

PLANT HORMONE-MEDIATED REGULATION OF STRESS RESPONSES IN FRUIT CROPS- A REVIEW

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November 6, 2020

Abstract

One of the challenges facing fruit crop production globally is the regional climate regimes are becoming more unpredictable year after year leading to various type of stress. The exact impact of these stress on fruit crops is difficult to predict. Plant hormones can improve tolerance against abiotic stresses by inhibiting or reducing the active oxygen (AOS) accumulation, electrolyte leakage, induce the expression of stress-specific genes, etc. Among the major hormones produced by the plants, ABA, SA, JA and ET are known to play major roles in mediating plant defence response against various abiotic stresses. Crosstalk networks among phytohormones mediated by diverse key regulators have been extensively investigated and documented in various research investigations. Many canvassers' recommended the use of phytohormones to counteract abiotic stress as increasing stress tolerance through conventional breeding methods requires longer time and also leads to inadequate adoptability of such cultivars under diverse cultivation environment for validation of performance and heritability. In this review, we summarize the roles of the major phytohormones present in fruit crops in regulating abiotic stresses responses with special focus on the significance of crosstalk between various hormones at biochemical and molecular level in generating a sophisticated and efficient stress response.

1. INTRODUCTION

Fruit crops are highly vulnerable to different environmental stresses. These stresses are grouped into two main categories- biotic and abiotic- based on the nature of stimulants. Biotic stresses are caused by various fungi, bacteria, viruses, nematodes, insects, and weeds. Whereas the second group is linked with the physiographic, climatic, and edaphic components of the environment affecting plant development and productivity (Verma A, 2016). The concern about these stresses in horticultural crops is important due to reducing annual production year after year by climate change (Bray et al., 2000). These stresses may cause morphological, physiological, biochemical, and molecular changes in plants (Dos Reis et al., 2012). Morphological changes like retarded shoot and root growth, flower drop, low fruit setting, deformed fruit shape are observed during abiotic stress conditions. Nutrient content and their proportion may change with the intensity of stress. To survive under unfavorable environmental condition plants need to regulate their growth and development (Wolters and Jurgens, 2009). They produce excessive reactive oxygen species leading to an oxidative stress condition in plants (Noctor et al., 2015). As a consequence of facing stressful situations, plants produce defensive biochemicals leading to neutralize the negative impact of abiotic stress (Herbette et al., 2007).

The exact impact of these stress on fruit crops is difficult to predict and it depends on numerous other climatic factors that are all always counted in predictive models. Most of the time, several abiotic stresses

occur and simultaneously affect plant growth and development. In this situation, studying individual stress separately without considering other stress factors is not adequate because plant response is unique and can be predicted but the similar results may appear by each stress factor applied individually (Mittler R, 2006). Plants do have root system architecture (RSA) to respond to changing environment and it facilitates lateral root branching which enables plants to withstand stress conditions (Lavenus et al., 2013). Moreover, abiotic and biotic components typically interact in a given ecosystem (Pandey P et al., 2017). Focusing on horticulture crops concerning abiotic stress is important because they are considered as cash crops and provide essential dietary elements (Shannon MC and Grieve CM, 1998).

According to the Global Burden of Disease study, nearly 3.4 million deaths can be attributed due to shortage of fruit and vegetable production and consumption yearly (<http://www.fao.org/3/a-i6807e.pdf>). Therefore, need to grow a vast amount of horticultural crops under diverse stress conditions becomes the most important goal for the current agriculture scenario to provide a properly balanced diet to every person. Since 2000, extensive studies were conducted to know the exact impact of climate change encompassing all abiotic stresses but only few research articles pay attention to fruit crops in terms of quality fruit production under abiotic stress conditions (Parajuli R et al., 2019). In that suggestion, increasing phytohormones biosynthesis and external application is the main concern to increase the tolerance against abiotic stress in fruit crops with a less economic burden. To maintain the normal plant physiological activities in plants, it is essential to understand clearly how these stress factors respond to different hormones at different stages of plant growth (Wien, 1997).

Traditional agronomical approaches do not have the potential to completely overcome the impact of environmental stresses. Therefore, it is important to use a modern molecular approach like marker-assisted selection (MAS), association mapping, QTL mapping, and whole-genome sequencing used to enhance the knowledge of tolerance in new cultivars. Limited work was accomplished at the DNA level to know stress tolerance in fruit crops (Gong et al., 2010). Several studies have shown that the stress tolerance influencing genes are present in the different fruit crops (Song et al., 2012). Generally stacking traits breeding method is used to introduce the numerous valuable genes for crop improvement but this method is inadequate because of the attribute segregation which disturbs the selection (Ainley et al., 2013). However, zinc finger nucleases are more useful for producing trait landing pads (Belhaj et al., 2013). There are three common methods of QTL model which are used in fruit crop improvement. Those are Single marker-assisted, simple interval mappings, and composite interval mappings, in which single marker-assisted QTL mapping are widely used (Collard et al., 2005). Till, now only few QTLs and genes have been identified in fruit crops which are involved in stress level regulating activities. The introduction and improvement of stress tolerance through a conventional breeding method does not provide the required result because of the linkage drag of unknown characters from donor parents (Asins, 2002). So the study of phytohormones becomes essential because they have some amount of stress regulation mechanism directly or indirectly without any negative effect on plants. Hence, it is necessary to understand the functional significance of major phytohormones in plants exposed to harsh environmental conditions. The current review presents an overview of the frontiers of phytohormones research in plant abiotic stress responses.

