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Utilization of phytohormones for successful crop production under environmental stress conditions

Mohammad Hussain Faiq, Mohammad Safar Noori*

Department of Agronomy, Faculty of Agriculture, Takhar University, Afghanistan

ABSTRACT

Stress is an external factor that exerts a detrimental effect on overall growth of a plant. Environmental stress is a serious threat for sustainable crop production, and a main cause for food insecurity. Agricultural crops are exposed to a variety of environmental stresses including extreme temperatures and unfavorable chemical and physical soil conditions. Drought stress adversely affects some physiological and biochemical processes in plants, including transpiration, translocation of assimilates and nutrient metabolism. Salinity stress is responsible for loss of turgor, reduction in growth, wilting, leaf abscission, reduction in photosynthesis and respiration, loss of cellular integrity, tissue necrosis and finally death of the plant. Drought and salinity stress negatively affects the growth and yield of crop plants more than all the other stresses combined. Cold stress affects cellular components and metabolism, and temperature extremes impose stresses of variable severity that depend on the intensity and duration of the stress. Many approaches are being used to alleviate the deleterious effects of environmental stresses on successful agricultural crops production in recent years. Application of phytohormones (Abscisic acid, Indole-3-Acetic Acid, Jasmonic acid and salicylic acid) is one of the curative measures to mitigate the environmental stresses in agricultural crops. Phytohormones play a significant role in enhancing stress tolerance and therefore, reduce the yield loss in crop plants. In this paper, the impacts of environmental stresses on productivity and physiological activities of crop plants, and the effective role of some phytohormones in alleviation of environmental stresses have been reviewed.

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*Corresponding Author:
Mohammad Safar Noori
E-mail: safar_noori@yahoo.com

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INTRODUCTION

Phytohormones which also called plant growth regulators (PGR) are organic compounds, other than nutrients, that modify plant physiological processes. Phytohormones called biostimulants or bioinhibitors, act inside plant cells to stimulate or inhibit specific enzymes or enzyme systems and help regulate plant metabolism. They normally are active at very low concentrations in plants. Today, specific Phytohormones are used to modify crop growth rate and growth pattern during the various stages of development, from germination through harvest and post-harvest preservation (Charles *et al.*, 1986).

Environmental stresses such as drought which often cause complex physiological, molecular, and biochemical changes in plants, may alter the levels and ratio of different endogenous PGR. Under environmental stress conditions, it is reported that exogenous application of Phytohormones may overcome much of the internal Phytohormones deficiency and could lead to reduced inhibitory effects caused by the stress (Ashraf & Foolad, 2007). From a practical point of view, application of

Phytohormones offers a potential approach to mitigating the inhibitory effects of drought-stress on plant growth and crop productivity.

Exogenous applications of Indole Acetic Acid (IAA) or 2, 4-dichlorophenoxyacetic acid (2, 4-D) were found to reduce the impact of drought on plant growth especially at heading and flowering growth stages. Moreover, ethephon was found to reduce the size of corn plants which in turn reduce water consumption especially when applied at early vegetative stages. Several other reports showed the importance of using plant growth regulators such as mepiquat chloride, ethephon and others, in improving plant tolerance to drought (Al-Tabbal *et al.*, 2006).

Plant growth and development is the integrated result of many environmental and endogenous chemicals (hormones). The action of hormones is very interesting. A single hormone can regulate many processes and at same time many hormones interact to influence a single process (Kucera *et al.*, 2005) and this is one of the differences between animal and plant

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hormones. Seed treatment with hormones is an important remedy to minimize problem of seed germination in stress conditions, due to their consistent effects on germination and growth (Atia *et al.*, 2009). Now a day where global warming is a critical problem for crop production, wide areas of agricultural land are subjected to moisture stress, and in some case, it makes the arable land liable to salinity stress (Muhie, 2018).

Environmental stresses caused by climate change and other factors could be a big challenge for successful and sustainable crop production. Therefore, it becomes necessary to overcome this problem by development of adaptation technologies and mitigating the deleterious impacts of environmental stresses to produce sufficient for the rapidly growing population. The aim of this study was to compile relevant information from reliable sources and review the impacts of climate change, environmental stresses on agricultural products and the role of Phytohormones on mitigating environmental stresses.

