress known as oxidative stress (Da Silva et al. 2013), leading to the excess generation of ROS, lipid peroxidation, and membrane injury, ultimately causing cell death (Abid et al. 2018). The plants survive in drought-induced oxidative stress in various ways such as altering growth pattern, phenology, phenotype, and morphology, and also follow several physiological mechanisms (Zandalinas et al. 2018), such as increasing enzymatic and non-enzymatic antioxidant activities (Da Silva et al. 2013; Abid et al. 2018). Lipid per-oxidation increased in growth phases of maize, while antioxidant enzyme activities especially superoxide dismutase reduced in the last phases (Li-Ping et al. 2006; Abdelaal et al. 2017).

#### 1.2.3 Salinity Stress

Among the abiotic stresses, soil salinity is another abiotic limitation that has threatened the agricultural productivity worldwide, predominantly in arid and semi-arid regions (Hussain et al. 2009; Huang et al. 2019; Yassin et al. 2019). It is estimated that approximately 800 million ha of arable lands across the globe are affected by soil salinity (Munns and Tester 2008). Under soil salinity, generally, plants face two types of stress such as osmotic stress and salt-induced ion toxicity (Munns 2005) which are linked with unwarranted Cl<sup>-</sup> and Na<sup>+</sup> toxicity, leading to the deficiency of Ca<sup>2+</sup> and K<sup>+</sup> and also other nutrients (Marschner 1995). ROS-mediated ion toxicity leads to chlorosis and necrosis (hampered the photosynthesis), as a result of the higher accumulation of Na<sup>+</sup> which inhibits numerous physio-biochemical activity in plants (Munns 2002; Kundu et al. 2018).

The damaging effect varies depending on growth environment, climatic conditions and genotypes (Islam et al. 2011; Tang et al. 2015). Based on salt-tolerant ability, generally, plants can be classified into three categories: glycophytes, euhalophytes, and halophytes (Munns 2005; Koyro 2006; Stepien and Johnson 2009; Tang et al. 2015). Glycophytes cannot grow in the presence of high salt levels (Munns and Termaat 1986); euhalophytes can grow in a medium level of salinity through developing different types of mechanisms (Larcher 2003); halophytes can be grown under high concentrations of NaCl (300–500 mM) as they could establish better salt resistance mechanisms (Parida and Das 2005; Flowers and Colmer 2015).

#### 1.3 Overview of PGRs Under Stressful Environment

The plant hormones commonly related to stress responses are abscisic acid (ABA) (Suzuki et al. 2016), ethylene (ET) (Dubois et al. 2018; Debbarma et al. 2019), salicylic acid (SA) (van Butselaar and Van den Ackerveken (2020), etc. While ABA has been mainly involved in the regulation of abiotic stress responses, ET, SA, and JA have been associated with responses of defense against pathogens, insects, or wounding. Auxins (AXs), cytokinins (CKs), gibberellins (GAs), brassinosteroids (BRs), and strigolactones (SLs) are also required in stress-triggered responding networks (Korver et al. 2018; Kanwar et al. 2017).

ABA is a molecule classified as sesquiterpene, and it is accumulated in plants growing under abiotic stressful conditions, which activates several responses. When the environment is optimal, ABA levels are reduced to promote plant growth. Regulations of ABA levels are essential for balancing defense and growth processes when plants are exposed to stressful environments (Vishwakarma et al. 2017). ABA levels are finely regulated by their biosynthesis, degradation or conjugation reactions, and the control of conjugate or free ABA transport to hormone action sites. The gene-encoding enzymes involved in ABA biosynthesis are upregulated under adverse environmental conditions, and it leads to an increase of ABA synthesis and/ or a decrease of ABA catabolism and regulates numerous ABA-mediated stress responses (Finkelstein 2013; Waadt et al. 2014; Tan et al. 2018). ABA-mediated responses involve a change in several proteins and anion channels for stomatal closure reducing the transpiration and water loss and limiting the carbon dioxide availability, which leads to reduced photosynthetic performance and increased ROS production (Mittler and Blumwald 2015).