2. Phytohormones

Plant hormones are bimolecular compounds required in small quantities (Fahed et al., 2015) to regulate normal physiological activities. These organic molecules manage the abiotic stress by forming complex signaling cascades from stimuli perception to abiotic specific gene expression (Azevedo et al., 2012). They play key roles in plants by modifying growth and development (Wani et al., 2016). They include gibberellic acid (GA), auxin (AUX), cytokinin (CK), abscisic acid (ABA), ethylene (ET), salicylic acid (SA) and jasmonates (JAs) which are involved in different stress regulation activities directly or indirectly. They act as a chemical messenger with highly complex regulation mechanism, these biomolecules allow plants to maintain normal growth plasticity even under stress conditions (Xu et al., 2016). Various studies have shown that different plant hormones can improve plant tolerance against various abiotic stress conditions (Ogawa et al., 2005) by inhibiting or reducing the active oxygen species (AOS) accumulation, electrolyte leakage, induce the expres-

sion of stress-specific genes and enhance the photosynthesis (Kang et al., 2004), as the AOS level increase in the cell can damage nucleic acid molecules, protein, lipids, and other biomolecules (Noctor and Foyer., 1998). Furthermore, DELLA proteins work collaterally with GAs, which leads to an increase in tolerance against environmental stresses (Achard et al., 2009). However, the identification of novel genes and its stress responses may prove to be a vibrant target for engineering abiotic stress tolerance in fruit crops. More information is needed to have celerity regarding the regulation of abiotic stress at hormonal levels in fruit crops along with how and which hormones regulate different abiotic stresses.

2.1 Role of Auxin in plant defense response

Auxin is an essential biomolecule that regulates cell elongation, cell division, apical dominance, differentiation, apical dominance, tropical response, and other biological activities in plants. Genes involved in various auxin-related pathways show variation in expression during stress conditions (Van et al., 2013). Auxin stimulates the initiation of lateral roots from primary roots at seedling stage in plants by promoting lateral root primordia (LRP) initiation through activation of root pericycle cells present opposite to xylem (Lavenus et al., 2013) with the help of multiple IAA and ARFs (Okushima et al., 2007). The members of Aux/IAA and ARF class showed variation in expression during cold stress conditions in Arabidopsis (Hannan et al., 2005). Cheong et al. (2002) showed fluctuation in auxin-related genes expression, including IAA2, IAA3, GH3-like protein, and SAUR-AC1, after damage caused by the environment (Kovtun et al., 1998). During oxidative stress conditions, expression of *PIN1*, and *PIN3* downregulated (Pasternak et al., 2005). Genome-wide study shows that the glutaredoxin (*GRX*) gene family exhibits differential expression patterns under different phytohormones treatment. Among them, *OsGRX8*, a member of *GRX*, has expression during different abiotic stress conditions (Garg et al., 2010). WES1, encoding auxin conjugating enzyme, is induced by drought, heat, cold, and oxidative stress conditions (Park et al., 2007). Under ABA, drought, and salt treatments, numerous auxin transport genes have shown differential regulation (Shen et al., 2010).

2.2 Role of GA in plant defense response

GAs are primarily growth-regulating phytohormone involved in various developmental processes, including germination, leaf expansion (Claeys et al., 2012), stem elongation (Iwamoto et al., 2011), flowering (Hyun et al., 2016) and trichome and reproductive organs development (Claeys et al., 2012). Recently researcher identified the role of GA under stress condition (Wang et al., 2017). GA signaling and metabolism is a vital critical factor for environmental stress-tolerant in resilient phenotypes. It modifies the physiological metabolism in plants with regulating sink and source relationships (Iqbal et al., 2011). The methylerythritol phosphate pathway synthesizes the gibberellic acids in plastids from trans-geranylgeranyl diphosphate, thus both GA and ABA share common precursors during biosynthesis (Banerjee et al., 2016). The pleiotropic action of GAs is modified by the degradation of DELLA proteins which belongs to the GRAS protein family (Colebrook et al., 2014). DELLAs may regulate the gene expression by acting as transcriptional activators in multiplexes with other transcription factors (TFs) (Hirano et al., 2012). In the same way, they also act as inhibitors by sequestering gene activating TFs (Feng et al., 2008). DELLAs have been observed to interact with the other phytohormone cascades at the molecular level (Bai et al., 2012) during stress conditions (Bai et al., 2008). In recent years, several tissue-specific GA dioxygenases have been identified as *CsGA2ox1*, *CsGA2ox2*, *CsGA2ox3*, *CsGA3ox2*, *CsGA3ox3*, and *CsGA2ox4* in *Camellia sinensis*, these genes are utilized as a candidate marker gene for abiotic stress tolerance breeding (Pan et al., 2017). *DREB2*, an AP2/ERF family protein was found to be induced by ABA, but suppressed by overexpression of the *DREB2* gene which may cause dwarfness in rice with GA deficient symptoms and normal growth was restored by exogenous application of GA. Expression of *OsGA2ox1*, *OsGA2ox2*, *OsGA3ox2*, and *OsGA2ox4* was significantly declined in the plants under stress condition especially to salt stress (Tang et al., 2017).

