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Plant Growth Regulating Phytohormones: The Potent Targets to Alleviate Abiotic Stress in Crop Plants —A Research Update and the Way Forward

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Abstract

The latest modifying models of global climate have changed to be an unadorned threat to the crops production. An extensive scale of biotic and abiotic stresses frequently impacts crop plants because of their stalkless characteristics. Crop plants failures are principally triggered by abiotic factors such as salt, heat, cold, floods, ultraviolet radiation and drought. For dealing with these harsh conditions, well-established mechanisms have been developed in plants, which perform a pivotal role in comprehending stress signals and assisting ideal development responses. Remarkably, the exploitation of plant growth regulating phytohormones for decreasing the adverse effect of abiotic stress has acquired much attention in current decades. For evasion of stress at various levels, including physiological, molecular, and biochemical, an erudite method is informed to be presented by phytohormones. Thus, labeling these phytohormones plays an important function in plant growth and overall development. Phytohormones can progresses tolerance against abiotic stresses by raising seed germination, seedling growth, root growth, leaf photosynthesis and antioxidant enzymes by dropping the accretion of reactive oxygen species, malonaldehyde, and electrolyte outflow. Current findings focus on the important function of a diversity of phytohormones counting, Abscisic acid (ABA), Salicylic acid (SA), Jasmonates (JA) and Ethylene (ET) in the abiotic stress tolerance improvement of crop plants. The contribution of Cytokinins (CKs), and some other novel phytohormones such as Brassinosteroids and Strigolactones in plant development has been acknowledged under normal and stress conditions. Therefore, this review is desired to recap the new progresses in the knowledge associated to phytohormones and their association in abiotic stresses of expectation, signaling, crosstalk, and the response processes. Therefore, such a review will be helpful in improving the pathway for sustainable agriculture development via involvement of phytohormones in improvement of abiotic stress tolerance of the crop plants.

Keywords: phytohormones, plant growth regulators, abiotic stress, plant tolerance, crop breeding.