ABA signaling begins with ABA receptors identified as RCAR/PYR1/PYL (regulatory components of ABA receptor/pyrabactin resistance 1, and protein/PYR-like proteins) receptors and protein phosphatases of type 2C (PP2C) as ABA receptors (Tischer et al. 2017). Binding of ABA to the receptor allows blocking of the active site of phosphatases and the release of a protein kinase from the PP2C complex. This protein kinase is part of sucrose non-fermenting-1 (SNF1)-related protein kinase 2 s (SnRK2s) subfamily which functions as link between guard cell movement and ABA signaling (Mittler and Blumwald 2015). ABA promotes the stomatal closure through a ROS wave, which allows the regulation of ROS-regulated Ca<sup>2+</sup> channels and the generation of synthesis of new ROS (Drerup et al. 2013). PP2C complex can be inhibited by the action of ROS; thus, ROS and ABA interact in a positive regulation triggering the stomatal closure and inducing the specific gene expression during stressful conditions (Mittler and Blumwald 2015). Furthermore, it has been reported the essential role of ABA signaling mediated by the SnRK2s modulating the tricarboxylic acid cycle and metabolism of organic acids involved in osmotic stress tolerance mechanisms (Thalmann et al. 2016). In addition, ABA homeostasis and signaling are modified by the presence of other PGRs. For example, ABA accumulation and upregulation of ABA signaling are affected by the synthesis of JAs in plants under dehydration treatments; both hormones trigger several drought plant responses (de Ollas and Dodd 2016).

Ethylene (ET) is a gaseous hormone with the simple  $C_2H_4$  structure; it increased the response to multiple stressful environmental conditions, such as salinity, drought, exposure to heavy metals, and high temperatures, among others (Llanes et al. 2016; Savada et al. 2017; Dubois et al. 2018). ET biosynthesis consists in the conversion of methionine into S-adenosyl methionine, which is turned to an aminocyclopropane carboxylic acid (ACC) by the action of ACC-synthase (ACS) enzyme. The induction and activation of ACS are regulated by environmental factors that trigger ET accumulation. For example, ACS genes are transcriptionally upregulated by drought (Dubois et al. 2017). In destination organs, ET triggers a signaling cascade through ethylene receptors, ERS1 and ERS2 (ethylene response sensor), ETR1 and ETR2 (ethylene resistance), and EIN4 (ET insensitive). In the absence of ET, these active receptors subsequently bind to kinase protein (CTR1), but in the presence of ET, it relieves CTR1 inhibition, and these receptors induce the expression of numerous transcription factors. Ethylene response factors (ERFs) have been reported as the last downstream components of ET signaling pathways (Meng et al. 2013). ERFs play essential functions in the abiotic stress responses through the regulation of several stress tolerance genes (Klay et al. 2018). Therefore, this hormone regulates leaf development and some senescence mechanisms and processes such as fruit ripening and germination in some species under stressful conditions, being ACC a long-distance root-sourced signal under stress.

SA is involved in numerous plant growth responses, such as photosynthesis, ionic homeostasis, and seed germination. In recent years, there have been increasing reports about SA new roles in plants under different environmental stresses (Ghassemi-Golezani et al. 2016; Singh et al. 2017). Foliar application of SA in soybean plants exposed to different levels of salinity enhanced the quantity and quality of several proteins (Farhangi-Abriz and Ghassemi-Golezani 2016). Exogenous SA increases the physiological, yield, and growth parameters in wheat plants under drought treatments (Kareem et al. 2017), while JAs are involved in diverse developmental processes regulating several responses to biotic and abiotic stress conditions, mediating defense responses against pathogens and herbivores, and controlling growth and reproductive development (Pérez-Salamó et al. 2018). Farhangi-Abriz and Ghassemi-Golezani (2018) reported that foliar sprays of SA and JAs reduce the sodium influx to cells of leaves and mitigate the oxidative and osmotic damages by the enhancing antioxidant enzyme activities and increasing glycine betaines, carbohydrates, and proteins in soybean plants under salinity. The JAs and SA signaling pathways were characterized in Arabidopsis plants in response to stressful environments (Ahmad et al. 2016; Zhou et al. 2019; Fu et al. 2020). It has been suggested that both PGRs induce antioxidant system genes that help to eliminate ROS. Indeed, studies on JAs signaling in wheat plants under different stress conditions demonstrated that JA is involved in the induction of some antioxidant systems to cope with the stress (Kang et al. 2013; Qiu et al. 2014; Shan et al. 2015). There are several evidence that JAs and SA may have convergence points with ABA generating a complex and integral network for abiotic stress responses (Zhao et al. 2014; Prodhan et al. 2018). Future researches in hormonal signaling may be explored to elucidate the links between SA, JAs, and ABA and the multiple stresses abiotic responses.

Modifications in plant architecture and growth pattern of plants under stressful environment are regulated by AX and CK pathway. The action of AXs has been found to be antagonistic to CKs (Bielach et al. 2017). Different plant tissues during stressful environment decrease the synthesis and signaling of AXs and CKs to increase the ABA sensitivity for the regulation of abiotic stress responses (Rowe et al. 2016; Abid et al. 2017). Thus, stress-induced growth inhibition involves the repression of AX- and CK-responsive genes. For example, Pospíšilová et al. (2016) described that the transgenic barley plants overexpressing a CK dehydrogenase gene showed greater tolerance to drought conditions. These transgenic plants showed altered root morphology resulting in better dehydration avoidance. In addition, some studies demonstrated that components of cytokinin signaling, such as cytokinin oxidase/dehydrogenase genes, are regulated by ABA (Huang et al. 2018). Recently, Bouzroud et al. (2018) reported that auxin response factors (ARFs) are involved in auxin signaling in tomato plants responses under stressful environments.