2.3 Role of abscisic acid in plant defense response

Absciscic acid (ABA) is a small organic molecule and classified as sesquiterpene (Roychoudhury et al., 2013). It plays an important role in mediating stress responses (Yang et al., 2011). When environmental conditions are unfavorable for plants growth, the ABA biosynthesis (Kim et al., 2010) and accumulation in various

plant tissues increases drastically and bind to its receptors to initiate signal transduction that leads to stress response at the cellular level (Ng et al., 2014). Diverse *ZEP* genes regulate the ABA biosynthesis in different species and plant growth stages but *NCED* genes have a major role in drought stress conditions in tomato (Burbidge et al., 1990), bean (Qin and Zeevaart, 1999) and avocado (Chernys and Zeevaart, 2000). A remarkable rise in the *NCED* transcript level observed under induced dehydration conditions (Xiong and Zhu, 2003). But the *NCED* expression not varied by exogenous ABA application. Exogenous ABA regulates the *ZEP*, *AAO3*, and *MCSU* genes. Both ABA degradation and biosynthesis have a significant role in ABA expression and adjusting plant stress responses and developmental strategies. *ABRE* and *DRE* like cis-elements are promoters of stress-inducible ABA genes (Xiong et al., 2001; Bray, 2002).

2.4 Role of ethylene in plant defense response

Ethylene has the same activities as ABA for senescence but it has a different site of action and regulates diverse biotic and abiotic stresses (Brodersen et al., 2005). Abiotic stress promotes the ethylene production by modulating the activities of ACC synthase and ACC oxidase. Underwater deficit condition, increase in ethylene level observed in avocado and orange (Upreti et al., 1999). One of the subfamilies of AP2/ERF transcription factors, Ethylene Responsive Factor VII group (ERF-VII) participates in growth and development processes and stress response mechanisms in plants (Yao et al., 2016). These proteins contain a conserved APETALA2 (AP2) domain necessary for protein-DNA interaction (Papdi et al., 2015). At the N-terminal, ERF-VII has highly conserved motif MCGGAI/V (N-degron) to regulate protein turnover and initiate a protein degradation pathway through an oxygen-sensing mechanism (Gibbs et al., 2014). The ERF-VII proteins not only participate in regulation under hypoxia stress but are also involved in biotic and abiotic stress and hormone response. At the vegetative stage, they enhance the drought-responsive genes expression to recovery from dehydration stress (Fukao et al., 2011).

2.5 Role of salicylic acid in plant defense response

Salicylic acid is a phenolic compound and the most common pathway in plants for SA synthesis is, the phenylalanine pathway and isochorismic acid pathway (An C et al., 2011). Most of the research evidence shows that SA can enhance tolerance in plants against various external stresses including salt stress, osmotic stress, chilling, heavy metal stress (Chen YE et al., 2016), and high light by activating the antioxidant system to protect photosynthesis (Gururani MA et al., 2015). SA has a key role in plants to gather hypersensitive response (HR) or systemic acquired resistance and it also modulates various physiological responses such as thermogenesis, ion absorption, and programmed cell death during stress conditions.

2.6 Role of jasmonic acids in plant defense response

Jasmonates (JA) are endogenous signaling molecules involved in the various developmental process and also in stress mitigating activities (Llanes A et al., 2016). JA is closely associated with plant resistance to abiotic stress by the physiological and molecular response. Under stress condition, JA alleviates the antioxidant system, accumulation of isoleucine, methionine, soluble sugars (Wasternack C, 2014), regulate the stomatal activities (Acharya BR and Assmann SM, 2009), expression of JA-associated genes (*JAZ*, *AOS1*, *AOC*, *LOX2*, *CO11*) (Hu YR et al., 2017) and interaction with other phytohormones (Yang J et al., 2019).

2.7 Role of brassinosteroids in plant defense response

Brassinosteroids (BRs) are a group of steroidal hormones that play pivotal roles in cell division and elongation, photomorphogenesis, reproductive development, and leaf senescence and also external stress response (Choudhary et al., 2012). BRs increase the activities of catalyzing and decrease the activities of peroxidase and ascorbic acid oxidase under stress conditions (Ahammed et al., 2013) and also regulate secondary metabolites (Vardhini and Rao, 2003).

2.8 Hormonal crosstalk in plant defense mechanism

The signaling pathways of different phytohormones are known to interact among themselves in various situations, such as biosynthesis of hormone-responsive transcription factors to regulate plant defense reaction.