1. Introduction

Sudden climate changes or seasonal fluctuations in weather cause severe challenge for the existence to crop plants. Meanwhile, these are stalkless organisms, they must deal with such ecological hostile situations. Among several ecological variations water logging, drought, high salinity, heat stress, cold stress and solar radiation are harmful for plant growth and development (Raza et al., 2020; Hossain et al., 2021). Therefore, these factors are causing reductions in crop production at a comprehensive scale (Achard et al., 2006; Gururani, Venkatesh, & Tran, 2015). Due to these dangerous surroundings, different abiotic stresses co-happen. For instance, salt stress can be often linked with drought (Ashraf & Foolad, 2007; Aslam et al., 2012; Slama et al., 2015). The lethal impact of salt has a harmful effect on root extension, and it regulates the capability to uptake water and nutrients Plants advanced effectual signaling, and response methods for dealing with these harmful conditions. Among these the utmost noticeable instances of these response methods applied by plants which is epitomized by the Phytohormones (PHs), and it can be well-defined as signal molecules of cell that performance as the chemical messengers in plants which have dominant roles in the rule of the response that plant display to the abiotic stresses (Fleet & Sun, 2005; Davies, 2010; Williams, 2011), This signaling pathways are joined in a complicated network which restrain physical or morphological activities to rapidly adjust to the ecological stresses. Previous study identified, plants have five resistance-associated metabolites against the abiotic stresses: the cuticle, reactive species scavengers, unsaturated fatty acid, compatible solutes, and molecular chaperones (proteins and subcellular structures stabilization). These self-protective metabolites are synchronized by an intricate controlling network that contains the involvement of the upriver signaling molecules as reactive oxygen species (ROS), hydrogen sulfide (H2S), stress PHs, polyamines (PAs), nitric oxide (NO), phytochromes, and calcium, as well as transcription factors (TFs) (M. He, C. Q. He, & Ding, 2018). Currently, nine PHs have been identified including auxins, cytokinins (CKs), salicylates (SA), ethylene (ET), brassinosteroids (BRs), jasmonates (JA), strigolactones (SL), and abscisic acid (ABA) (Su et al., 2017). ABA, SA, ET, and JA have been acclaimed to have an essential function among these nine PHs in the plant's responses against ecological stresses (Peleg & Blumwald, 2011; Wasternack, 2014). Currently, one research group evaluated BRs, CK, GA, ET, SA and JA show an essential function in the drought tolerance by controlling the cellular functions by cell signaling (Yadav et al., 2021). The BR and SL form a new plant hormone for improving significance because of their association in the response to different environmental stresses for example, drought and high temperature (Su et al., 2017; Brewer, Koltai, & Beveridge, 2013; Nolan et al., 2020). Melatonin, a plant hormone which can regulate various physiological activities for example seed germination, growth, rooting, photosynthesis, and tolerance against abiotic and biotic stresses (Maheshwari, Dheeman, & Agarwal, 2015). Polyamines concentration is high and located within the plant (conversely to PHs), are essential for plant growth and development under stress conditions (Liu et al., 2007). PHs homeostasis is regulated by the regulation of metabolic pathways, and transportation (Pieterse et al., 2009; Iqbal, 2014). Currently, hormone-biosynthetic pathways are used to know the amalgamation of hormonal circuits into molecular methods which is linked with stress responses. Hence, decoding how plants can more accept ecological stresses with the minimum in their yield is the main target for the researchers. Figure 1 indicates stress tolerance mechanisms of PHs in plants (Egamberdieva et al., 2017). This analysis objects to improve the knowledge of the impacts of abiotic stresses on Phytohormones and their functions in plant physiology to clarify the mechanisms of phytohormone against abiotic stress in plants. This evidence can be useful in onward-thinking solutions for improving climate friendly crop plants in this vigorously changing world. Figure 2 points out the essential role of these phytohormones.