Impacts of Climate Change on Crop Production

Climate change may be a change in the mean of the various climatic parameters such as temperature, precipitation, relative humidity and atmospheric gases composition etc. and in properties over a longer period and a larger geographical area. It can also be referred as any change in climate over time, whether due to natural variability or because of human activity (Abewoy, 2018). The changing patterns of climatic parameters like rise in atmospheric temperature, changes in precipitation patterns, excess UV radiation and higher incidence of extreme weather events like droughts and floods are emerging major threats for crop production (Tirado *et al.*, 2010). Rainfed agriculture will be primarily impacted due to rainfall variability and reduction in number of rainy days (Venkateswarlu & Shanker, 2012).

Temperature

Fluctuations in daily mean maximum and minimum temperature is the primary effect of climate change that adversely affects crop production, as many plant physiological, bio-chemical and metabolic activities are temperature dependent. High temperature causes a significant alteration in morphological, physiological, biochemical and molecular response of the plant and in turn affects the plant growth, development and yield (Abewoy, 2018). High temperature can cause significant loss in tomato productivity due to reduced fruit set, and smaller and lower quality fruits (Bhardwaj, 2012). The temperature fluctuations delay the ripening of fruits and reduce the sweetness in melons. Warm humid climate increase the vegetative growth and result in poor production of female flowers in cucurbitaceous vegetables like ash gourd, bottle gourd, pumpkin that causes low yield (Ayyogari *et al.*, 2014).

Drought

Drought is a major problem in arid and semi-arid regions, which is the primary cause of crop loss worldwide, reducing

average yields for most of the crop plants by more than 50% (Sivakumar *et al.*, 2016). It adversely affects the germination of seeds in vegetable crops like onion and okra and sprouting of tubers in potato (Ayyogari *et al.*, 2014). It has been suggested that water stress at flowering stage reduces photosynthesis and the amount of photosynthetic assimilates allocated to floral organs and might thereby increase the rate of abscission. Apart from inhibiting the photosynthetic rate through reducing stomatal conductance (Yordanov *et al.*, 2013), drought stress also induces metabolic impairment (Dias & Brüggemann, 2010). The photosynthesis and photosynthetic capacity are reduced during limited water conditions. Further, the biochemical capacity was also affected by the water stress as indicated by a decrease in sucrose phosphate synthase (SPS) and invertase activities, which affect the availability and utilization of sucrose. The SPS is considered to play a major role in the resynthesis of sucrose and sustain the assimilatory carbon flux from source to developing sink (Isopp *et al.*, 2008).

Plants have developed two strategies to resist drought: drought avoidance and dehydration tolerance (Blum *et al.*, 1982). Drought avoidance refers to plant's abilities to maintain high water status when water is scarce. For instance, plants grow long roots to reach deep soil moisture or reduce water loss by closing stomata on the leaf surface. When moisture is limited, the stomata close to slow transpiration and conserve water. However, at that time, CO₂ supply is decreased, consequently, reducing photosynthesis. Stomata play a major role in plant adaptation to stresses. Drought tolerance refers to plant's ability to withstand loss of water content and regrow when moist conditions return. Resurrection plants can withstand about 90% water loss, whereas most other plants can withstand about 30% water loss or moderate dehydration (Hara *et al.*, 2012).

The detrimental effects of drought stress on plants are a consequence of osmotic strain on cytoplasm. In many plants, drought stress decreases stomatal conductance and transpiration rate (Yokota *et al.*, 2006). Under drought stress condition, stomatal closure helps to maintain higher leaf water potential and hence, high leaf water content; however this often leads to decreased leaf photosynthesis (Chaves *et al.*, 2002). The limitation of CO₂ assimilation imposed by stomatal closure reduces the internal CO₂ concentration in leaves and induces an imbalance in photosystem II (PSII) photochemical activity, thereby altering the electron requirements for photosynthesis and consequently leading to increased susceptibility of PS II to photo-damage (Murata *et al.*, 2007). Drought stress causes oxidative damage through an increase in reactive oxygen species (ROS) such as superoxide radical, hydrogen peroxide, and hydroxyl radical, which may cause various cellular damages including, protein oxidation, nucleic acid damage and peroxidation of membrane lipids (Gill & Tuteja, 2010; Sharma *et al.*, 2012).