Brassinosteroids are a group of PGRs classified as polyhydroxy steroidal compounds with strong growth and development promoting potential. More than 70 compounds have been identified from plants, being 28-homo-brassinolide, 24-epibrassinolide, and brassinolide the most bioactive compounds isolated (Vardhini and Anjum 2015). BRs play an essential role in several developmental processes such as shoot and root growth, floral initiation, and fruit development. Recent studies have shown the potential of BRs in the induction of components of antioxidant defense mechanisms decreasing ROS accumulation and increasing the protection of photosystems in plant abiotic stress responses (Vardhini and Anjum 2015; Sharma et al. 2017). Moreover, BRs could modify the architecture of cellular walls and the adjustment of cellular membranes to preserve the functionality of membranes during adverse environmental conditions. Indeed, BRs signaling have been reported to be critical for inducing expression of several enzymes involved in the loosening and extension of cellular walls (Guo et al. 2009) and increasing of pectin methylesterases enzymes (Yang et al. 2014), which are associated with the stress tolerance mechanisms. BRs also regulate several stress-responsive transcription factors by a negative regulator of BRs signaling called BIN2, which can regulate some transcription factors that activate numerous stress tolerance genes (Xu et al. 2015; Eremina et al. 2016; Chen et al. 2017).

Strigolactones (SLs) constitutes a small group of PGRs represented by carotenoid-derived compounds. SLs are germination-stimulating compounds in root parasitic plants such as *Striga*, *Orobanche*, and *Phelipanche* species (López-Ráez et al. 2017). Application of SLs in some plants suggests that SLs could play essential roles in the tolerance of abiotic stress factors, by regulating growth and development responses, source/sink transitions, and nutrient distribution (Saeed et al. 2017). SLs signaling and their action on the architecture of plants implicate that SLs interact with other PGRs, particularly AXs and ABA (Cheng et al. 2013) although there is emerging evidence for cross-talk between the signaling and function of SLs.

#### 1.4 PGR-Induced Changes in the Agronomic Traits of Crop

Exogenous application of plant growth hormone like SA produces resistance against several abiotic stresses like moisture deficiency, salt stress, high-temperature stress, and heavy metal stress (Singh and Usha 2003). Earlier studies also showed that exogenous application of salicylic acid increased the resistance in *Cicer arietinum* against moisture stress (Khan et al. 2017) as well as also mitigated the drastic effects of lead (Pb) and mercury (Hg) (Kim et al. 2014). Putrescine (Put) also played a positive role in minimizing the drastic effects of abiotic pressures on crops by its acidic neutralization and stabilized capability of the cell membrane (Zhao and Running 2010). Application of plant growth regulator Put enhanced resistance in plants against moisture stress, ROS production, salt stress, and low-temperature stress in various plants (Duan et al. 2008). In spite of producing resistance against abiotic stresses, plant growth regulators also play an imperial role in various growth phases of plants (Pal et al. 2015).

#### 1.4.1 Interactive Effect of PGRs on Growth and Yield Traits

In legumes, leaf area index and other growth-related traits were affected by various PGRs (Ullah 2006). Plant growth-related parameters like leaf area index (LAI), leaf area duration, crop growth rate (CGR), net assimilation rate, and total dry matter production were significantly affected by plant growth regulators. Grain yield is directly proportional to LAI, CGR, and net assimilation rate (NAR). Yield and quality traits of *Cicer arietinum* were significantly influenced by plant growth regulators, and also PGRs increased protein synthesis, seed yield, and straw production (Kumar et al. 2003). PGR application with twice rate increased bud's retention percentage (Gupta et al. 2007). Neelima et al. (2006) revealed that triacontanol alone or with KNO<sub>3</sub> improved pod development, hundred-grain weight, biomass, HI, as well as grain yield at harvest as well as reduced leaves senescence in *Cicer arietinum*. Rao et al. (2005) studied that yield-related traits including floral sustainability, pod formation percentage, pod number, and grain weight were increased by application of gibberellic acid and cystocele levels.