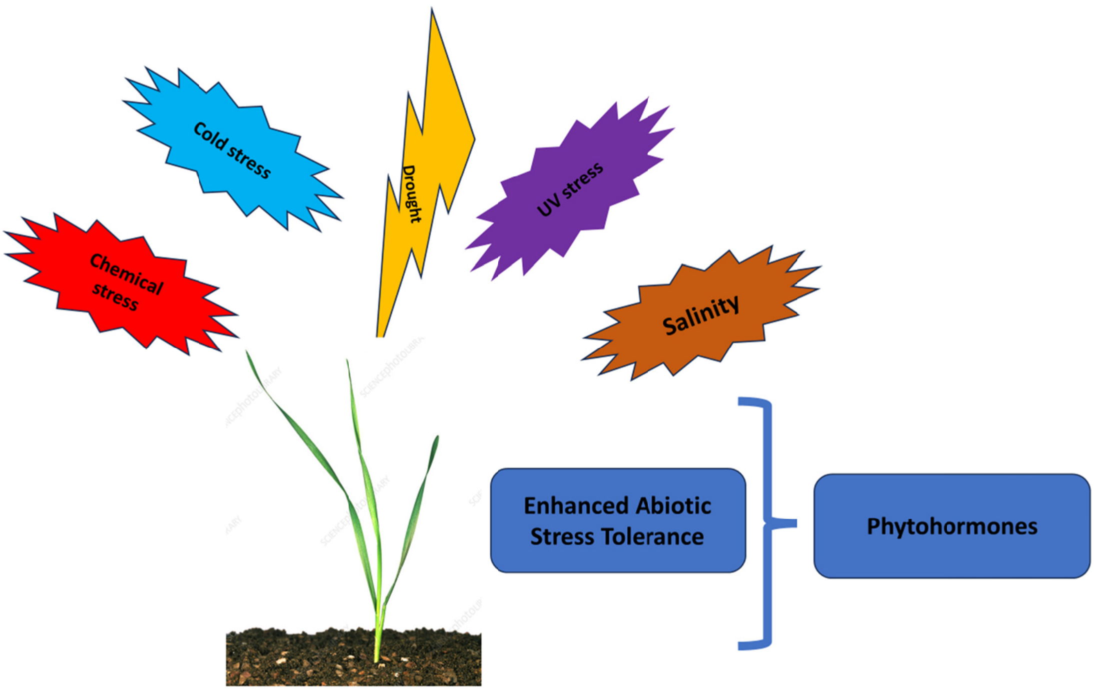

Figure 1. Schematic diagram of mechanism of plant abiotic stress tolerance regulated by phytohormones

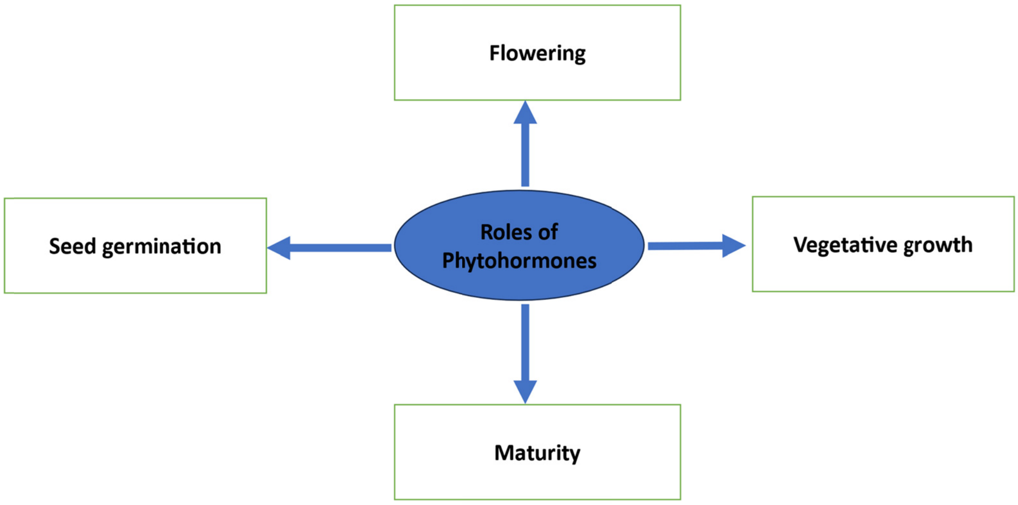

Figure 2. The role of phytohormone on plant reproduction

1.1 Overall Impacts of Abiotic Stress on the Crop Plants Growth and Development

During their whole life cycles, plants deal with several stresses (Figure 3). Many abiotic stressors trigger crop losses by influencing crop production, including heat, drought, salinity, heat, and nutrient shortage stresses (Andreotti, 2020). Abiotic stresses affect not only crop production but also the trait quality which is causing physiological and biochemical variations (Rao, Shivashankara, & Laxman, 2016). Current climatic changes cause many abiotic stresses to the crop plants. Climate change is also considered as a severe challenge for which the agriculture division has to suffer in the very near future (Francini & Sebastiani, 2019; Shahid et al., 2021; Gao et al., 2022). For the abiotic stressors plants decrease mainly leaf water potential, photosynthesis, membrane integrity, plant growth, and crop production (Ullah et al., 2018). Therefore, the horticulture sector is enthusiastically looking for advanced agronomic implements that will be able to deal with the difficulties of these environmental stressors to sustain the overall quality of the crop production.