In response to drought stress, plants may accumulate low molecular weight osmolytes such as sugars and specific amino acids. Accumulation of these compatible solutes helps plants to maintain turgidity and hence normal metabolic processes,

and this solute accumulation has been suggested as a major mechanism underlying adaptation and/or tolerance of plants to drought stress through osmotic adjustment (Munns, 2002; Yokota *et al.*, 2006).

Salinity

Salinity is a serious problem that reduces growth and productivity of crops in many salt-affected areas. Excessive soil salinity reduces productivity of many agricultural crops, which are particularly sensitive throughout the ontogeny of the plant. Salt stress causes loss of turgor, reduction in growth, wilting, leaf abscission, decreased photosynthesis and respiration, loss of cellular integrity, tissue necrosis and finally death of the plant (Cheeseman, 2008). Salt stress causes suppression of growth and photosynthesis activity and changes in stomata conductivity, number and size in bean plants. It reduces transpiration and the cell water potential in salt-effected bean plants (Kaymakanova *et al.*, 2008).

Salinity stress in plants is multifactorial, including osmotic stress and cellular sodium toxicity, such as inhibition of vital enzymes and metabolic processes (Ward *et al.*, 2003). Simply, in response to salinity stress, the reduction in growth occurs in two phases: a rapid response to the increase in external osmotic pressure and a slower response due to the accumulation of Na⁺ in leaves (Munns & Tester, 2008). Salt stress destroys the ionic homeostasis in the water potential and ionic distribution. Photosynthetic processes are severely affected by salinity; thus, salt stress directly reduces carbon fixation and biomass production in plants (Munns, 2002). More than 20% of irrigated lands are affected by high salt content.

Cold stress

Cold triggers cell death by cytoplasmic dehydration and ice formation in the cell wall. Plants of tropical or subtropical origin suffer severe damage at temperatures between 0 and 15°C. However, plants from temperate regions become cold tolerant and are still able to grow near the freezing point. Plants develop adaptation to cold stress. Plant cells synthesize and accumulate cryoprotectant solutes and cryoprotective proteins that stabilize cellular membranes and enhance antioxidative mechanisms (Mahajan & Tuteja, 2005). Low temperature triggers rigidification of membranes by increasing desaturated phospholipids in membranes (Anchordoguy *et al.*, 1987). Furthermore, cells also accumulate osmolytes, such as sugars, polyalcohols, aminoacids, polyamines, quaternary ammonium compounds, and antifreezing proteins because sucrose and proline-rich proteins trap water by creating hydrogen bonds to prevent dehydration of the cytoplasm, and accumulation of these compounds causes the freezing point within the cell to drop. In addition to sucrose and proline, some pathogen-related proteins, which may interact with ice to prevent damage from ice crystal dynamical growth, are also induced to function in cold tolerance (Thomashow, 1999). Cold stress is responsible for a range of physiological disturbances in chilling-sensitive plants and can cause chilling injury and death of many agricultural plants. Low temperature stress is a harsh constraint, which

negatively affects vegetable crops productivity. However, several mechanisms in plants are involved in alleviating cold stress through natural tolerance system. Utilization of plant growth regulators as a new approach is very promising in plant response to environmental stresses (Atayee & Noori, 2020).

Utilization of Phytohormones for Alleviation of Environmental Stress

Flexibility in the growth patterns of plants is partly achieved by the action of phytohormones. They together form a signaling network which regulates plant response to different abiotic as well as biotic stresses. Several reviews in this regard add to the recent knowledge of hormonal cross-talk responsible for plant stress responses (Arc *et al.*, 2013; Denancé *et al.*, 2013). Phytohormones are the signaling chemicals which control almost all aspects of plant life. Plants have successfully evolved through their developmental processes to face the challenges of environmental cues.