To regulate the balance between seed dormancy and germination, the cross talk of ABA with GA, mediated by DELLAs is a key mechanism for evading early abiotic stress conditions. The signaling pathways of SA and JA are known to interact at various points to regulate the numerous biotic stress antagonistically (Bari R and Jones JD, 2009). Different studies evidenced that SA-facilitated suppression of JA-responsive genes like PDF1.2, LIPOXYGENASE 2 (*LOX2*), and VEGETATIVE STORAGE PROTEIN (VSP) was abolished in *npr1* mutant plants (Spoel SH et al., 2003). Both JA and ET pathways stabilize *EIN3* and thus exhibit resistance to necrotrophs (Zhu Z et al., 2011). Auxin associate with ethylene to regulate root development under drought and salinity stress conditions. Furthermore, benzothiadiazole S-methyl ester (BTH), SA analog, treated Arabidopsis suppress the several auxin-responsive genes. SA signaling minimizes the TRANSPORT INHIBITOR RESISTANT 1 (TIR1)/ AUXIN SIGNALING F-BOX (AFB) gene expression (Wang D et al., 2007).

Cytokinins also known to crosstalk with SA and others signaling cascade to regulate plant defenses. For instance, ARABIDOPSIS RESPONSE REGULATOR 2 (ARR2) (cytokinin-activated transcription factor), a type BARR, interacts with TGA3 (bZIP-type transcription factor) and promotes SA defense responses in an NPR1-dependent manner (Choi J et al., 2010). A majority of the time, ABA suppresses the CYTOKINE OXIDASE. ARABIDOPSIS HISTIDINE KINASE (AHKs) functions as cytokinin receptors and regulates drought and salinity response and also ABA signaling, while *AHK2* and *AHK3* decent osmotic stress response and ABA signaling (Tran LS et al., 2007). ARABIDOPSIS HISTIDINE PHOSPHOTRANSFER PROTEINS (AHPs) negatively control responses to drought stress by losing activity of AHP (

Acute Hepatic Porphyrias) genes resulted in the up-regulation of ABA-responsive genes and thus a strong water stress tolerance phenotype (Nishiyama R et al., 2013).

3. Hormone functions and cross-talk toward stress tolerance in fruit crops

3.1 Hormonal regulation of growth responses under water stress conditions

Horticulture products are usually sold on a fresh weight basis in the market and yield is predominantly determined by water content (Marcelis et al., 1998). Plants adopted morphological, physiological and biochemical responses and molecular level to mitigate or minimize the effect of drought stress (Conesa et al., 2016). Drought is responsible for the drastic reduction in productivity (Medici et al., 2014). Flooding also produces the same impact as drought on horticulture crops by creating an anaerobic respiration zone around the root (Issarakraisila et al., 2007) and upsurges the soil-borne diseases (Rao and Li, 2003). Thereby, relevant reports about several hormones influence the inflection of water stress in fruit crops that have been produced and some are commented next.

Some studies show that ABA-induced auxin regulates the root growth and root cell differentiation (Xu et al., 2013) and modulate proton secretion at root tips under drought stress condition. Also, ABA-mediated auxin transporter inhibits lateral root growth under moderate water stress conditions (Shkolnik- Inbar and Bar-Zvi, 2010). At the genetic level, *ABI3* (ABA insensitive 3) interact with Aux/IAA or ARF proteins and LR growth inhibited in mutants of *ABI3* mutants by attenuation of auxin responses. In contrast, *ABI4* overexpression harms LR development. Some of the research work provided evidence that drought can affect the expression of core abscisic acid signaling constituents, equivalent to ABA, PYR/PYL/RCAR ABA receptors, subclass III SnRK2 protein kinases and protein phosphatases 2C (PP2C) (Weiner et al., 2010). ABA non-functional mutants are extra vulnerable to drought and salinity as compared to transgenic plants which can induce much hormonal response (Qin and Zeevaart, 2002). PYR/PYL/RCARs, PP2C, SnRK2s, and bZIP transcription are incorporated by the ABA-facilitated signaling pathway during water stress conditions. Zhung et al. (2012) proved that *OsPIN3t*, auxin influx carrier involved in drought stress conditions and overexpression of *OsPIN3t* upregulate drought-responsive genes, *OsDREB2A* and *OsAP37* and improve the tolerance against drought. ABA is known to regulate the balance between intrinsic growth and external responses. *AtABCG25* acts as ABA transporter in cell membrane and export ABA from the cytoplasm to outside of the cell. Reduced transpiration observed when *AtABCG25* overexpressed. Kuromori et al., (2016) observed that *AtABCG25* over-expression stimulated a local ABA response in guard cells and

increase the drought tolerance, probably resulting from the maintenance of water content.

Jasmonic acid also regulates the water loss under drought conditions by regulating stomatal opening and closing (Savchenko T et al., 2014). Jasmonate ZIM-domain proteins (JAZ) are regulators in the JA signaling pathways. *OsJAZ1* play a negative role for stress tolerance in rice under drought condition with the ABA and signaling pathways (Fu et al., 2017). Seo et al. (2011) demonstrated that *OsHHLH148* acts as a transcriptional regulator and up-regulates *OsDREB1* and *OsJAZ* under dehydration condition. Furthermore, Ge et al. (2010) found that JA accumulation could promote leaf senescence, improve plant survival by preventing excessive water loss. Foliar application of MEJA on soybean plants can improve water stress tolerance with an increase in sugars, phenolic compounds, and flavonoids in leaves (Mohamed HI et al., 2017).