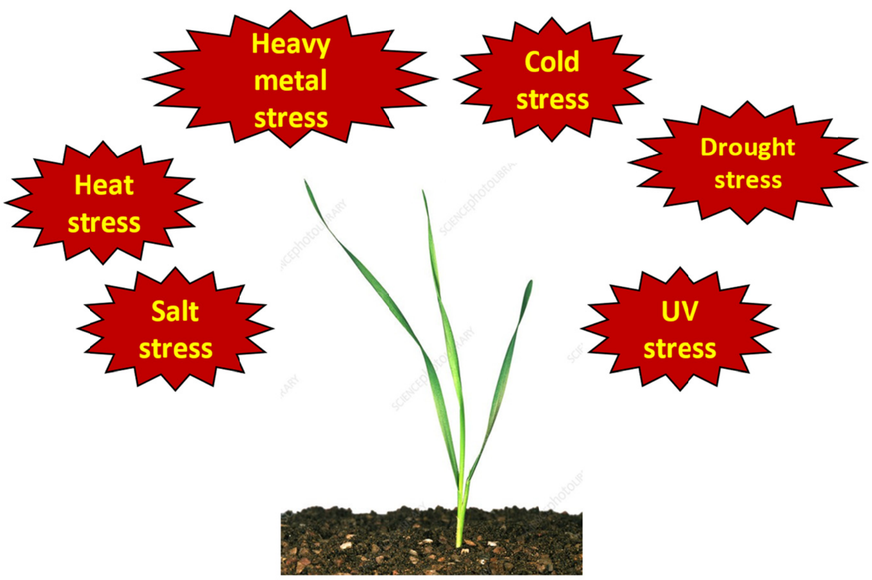

Figure 3. Schematic diagram of different stress factors that affect crop plants growth and development

1.2 Phytohormones and Their Beneficial Functions in Plants Under Abiotic Stresses

Abiotic stresses, for example drought, heat, flooding, high soil salinity, cold, and oxidative stress are not only decline ecological assets but also decrease crop's growth and production by decreasing the nutrient uptake (EL Sabagh et al., 2020; Javeed et al., 2021). Plant nutrients extremely effect the biochemical and physiological activities of plants (Raza et al., 2020). Furthermore, the shortage of the necessary nutrient's brakes down crop's growth and development, as a result, it can cause to the death of plants (Bennett, 1993; Balakrishnan, 1999). Genetic engineering methods are considered as the best method to breed stress-tolerant plants. However, inadequate success is attained in this field. Therefore, Phytohormones are the potential applicants to defend crop plants from the adverse effects of abiotic stresses. Phytohormones are extensively implied in abiotic stress tolerance, and these are known as the key regulators of responses in plants under several abiotic stress conditions. The mechanism processes can be modified with different hormones. Therefore, sometimes a single hormone is detected to control cellular and developmental activities (Ciura & Kruk, 2018). The essential Phytohormones for the plant's growth and development (Figure 4) support plants to help reproduction against the biotic and abiotic stressors (Sytar et al., 2019). Thus, the application of these crucial phytohormones is supportive as well as beneficial for increasing crop stress tolerance improvement research.