Abscisic acid (ABA)

This hormone has a major role in stress signaling causing an immediate response like hydraulic signal that triggers ABA biosynthesis in the system (Raghavendra *et al.*, 2010). Phytohormones can mediate a wide range of plants' responses, from rapid (e.g. stomata closure) to long term adaptations by modulating the programs of plant growth and development. ABA as a growth inhibitor, acts in stress conditions like drought. Plant hormones have an important role in the response mechanism against abiotic stress (Franklin, 2008). ABA as a stress-responsive signaling molecule is the most well studied hormone in the past decade. In the recent past, a lot of research has been done in the field of elucidation of the core ABA-signaling pathway and proper identification of ABA receptors. For example, less water availability is first confronted by the plant roots which results in stomatal closure of leaf and thereby resulting into reduced transpiration to a great extent by the action of the stress hormone ABA (Wilkinson & Davies, 2002). Many recent experiments on plant hormones have shown that ABA has the potential to elevate the abiotic stress tolerance in various plant species (Tiwari *et al.*, 2017). In addition to its regulatory functions in development it has also a key role to play in coordinating different signal transduction pathways in environmental stress responses (Wolters & Jürgens, 2009).

Indole-3-Aacetic Acid (IAA)

IAA plays a major role on regulating plant growth. It controls vascular tissue development, cell elongation, and apical dominance (Wang *et al.*, 2001). Plants exposed to drought stress can recruit IAA as an endogenous, signal to initiate adaptive responses (Wang *et al.*, 2008; Zhu, 2002) Reports have shown that the adaptation to drought was accompanied with an increase in the IAA content (Sakurai *et al.*, 1985; Pustovoitova *et al.*, 2004). Drought stress significantly decreases IAA and GA concentration in leaves than that of control (Xie *et al.*, 2003).

Jasmonic acid (JA)

Jasmonic acid and its methyl ester play a significant role in plant growth and developmental processes under changing environmental as well as other biotic stresses. It has been established that JAs are emerging players in alleviating the deleterious effects under adverse conditions. They induce resistance against many biotic stresses. In plant systems, they regulate gene expression which controls overall plant growth, antioxidant metabolism, osmolyte synthesis, metabolite accumulation, and physiological parameters. These hormones are produced only under abnormal conditions such as heat, cold, or salinity to protect the plant and induce tolerance against environmental stress conditions (Siddiqi & Husen, 2019).

JA is a proven endogenous regulator of stress responses and overall plant growth and productivity. Post application in stressed plants with 30- μ M JA and 24 and 4 h after NaCl treatment, effectively removed salt inhibition on dry mass production. Walia *et al.* (2007) have reported that the induction of JA-responsive genes in barley was considered as a crucial aspect under salinity. Stomatal closure in plants limits the transpiration to retain water under drought conditions. Stress-induced production of JA interacts with ABA-mediate stomatal closure by stimulating the influx of extracellular Ca_2^+ or/and by activating $\text{H}_2\text{O}_2/\text{NO}$ signaling (Harrison, 2012). Many JA-associated signaling genes are regulatory drought stress (Huang *et al.*, 2008). Stomatal aperture of *Arabidopsis* leaves has been found to be drastically reduced when treated with methyl jasmonate (MJ) for 10 min (Munemasa *et al.*, 2007). JA is helpful in regulating plant response under water scarcity (Liu *et al.*, 2005). However, a combination of indole 3-butyric acid (IBA) and MJ is more effective for growth promotion under normal condition.

IBA alone is ineffective under stress, although MJ enhances both the growth and yield. JA application, however, enhanced accumulation of osmolytes while carotenoids enhanced antioxidant enzyme concentration which prevented the plants from damage by excess metal ions (Poonam *et al.*, 2013). Pigeon pea exposed to JA showed accumulation of proteins, total chlorophyll and carotenoids, and reduced the effect of copper (II) on the growth of seedlings. Heavy metal stress is also alleviated by activating the antioxidant system (Yan *et al.*, 2013). MJ strengthened tolerance in *Arabidopsis thaliana* plants against copper and cadmium stress through accumulation of chelating ligands which form complex with metal ions and prevent their availability to plant.