Mango orchids present in the rainfed area can survive for a long period by adopting drought-tolerant mechanisms (Chacko, 1986) and they set fruit when daily average temperature more than 20°C. But flooding for more than 2 weeks can significantly reduce root dry weight (Larson et al., 1991), net CO₂ assimilation, stomatal conductance, and transpiration rate (Schaffer et al., 1992). Grape plants develop large-sized vessels in the xylem to transport water under drought conditions (Serra et al., 2013). Grafting high yielding commercial varieties scions on drought-tolerant rootstocks helps to overcome the water stress (Kodur et al., 2010). Initially ABA concentration is an increase in stressed roots, and later it is transported to the leaves to reduce the photosynthesis and partially transpiration. Pomegranate is considered to be both winter hardy and drought-tolerant plant (Aseri et al., 2008). Mild to severe drought stress during the reproductive stage may reduce the fruit size by 10–50 % in cluster apple. Whereas 50 ppm GA₃ application along with wheat straw mulch gave the highest net income (Patel et al., 2010) with good fruit setting during water stress conditions. Custard apples are very sensitive to salt in irrigation water and should not exceed an electrical conductivity of 800 µS/cm (George et al., 1999). Ber plants are comparatively more resilient for water stress by producing pubescent leaves with a large number of stomata arranged in the interveinal regions, whereas the adaxial surface is glabrous, with few comparatively sunken stomata (Clifford et al., 2002). The date palm tree has naturally evolved as drought and salt-tolerant plants through selection (Zaid and deWet, 2002) with an adaptation capacity more than barley for saltwater (Furr and Armstrong, 1975). In litchi, ABA content in leaves increased with the drought (Stern et al., 2003) by inhibited CO₂ assimilation in litchi leaves (Damour et al., 2008).

Application of paclobutrazol (gibberellin biosynthesis inhibitor) can induce stress protection in apple (Swietlik and Miller, 1983), strawberry (Navarro et al., 2007), and peach (George and Nissen, 1992) under drought conditions. In flood soil, PM ATPase stimulates the accumulation in putrescine to support cell homeostasis and nutrient acquisition (Bertini et al., 1997) with a reduction in superoxide radicals and H₂O₂ accumulation. GA interferes with the ethylene and ABA biosynthesis by upregulating ethylene response factor (ERF) domain proteins SNORKEL1 and SNORKEL2 to minimize the negative effect of excess water (Hattori et al., 2009). During drought, *IAR3* (IAA-Ala Resistance3) involved in lateral root production, free auxin production (Kinoshita et al., 2012). It stimulates the gibberellin production and inhibits the ABA synthesis for plant accumulation under submerged conditions (Colebrook et al., 2014). ABA level shows a decrease with an increase in hydration, but PA or DPA levels either increase or remain unaltered (Zhou et al., 2004). ABA restrict their water loss through controlled transpiration (Thompson et al., 2007) and regulates the influx or efflux of K⁺. The decline in cytokinin concentration under soil moisture deficit conditions observed in grapevines (Satisha et al., 2005) and partial root drying harmed the xylem cytokinin concentration with a distinct increase in xylem sap pH (Stoll et al., 2000). During water stress conditions enhances ethylene production in orange (Ben-Yehoshua and Aloni, 1974), avocado (Adato and Gazit, 1974), and in many other plant species leads to increased senescence of fruits/ leaves and reduced growth. The ethylene production indirectly depends on the magnitude of stress, stress intensity, and stress duration (Upreti et al., 2000).

Under flood, condition roots trigger the ACC synthesis, which later oxidized to ethylene when it reaches shoots and cause nastic movements of the leaves and promote aerenchyma tissue formation to mitigate oxygen deficiency (Colmer, 2003). External application of polyamines ameliorates the drought stress in pomegranate

by increasing proline concentration (Amri and Mohammadi, 2012) Polyamines stabilize membranes and forming potential of higher buffering and antioxidant capacity (Roy and Sengupta, 2014). The balance of auxin levels (IAA) required for the adaptive recovery growth of litchi plants after release from the stressed environment. Although the levels of cytokinins decreased and levels of ABA increased (Krishna, 2012).

Some signaling molecules include inositol (Sengupta et al., 2008); polyamines (Rangan et al., 2014), and various involved in minimizing the water stress with minimum biomass loss. They may induce the production like protective proteins such as dehydrins; late embryogenesis abundant (LEA) proteins; heat shock proteins (HSPs) (Juszczak and Bartels, 2017). LEA proteins, dehydrin, lipid transfer proteins saturate enzymes, RAB (responsive to ABA) are associated with the protection of cellular structures (Cushman and Bohnert, 2000). AREB1/ABF2, AREB2/ABF4, and ABF3 like bZIP transcription factors are induced by dehydration, salinity, or ABA treatment under drought condition (Yoshida et al., 2010).