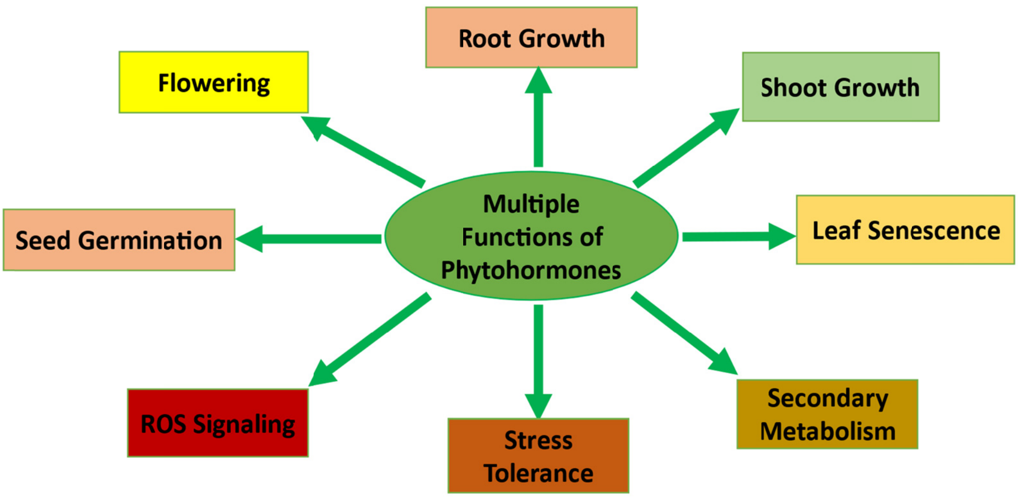

Figure 4. Schematic diagram for multiple Functions of phytohormones

2. Phytohormones

2.1 Abscisic Acid

Abscisic acid (ABA) had been discovered in1960s. ABA is responsible for seed dormancy, and stomatal opening and closing. It is also responsible for the adjustments of a plant to environmental stresses. Under water deficit conditions, ABA can be biosynthesized in roots and transferred to leaves to enhance its amount in the leaves. Furthermore, this biosynthesized ABA initiates signaling cascade in the cells to control turgor of cell (Danquah et al., 2014; Awan, Khurshid, & Mehmood, 2017). In the abiotic stress response, ABA begins stomatal closure to decrease cell growth (Peleg & Blumwald, 2011). ABA is essential in plant-water interaction (Arkhipova et al., 2020). Phosphatase and kinase play a role in arbitrating quick responses to abiotic stresses in ABA signaling (Dar et al., 2017). This ABA Signaling pathway is originated from carotenoids transformed to neoxanthin (Nambara & Marion-Poll, 2005). After that, conversion of xanthoxin, its oxidationcauses ABA production. The biosynthesis of ABA has been stated as an alternative method of ABA synthesis in plants uncovered to abiotic stresses (Xu et al., 2013; Llanes et al., 2014). Furthermore, ABA control physiological responses by cooperating with the other PHs to response against abiotic stresses (M. He, C. Q. He, & Ding, 2018). ABA activates an range of biochemical defenses for example biosynthesis of antioxidants, heat shock proteins, ROS detoxifying enzymes, and unsaturated fatty acids which help plants to deal with abiotic stress to decrease the adverse effects on exposed plants to abiotic stress (Ashraf & Foolad, 2007; H. Chen, X. Chen, & Zheng, 2013; Lee & Suh, 2015; Huang et al., 2016).

2.2 Ethylene

Ethylene (ET) is crucial for many fundamental morpho-physiological processes, for example seed germination flowers development and initiating plant responses against different abiotic stresses. ET controls many biochemical responses of plants who deal with abiotic stresses such as cold, drought, heat, waterlogging, and salinity (Awan, Khurshid, & Mehmood, 2017). ET homeostasis is essential for cold stress tolerance. High ET concentration is essential for salt stress tolerance, for example salt tolerant Arabidopsis plants. The high ET concentration can actively deal with salt stress by sustaining ROS production (Yang et al., 2017). Additionally, it is crucial to response against external wounding, UV radiation, pathogen attack, and nutrients deficiency. ET biosynthesis is responsible in response to damage of plants (Kendrick & Chang, 2008). The biosynthesis of ET has been enumerated in various plant tissues which are exposed to various abiotic stresses (Kendrick & Chang, 2008). The mechanism for ET biosynthesis initiates with S-Adenosyl methionine (SAM) which is produced in many crops' plants. 1-aminocyclopropane-1-carboxylic acid (ACC) synthase makes the first chain reaction for converting SAM to ACC, and methylthioadenosine (MTA), which steps recycled to L-methionine. Furthermore, the ET biosynthesis pathway is affected by ACC, which decreases biosynthesis rate and increases the ethylene levels in many plant's tissues (Maheshwari, Dheeman, & Agarwal, 2015).