Cold stress (chilling and freezing) affect crop productivity because many crops are sensitive and intolerant to low temperature. Acute temperature variation damages the plants (Schwartz *et al.*, 2016). Usually, chilling and freezing stress lead to chlorosis, necrosis, membrane damage, changes in cytoplasm viscosity, and changes in enzyme activities (Ruelland & Zachowski, 2010), leading to death of plants. Experiment on *Arabis alpina* belonging to Brassicaceae family showed variation in JA and other hormones under chilling and freezing conditions (Kolaksazov *et al.*, 2013). All tolerant and

non-tolerant plants showed very high level of JA at normal temperature of 22 °C. After chilling stress at 4 °C, the tolerant plants did not show considerable change in JA relative to 10-fold reduction in nontolerant plants. JA induces accumulation of resveratrol in *Vitis vinifera* which is a healthy compound for human consumption (Verpoorte *et al.*, 2000). It also induces the formation of many compounds of pharmaceutical interest and antioxidants such as flavonoids and vitamins (Martin *et al.*, 2013). JA reduces chilling injury in *Cucurbita pepo* through its regulation of ABA and polyamine levels. MJ can also enhance the accumulation of ABA in the exocarp tissue of Zucchini squash (Wang & Buta, 1994). Perhaps, MJ causes an alteration in tissue metabolism followed by an increased synthesis in ABA at chilling temperatures. JAs produce thermo tolerance in plants, and exogenous application of low dose of MJ has been shown to maintain the cell viability by controlling electrolyte leakage in heat stressed *A. thaliana* plants (Clarke *et al.*, 2009).

Salicylic acid (SA)

SA is a conservative compound of some biotic and abiotic stresses. It acts as important molecular signal for plants adjustment under abiotic stress (Waseem *et al.*, 2006; Arfan *et al.*, 2007)]. In plants various physiological processes are regulated by SA such as growth, transpiration rates, photosynthetic processes and stomatal regulation, ion uptake and transport (Gunes *et al.*, 2005). Moreover, salicylic acid also reduces negative effects of various abiotic stresses by increasing internal level of other plant growth regulators in plants (Sakhabutdinova *et al.*, 2003). Wheat is consumed as food by about 35% of the human population. Wheat is a staple food so, wheat plant growth and yield under different abiotic stress condition is compulsory (Zhu *et al.*, 2000). Salicylic acid (SA) exogenous application could modify the physiological and morphological capacity of wheat plants in water stress condition. SA application via root enhanced water stress tolerance of wheat seedlings and alleviated the effect of drought (Saboon *et al.*, 2015).

Safar-Noori (Safar-Noori *et al.*, 2018) found that SA applied with a higher rate of K fertilizer alleviated drought stress and increased the grain yield of wheat under stress condition. Furthermore, SA application increased grain crude protein and mineral content. A pot experiment was conducted to determine drought mitigating effect of SA and L-Tryptophan. Maize seeds were sown in pots filled with soil. Salicylic acid and L-Tryptophan were sprayed at 3-4 leaves stage @ 100, 150, 200 ppm and 5, 10, 15 ppm, respectively. Drought stress was induced by withholding water after five days of Salicylic acid and L-Tryptophan application. Significantly higher relative water content, leaf membrane stability index, chlorophyll and potassium content were found in plants treated with 100 ppm Salicylic acid and 15 ppm L-Tryptophan compared with other treatments and control plants. Thus, foliar application of Salicylic acid and L-Tryptophan can play a role to reduce the effect of drought in maize (Rao *et al.*, 2012).

Exogenous application of SA has been shown to induce plant stress tolerance. Many research finding highlighted the protective effects of exogenous SA on plants against salinity

(Wang & Li, 2006), drought (Singh & Usha, 2003), and high temperatures (Ashraf *et al.*, 2010). For example, treatment of common bean (*Phaseolus vulgaris* L.) and tomato (*Solanum lycopersicum* L.) plants with SA increased their drought tolerance (Senaratna *et al.*, 2000). Exogenous application of SA also has been reported to modulate activities of intracellular antioxidant enzymes superoxide dismutase and peroxidase (POD) and increase plant tolerance to environmental stresses. Stomatal regulation is a key process involved in the maintenance of photosynthetic capacity in plants under stress conditions, and thus SA-induced regulation of stomatal closure could reduce moisture losses in plants under drought stress. Exogenous application of Phytohormones enhance plant performance under drought stress by modulating various physiological and biochemical processes which are negatively affected by water stress. Application of SA increases total soluble proteins, chlorophylls a and b, and POD activity. It indicates that both SA and chlormequat chloride (CCC) were effective in alleviating adverse effects of drought stress in wheat. The beneficial effects of SA and CCC in reducing the adverse effects of drought stress may be due to improving stomatal regulation, maintaining leaf chlorophyll content, increasing water use efficiency, and stimulating root growth (Anosheh *et al.*, 2012).