Genomics and crop physiology studies of waters stress provide accurate information to breeders for plant improvement (Tuberosa and Salvi, 2006). Plants have sets of drought regulatory genes, which activated during the water-stress condition to minimize the hassle condition (Wohlbach et al., 2008). In plants at the initial phase of drought, water stress stimulate the production of ABA, which induce the expression of genes (Ding et al., 2016) like, *RD29A*, *RD29B*, *KIN2* and *RAB18* (Yao et al., 2012), *rd22* (Abe et al., 1997) and *PYL8* (Lim et al., 2013). SUBA-1 allele induces the negative regulation of ethylene in plants to survive under prolonged submerged condition (Xu et al., 2006). Over-expression of the *ESKIMO1* gene in Arabidopsis (Bouchabke-Coussa et al., 2008) and pro biosynthesis gene in *Cicer arietinum* (Bhatnagar-Mathur et al., 2009) were observed during artificial drought condition. Several transcription studies show, how plants recover after mild drought condition as compared to complete irretrievable inhibition of photosynthesis under severe drought (Watkinson et al., 2003). Most of the time, MYC, MYB, DRE-binding protein (DREB)/ C-repeat-binding factor (CBF), ABA-binding factor (ABF) and mainly cis-elements ABA-responsive element (ABRE) transcription factors present in ABA biosynthesis cycle are involved in drought stress management (Bartels and Sunkar, 2005).

3.2 Hormonal regulation of growth responses under high-temperature stress condition

The temperature has a major influence next to moisture for plant growth and development. In optimum temperature, the plants may grow faster and comes to flowering even earlier than normal. Those plants grown under cool conditions, they produce more upright leaves, but under warm humid conditions, they are more horizontal to downward (Ravi et al., 2013). Under subtropics, banana plant development is slower than in the tropics irrespective of yield and bunch size and they need optimum temperature around 22°C and stops growing above 39°C and below 10°C. When temperature crosses the sunburn critical temperature (>38°C). Pomegranate can tolerate drought by morphological and/or physiological modification which enables them to avoid or postpone desiccation in the semiarid zone (Save et al., 1995). Custard apple normally requires a hot and dry climate during flowering and high humidity for a good fruit setting. Even they can tolerate extreme temperatures (below freezing and up to 40°C). Soil temperatures below 10°C may cause severe chilling injury leading to loss of cell membrane stability (Maritza et al., 2004).

Most of the time-temperature in the plant is regulated by the transcription regulators like *HSFs* by activation of many heat shock responsive genes and heat shock proteins. A large number of *HSFs* and *Hsps* genes are identified in different crops from available genome sequence information and they are involved in heat shock regulatory network (Hu et al., 2009). There are 25 *HSFs*, 29 *sHsps*, 26 *Hsp70*, 9 *Hsp90*, and 10 *Hsp100* family genes that were identified in rice crop, 35 *DcHCFs* in carrot, 21 *HSFs* in *Arabidopsis thaliana*, 28 in *Populus trichocarpa*, 16 in *Medicago truncatula*, 52 in *Brassica rapa*, 25 in *Zea mays*, and 26 in *Glycine max*, respectively (Huang et al., 2015). When temperature crossed 45°C, the *HsfA1* gene activated in the tomato plant to minimize the impact of high temperature (Mishra et al., 2002). Whereas, *Hsp101* (mitochondrial transcription termination factor-related protein) in Arabidopsis enhanced the thermo-tolerance via mitochondrial oxidative damage control (Kim et al., 2012). Nearly 5% of transcriptomic activity observed and chaperones conquer only a minor part during heat stress conditions (Larkindale and Vierling, 2008). They mainly involved in metabolism of calcium and phytohormone signaling protein phosphorylation (Saidi

et al., 2011). For maintaining photosynthesis and transpiration under stress conditions, Chloroplast protein synthesis transcription factor accumulation is mandatory (Ristic et al., 2008). Under high-temperature stress condition, polycationic nature of polyamines stabilize the membrane structural integrity and facilitates their strong binding to nucleic acids, proteins, and membranes (Childs et al., 2003).

3.3 Hormonal regulation of growth responses under chilling stress condition

Low-temperature (chilling) stress may causes dehydration in plants by limiting water uptake and stomatal activities (Mahajan and Tuteja, 2005). Plants differ in their response to chilling (0-15°C) and freezing (< 0°C) (Xin and Browse, 2001). In general, initially chilling symptoms appear in the cell membrane by forming flexible liquid crystalline cell membranes into a solid gel phase (Farooq et al., 2009). Whereas in fruit crops, chilling may cause a delay in fruit ripening and fruit deformation. Low temperature during storage may cause browning, reddening, woolliness, and mummification (Lurie and Crisosto, 2005). Incidence of frost during fruit development forms ice crystals in subcellular space and damages the plant cell activities, in severe condition, complete plant death may also occur (Levitt, 1980). The intensity of frost damage also depends on the physiological condition of plants (Proebsting and Mills, 1978). It affects cell membrane integrity, ion leakage, biomolecule activities, and gene expression (Dhanapal and Crisosto, 2013). In fruit crops, chilling can suppress the photosynthesis by reducing photosystem II efficiency (Allen et al., 2000). Different phytohormones have a role in cold stress is yet to be discussed in detail.