2.3 Salicylic Acid

Salicylic acid (SA) is one of the most essential growth controllers of almost all plants. The concentration of SA is 1 µg g^{-1} of fresh biomass of soybean, rice, and barley crops. It is known as a growth regulator of all biochemical and physiological processes in plants. It improves the plant's resistance to many pathogens that have been identified already in plants (Misra & Saxena, 2009). Moreover, SA application lessened the harmful effects of salinity (Horváth et al., 2007). SA was produced in the 1960s from cinnamic acid (CA) by using two pathways. One pathway implies a side chain of CA, which creates benzoic acid, which synthesizes SA in crops plants including tobacco (Yalpani, Shulaev, & Raskin, 1993). The second pathway implicates CA, which creates coumaric acid which subsequently synthesizes SA. Trans cinnamate-4-hydroxylate causes to catalyze this reaction (Alibert & Ranjeva, 1971).

2.4 Jasmonates

Jasmonates are a wide-ranging group, and it is casing many compounds, for example jasmonic acids (JAs), jasmonic acid methyl ester (JAME) etc. These are implicated in plant responses to abiotic and biotic stresses. Jasmonates are located in plant's body. Though, root, shoot, fruits, and leaves are observed at extremely high concentrations. The producing method of JAs initiates at linolenic acid and ends at (+)-7-epi-JAs (Wasternack, 2007). Leaves and roots are the main organs of plants which synthesize Jasmonates mostly. Peroxisomes and chloroplasts are the primary organs of plants of the Jasmonates biosynthesis process (Cheong & Do Choi, 2003). Previous study identified that seed germination, development of the plant's reproductive organs, leaf movements and senescence, root growth, gravitropism fruit ripening and the formation of the tubers are regulated by Jasmonates (Wasternack, 2014). Further, Jasmonates have a key function in abiotic stress tolerance. Therefore, many studies were focused on Jasmonates because of having an important role on plant's response against abiotic and biotic stress (Takeuchi et al., 2011). Jasmonates regulated plant responses are observed against drought stress (Sasaki-Sekimoto, Taki, & Obayashi, 2005) cold stress, UV-stress, temperature stress and salinity stress (Yoshikawa, Honda, & Kondo, 2007). Additionally, Jasmonates regulated metabolites production (Chen et al., 2006) is implied in plant movements which is related to the circadian rhythms and study informed that jasmonates control microbe-related symbiotic relationships (Wasternack, 2007). The jasmonates are also responsible for abiotic stress regulation in papaya and *Arabidopsis thaliana* (A. thaliana) (Arbona, Argamasilla, & Gómez-Cadenas, 2010; Brossa et al., 2011) Arbona et al., 2010; Brossa et al., 2011) is also observed. Moreover, Jasmonates are involved in salt stress tolerance in glycophytes such as barley and others have been identified.

2.5 Cytokinins

Cytokinins (CKs) are key Phytohormes often and involved in many processes in plants for example, plant growth, development, and nutrients enhancement (Roy & Chakraborty, 2023). Cytokinins are also involved in tolerance against abiotic stresses (Pospíšilová, 2003; Danilova et al., 2016). Furthermore, when the plants are stressed by salt stress Cytokinins are triggered. Cytokinins can remarkably enhance salt stress tolerance by relating it to other plant hormones (Iqbal, Ashraf, & Jamil, 2006). Cytokinins are adenine products which were identified in plants at very lower concentration (Sakakibara, 2006) produced genetically modified tobacco plants which are transmitting Agrobacterium tumefaciens isopentenyl transferase gene (IPT). These genetically modified tobacco plants are remarkably tolerant against leaf senescence and consequently these tobacco plants have outstanding water stress tolerance levels. Hence, Cytokinins can shield photosynthesis during drought stress in the genetically modified plants (Rivero et al., 2010). Additionally, latest investigations have recommended that cytokinins are truly engaged against salt stress. Many research results have indicated that Cytokinins assist plant's growth under osmotic stress condition. Also, many studies have reported that Cytokinins can enhance plant's drought tolerance capability. But the method of drought tolerance by Cytokinins is still unclear.