#### 1.4.2 Role of PGRs in Plant Physiology

#### 1.4.2.1 Role of PGRs on Chlorophyll Contents

Chaloupkova and Smart (1994) revealed that the application of plant growth regulators and other inputs like pesticide application usually declined chlorophyll pigments. Additionally, chlorophyll pigments also were suppressed by the AA application. Samet and Sinclair (1980) studied that application of abscisic acid causes falling of older leaves, while newborn leaves have little effect of abscisic acid. Xanthophyll intermediate produces abscisic acid. Taiz and Zeiger (2010) studied that chloroplasts and other plastids are the hosts for producing early phases of abscisic acid.

#### 1.4.2.2 Role of PGRs in Photosynthesis

Giordano et al. (2000) observed that in legume crops due to sulfur (a growth hormone) deficiency exhibited minimum growth and photosynthetic efficiency. Li et al. (2007a, b) revealed that sulfur in the liquid condition of apoplast induces ROS that decreases photosynthetic efficiency of the plant and ultimately reduces plant yield. Root/shoot ratio is increased by kinetin application that may be accredited to cytokinins regulating photosynthesizing activity due to kinetin treatment that is associated with improving total biological yield with the rise in photosynthesizing activity. Application of cytokinins promoted photosynthesis efficiency mainly by means of improvement in leaf chlorophyll content (Caers and Vendrig 1986).

#### 1.4.2.3 Role of PGRs on Protein Contents

Gupta et al. (2007) observed positive effect of plant growth regulators on the protein content in *Cicer arietinum*. Cumulative effects of plant growth regulators and sulfur on maximizing content of protein in *Cicer arietinum* also as reported by Yadav and Bharud (2006) through combined foliar application of gibberellic acid, NAA and cycoel, benzyladenine, biforce, and biopower. Mandavia et al. (2006) reported that foliar-applied SA and brassinolide improved protein contents in chickpea seeds. Ali and Bano (2008) documented that at flower initiation and grain formation stage, maximizing protein concentration and sugars contents of leaves are directly proportional to nodule activity; therefore, reduction in chlorophyll contents and protein contents become more vulnerable in older leaves than younger leaves.

#### 1.4.3 Role of PGRs in Nodule Formation

Effects of PGRs (indoleacetic acid, gibberellic acid, and kinetin) on hemoglobin synthesis in *Cicer arietinum* nodules were noticed that almost all growth regulators showed an overall positive influence on the synthesis of hemoglobin (Jain et al. 2008). Scherer and Lange (1996) studied that kinetin is a plant growth regulator which improved the efficiency of nitrogenase enzyme of root nodules of *Cicer arietinum* as well as improved the biomass of pink bacterial tissues; it also enhanced leg hemoglobin percentage and nodule bacterial treatments over control. Kinetin causes increase in leg hemoglobin content and nodule bacteroid region over the

control. The nitrogen-fixing capacity of sulfur-deficient plants is significantly reduced, which is an important factor for the low level of nodule development and low production of nitrogenase and hemoglobin (Ereifej et al. 2001). Ali and Bano (2008) revealed that nodule formation is positively affected by exogenous application of ABA and kinetin in *Cicer arietinum*.

#### 1.5 Impact of PGRs on Abiotic Stress Tolerance

The prospective roles of PGRs for abiotic stress tolerance and their earlier evidence are discussed in Table 1.1.

#### 1.5.1 Impact of PGRs on Drought Stress Tolerance

Various abiotic stresses like moisture deficiency are ameliorated by the application of ABA (Keskin et al. 2010). High cellular ABA promotes changes in stomatal conductance, root hydro-conductivity, photosynthesis, distribution of biomass between roots and shoots, water family members of plants, the formation of osmolytes, and the synthesis of stress-touchy proteins and genes to ensure resistance to moisture stress (Finkelstein et al. 2008; Kim et al. 2010). Water stress produces abscisic acid accretion in the leaves of many plants (Upreti and Murti 2005; Satisha et al. 2005). The increase in ABA allows flora to restrict water loss via transpiration after the stomata are closed and improves the plant's water reputation after the underpinning hydraulic conductivity increases (Thompson et al. 2007). Zhang et al. (2006) observed that abscisic acid also plays an important role in the transfer of materials from roots to stem by regulating stomatal conductance, allele exhibition, and catabolic variations under moisture deficit conditions.

#### 1.5.2 Role of PGRs on Salt Stress Tolerance

The role of PGRs in regulating various physiological and biochemical processes and physiological characteristics of numerous crops underneath salt strain has been broadly elucidated (Fatma et al. 2013). The concentration of these plant genetic resources in plants may be a determinant of increased tolerance/sensitivity because the expression of stress-related proteins in crops is increased under stress conditions (Hamayun et al. 2010).

Due to the different plant growth regulators, plant growth may change under a persistent salt environment (Iqbal et al. 2012). Jackson (1997) proposed that changes and reductions in plant growth under stress are attributed to low endogenous levels of plant growth regulators. The exogenous application of plant growth regulators