ABA acts as a messenger in the regulation of water level in plants (Mahajan and Tuteja, 2005). Same as ABA, auxins involved in defense response against abiotic stresses in plants (Wolters and Jurgens, 2009). It more intricately involved in the various developmental process like fruit development, root initiation in grafting, root growth, and development (Depuydt and Hardtke, 2011). Members of the auxin-responsive *GH3* gene family also has cold stress-responsive activities. *OsGH3-2* found to modulate both endogenous free IAA and ABA homeostasis and differentially affect cold tolerance in rice (Du et al., 2012). However, the role of auxin remains unclear under stress conditions in fruit crops. Brassinosteroids avoid ions leakage in chilled stressed rape seeds (Janeczko et al., 2007), whereas it improves the antioxidant defense in young grapevines to avoid the negative impact of cold stress (Xi et al., 2013) by biosynthesis of de novo or activation of enzymes (Bajguz, 2000). When chilling sensitive banana plants were treated with SA (0.5mM) caused an increase in SOD, CAT, and APX activities when plants are induced to very low temperature (Kang et al., 2003). Wang and Li (2006) also showed that SA treated grapevines decreased lipid peroxidation and electrolyte leakage and induced cold tolerance.

GA also plays an important role in the low-temperature condition. It enhances the bolting and flowering in *Limonium gmelinii* plants when GA sprayed at 500 mg L⁻¹ (Guda et al., 2000). GA inhibits the sucrose formation from starch and mannitol (Ogasawara et al., 2001). This outcome suggests that the GA application enhances the rapid tissue enlargement and differentiated to resist the cold stress in plants (Jacobsen and Olszewski, 1993). Chilling causes discoloration to the peel of the ripened fruit by coagulating latex in latex ducts. The exogenous application of methyl jasmonate enhanced soluble protein and antioxidant content under cold stress in banana plants (Zhao et al., 2013). Cold stress also enhances the ethylene biosynthesis (Zhao et al., 2014). Zhao et al. (2009) reported that ethylene levels in plants and cold tolerance are positively correlated up to a certain level.

Chilling can induce the expression of jasmonic acid biosynthesis genes, including allene oxide synthase (*AOS1*), oxide cyclase (*AOC*), and lipoxygenase (*LOX2*). Recent studies show that, in banana, two MYC2 TFs are activated following the exogenous application of MeJA in the cold storage condition and enhances the expression of an inducer of CBF expression (ICE-CBF) cold-sensitive pathways genes (Zhao ML et al., 2013). In MeJA induce chilling tolerance, the *MaMYC2* transcription factor in coordination with *MaICE1* reduces lipoxygenase activity and increases antioxidant synthesis. Cao et al. (2009) found that ascorbate peroxidase (*APX*), catalase (*CAT*) and superoxide dismutase (*SOD*) activities in MeJA treated loquat fruits.

To manage the chilling injury, SA and MeSA treatments are given, which are easy to set up, less expensive, and applicable to any crops. They increase the AOX transcript level and reduces the chilling incidence.

When plants are treated with SA and MeSA before chilling induces the HSPs biosynthesis and increases the tolerance against chilling injury (Ding et al., 2001). Different genetic studies show that many auxin-responsive genes are involved in cold stress (Jain and Khurana, 2009). Likewise, *PIN1* and *PIN3*, an auxin transporter mediate root gravity response during the early phase is inhibited by cold stress (Shibasaki et al., 2009). Zhao et al. (2009) in tomato found a positive relationship between ethylene and freezing tolerance from the negative effects of 1-methyl cyclopropene, which inhibit ethylene biosynthesis on freezing tolerance. For freezing tolerance, the RARE COLD INDUCIBLE 1A (*RCI1A*) gene interacts with ACC synthase. Dehydration-responsive element-binding proteins/C-repeat binding factors (*DREBs/CBFs*) interact with dehydration-responsive elements/C-repeat-elements (*DRE/CRT*) to execute a highly coordinated transcriptional response to cold signals. C-repeat-binding factors (*CBF*) cold response pathway is found in freezing-tolerant (FT) plants (Skinner et al., 2005) and in freezing-sensitive (FS) plants (Zhang et al., 2004).

3.4 Hormonal regulation of growth responses under salinity stress condition

Soil salinity induced by excessive accumulation of sodium chloride (NaCl) (Munns and Tester, 2008). When salt content in irrigation water crossed the threshold level may harm osmotic adjustment, ion uptake, osmotic adjustment, photosynthesis, stomatal conductance, protein synthesis, nucleic acid production, enzymatic activity, and hormonal stability (Raga et al., 2016). Based on salt stress tolerance potential, plants have been classified into two major groups; i) halophytes have the potential to survive and reproduce even when salt concentration nearly 200-mM NaCl and ii) glycophytes are not able to survive under salt stress condition (Patane et al., 2013). Glycophytes produce stress symptoms like decreased in total leaf area and leaf growth, marginal and tip yellowing and tip scorching, marginal and tip scorching of leaves, yellowing and bronzing, early leaf drop, twig dieback, blackening, necrosis, and leaf burning (Bernstein et al., 2004). Structural disorders were found in both sensitive and tolerant genotypes, such as an increase in leaf thickness, excessive chloride accumulation with reduced Mg²⁺, and loss of chlorophyll content (Aranda et al., 1998).