2.6 Strigolactones

Strigolactones (SLs) were first revealed as an "natural signal" for parasitic seed germination. Hemiparasite plants need a living host for germination and development. Afterwards, these were labelled together as strigolactones (CE, 1972). Several strigolactoneS for example GR7 and GR24 have shown their function in reproductive development, shoot branching, root development and leaf senescence (Gomez-Roldan et al., 2008; Kapulnik et al., 2011; Ruyter-Spira et al., 2011). The main roles of Strigolactones are related in the developmental processe of plants (Hayward et al., 2009). Strigolactones are implicated in the symbiosis interaction of microbes and plants. Various studies have reported the importance of Strigolactones for controlling several physiological activities against different abiotic stresses for example drought, salinity, heat stress, cold stress, and nutrient starvation (Marzec, Muszynska, & Gruszka, 2013) identified that the application of GR24 in rice young plants developed in well growth and photosynthesis level. These findings indicated that Strigolactones can decrease the injury of crop plants affected by salt stress. Similarly, these findings indicated that Strigolactones can enhance the crop yield. The plants make Strigolactones in high concentration while facing nutrient deficiency (Umehara et al., 2008). Strigolactones also exhibited an important role in phosphorous deficiency (Marzec, 2016).

2.7 Brassinosteroids

Brassinosteroids (BRs) control various physical activities in plants including cell division, reproduction, and growth (Nolan et al., 2020). Brassinosteroids were syntheseized from Brassicanapus pollen (Grove et al., 1979). The Brassinosteroids help to organize the tropical responses of plant organ. Brassinosteroids assist the lateral root development (Bao, Locovei, & Dahl, 2004). Brassinosteroids crosstalk applies a significant long-distance impact (Symons et al., 2008). The Brassinosteroids metabolism is responsible to conserve the preferred levels of biologically active Brassinosteroids in the cells. Moreover, a very low amount of Brassinosteroids is adequate to begin the developmental processes in stress conditions. Various studies have reported that the abiotic stress tolerance of plants was achieved by the application of Brassinosteroids (Kagale et al., 2007). Oppositely, a high amount of Brassinosteroids treatment is observed to reduce the plant growth and development (Belda-Palazon et al., 2018). Brassinosteroids control the ROS level in stressful conditions. Brassinosteroids decrease photosynthesis inhibition rate (Ogweno et al., 2008) have identified that Brassinosteroids raise drought tolerance in Arabidopsis. Furthermore, another researcher has observed the lessening impact of Brassinosteroids against salt stress in lettuce. Moreover, some phenotypical characteristics are controlled by Brassinosteroids including inflorescence structure and plant height. Overall, these results exhibited that Brassinosteroids are powerful Phytohormones.

3. Conclusion

The difficulties related with different abiotic stressors have been increasing day-by-day and drawing concentration of the biologists to evade dangers to crop yield in near future. Phytohormones have appeared as a beneficial method in present abiotic stress problem as Phytochromes can defend the plants from several abiotic stress factors by increasing depressing oxidative destruction, and by increasing plant development. Hence, in abiotic stress lying areas the crop yield's sustainability can be retained by the phytohormones' application. Besides, developing the abiotic stress tolerant plants, the utilization of these phytochromes is also identified for enhancing seed germination by destroying the seed dormancy. This review is an effort to present beneficial insights about the utilization of the phytohormones and the functions performed by these phytohormones for increasing the plants' abiotic stress tolerance ways. Moreover, for more understanding phytohormones' growth-regulation methods, recently, phytohormones crosstalk inquiries have been made. In upcoming research, the goal of updating with the genetic engineering of abiotic stress-tolerant crop plants can be associated with the trickeries of these beneficial phytohormones level and their action at the developmental stage in the proper organs.

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