Among SA concentrations, 300 μM SA had better effects on plants as compared to others. Plants treated with 300 μM SA showed the highest values for net photosynthesis rate, transpiration rate and proline concentration. The application of 300 μM SA showed the highest leaf area. It seems that the application of SA in 300 μM concentration improves plant functions in both normal and stress conditions (Afshari *et al.*, 2013). Although there has been more investigation recently on the use of PGR affecting plant growth and yield production under stress, more has yet to be researched on the use of such products to enhance plant growth under stress due to the following: 1) different crop species respond differently under stress, 2) the response of crop plants (due to plant physiological differences) to different PGR is different, 3) the type of stress is a determining factor in the effectiveness of PGR and 4) the type and the effective amount of PGR is a function of different parameters including climate, plant species and the combination of PGR (Baena-González & Hanson, 2017; Kamran *et al.*, 2018).

The combined use of SA+GA₃, was the most effective treatment, followed by the use of SOD, the single use of SA and benzyl adenine (BA₆) also significantly affected wheat physiology and nutrient uptake under stress, indicating the importance of such plant hormones for wheat growth under stress. The possible molecular mechanisms, which may increase the tolerance of the treated wheat plants with PGR, under the stress, have been presented. Accordingly, the tested PGR are able to alter wheat physiology, including the activation and the expression of the stress genes and plant hormonal signaling and cross talk so that the wheat plants would be able to tolerate the stress and their physiology and nutrient uptake enhance. The treatment of wheat plants with the PGR tested in the presented research is recommendable to improve wheat physiology, and nutrient uptake, and subsequent wheat growth and yield under drought stress.

SA may improve heat tolerance in a concentration-dependent manner. Low concentrations (0.01–0.1 mM) of SA treatment to mustard plants via spraying increased heat tolerance (Dat *et al.*, 1998). Tobacco treated with 0.01 mM SA exhibited enhanced thermotolerance, whereas a treatment with 0.1 mM SA had no protective effect (Dat *et al.*, 2000). In grape leaves, SA pretreatment alleviated the decrease of photosynthesis rate under heat stress, in part through maintaining a high Rubisco activation state and rapid recovery of PSII function (Wang *et al.*, 2010).

CONCLUSION

Crop production and consumption is vital for the survival of human. However, environmental stresses, such as drought, salinity, cold, and heat impose adverse effects on the growth, productivity and trigger a series of morphological, physiological, biochemical, and molecular changes in plants, which may lead to suppressing plant growth and development, reducing crop productivity, or plant death. Consequently, hunger is a significant global problem. For reducing malnutrition and alleviating poverty in developing countries, there is a need to develop sound adaptation strategies to alleviate environmental stresses by utilizing the different Phytohormones. Plant growth regulators are very promising in plant response to environmental stresses. This review paper highlighted the role of Phytohormones application in enhancing the cold stress tolerance in vegetable crops and can be utilized as an effective strategy. Development of methods to enhance stress tolerance in plants is crucial and attracts considerable attention. However, more research is required to elucidate the effect of different Phytohormones on various agricultural crops and find appropriate PGR and specific dose/concentration to obtain satisfactory result.

AUTHORS' CONTRIBUTIONS

Both authors have equally contributed in conceptualization, writing, review and editing of this article.

ABBREVIATIONS

ABA: Abscisic acid; CCC: Chlormequat chloride; IAA: Indole Acetic Acid; GA: Gibberellic acid; H₂O₂: Hydrogen peroxide; JA: Jasmonic acid; MJ: Methyl Jasmonate; PGR: Plant Growth Regulators; POD: Peroxidase; ROS: Reactive Oxygen Species; SA: Salicylic acid

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