Osmotic regulation is one of the most important mechanisms to avoid osmotic stress by accumulating metabolites like glycine, betaine, proline, mannitol, and soluble sugars (Houimli, 2010). Morphologically some level of salinity stress can be minimized in fruit crops by grafting of salt-sensitive improved high yielding cultivars on salt tolerance rootstocks (Munns et al., 2006). Under mid salinity stress, reduction in lateral root (LR) elongation and an increase in the number of LRs observed. Besides, the reduction of LRs numbers observed in auxin signaling mutants *axr1*, *axr4*, and *tir1* completely blocked auxin influx (Zolla et al., 2010). Even at low salt stress can suppress auxin efflux carrier *PIN2* and also decrease the *PIN2* : GFP concentration in root tips. It suggests that salt regulates both transcription and posttranscriptional activities (Zhao et al., 2011). High salt concentration causes rapid degradation of amyloplasts in root columella cells thereby reduce the gravity response in roots (Sun et al., 2008). The development of LRs by salt overly sensitive 3 (*SOS3*) under salinity stress conditions has been reported by auxin redistribution activities (Zhao et al., 2011). Mutants of *SOS3* do not accumulate auxin in plant aerial parts. The NAC transcription factors have a key role in plant growth and stress responses. NAC1 and NAC2 proteins promote lateral root formation in Arabidopsis. AtNAC2 gene expression was induced by auxin, ethylene, and ABA. Under salt stress condition auxin receptor mutants *tir1* suppressed. NaCl also downregulate TIR1 expression (Xie, 2000)

When rootstocks of *Microhyla zeylanica* are used to cultivate mango under 60-mM NaCl salinity condition, plants maintained a higher photosynthetic rate with greater K⁺ /Na⁺ ratio in roots and lesser in leaf/root Na⁺ (Schmutz, 2000). Whereas *Pistacia atlanticarootstock* gave the better result as compared to *Poly-cythemia verarootstock* when used in pistachio plants under salinity stress (Tounsi et al., 2017). External application of 30-mM/L calcium nitrate for citrus plants significantly reduced Cl and Na⁺ uptake by the root system and also enhanced the growth attributes and gaseous exchange mechanism (Banuls et al., 1997). In olive plants, a reduction in stomatal conductance and photosynthesis observed when soil NaCl content crossed the 100 mM level (Tabatabaei, 2006). Jujube plants have more potential to resist salinity compared to other cultivated fruit crops, in which two wild Indian jujube (*Ziziphus rotundifolia* and *Ziziphus nummularia*) were found to be more resistant to saline conditions due to higher stomatal conductance, higher CO₂ assimilation, higher hormonal regulation, antioxidants accumulation and better nutrients translocation

(Meena et al., 2003) by accumulating high amount of Na^+ in roots through restricted translocation and high K^+/Na^+ ratio to keep ionic balance in leaves (Mohammadkhani, 2018). Number fruit crops are identified which can store excess K^+ in leaf, stem and other tissues to mitigate the negative effect of Salinity. The lowest Cl ion concentration and high K^+ were recorded in lemon (Gimeno et al., 2009) and fig (Zarei et al., 2016) plants when these plants are irrigated with water containing 50-mM NaCl with 10-mM potassium nitrate. *Arbuscular mycorrhiza* like fungi can increase the stress tolerance potential in trifoliate orange by accumulating a low amount of Na^+ and Ca^{2+} while higher K^+ , proline content, and carbohydrate content.

Proline can help to store carbon and nitrogen and maintains the structural integrity of cell membranes and proteins by purifying free radicals (Jalili et al., 2009) and it maintains the buffering capacity of cells against salinity (Heidari, 2012). Fozouni et al. (2012) demonstrated that *Vitis vinifera* table grape significantly increases the proline accumulation with increased salinity. But it harms photosynthesis by degrading chlorophyll content (Behboudian et al., 1986). The optimum value for the soil K/Na is 2.5 for the banana if this proportion exceeds by 8% can cause economic loss. Salt tolerant fruit crops have succulent organs, salt exclusion, excretion of salts, and accumulation of ions in the tonoplasts to maintain osmotic regulation. Pomegranate tissues can accumulate sodium, chlorine, and potassium ions without any stress symptoms in response to saline water irrigation and it can tolerate salinity up to 40 mM NaCl but at higher NaCl concentration ($>40\text{mM}$) affects the main stem length, number of internodes and the leaf surface area (Naeini et al., 2006) and decrease in soluble sugar accumulation was observed (Naeini et al., 2004). Date palm plants are considered as one of the exceptional halophytic plants and it can survive under severe salt stress conditions. Ramoliya and Pandey (2003) found that some datepalm cultivars adopted salt exclusion mechanisms and they can endure high soil salinity levels (up to 12.8 dS m^{-1}) with no visible effect on the seedlings (Greenway and Munns, 1980). Litchi trees should not be irrigated with water with salt contains more than 0.5 dS per m electric conductivity. If salinity level exceeds, symptoms like tips and margins die were observed in old leaves also.

When chloride content in plants crossed the toxic level induce the production of ethylene precursor ACC, leads to leaf senescence. In counteract to ethylene activities, plants trigger the biosynthesis of ABA to reduce ethylene production (Arbona et al., 2006). Silver thiosulfate and phosgene synthetics are also used externally to inhibit the ethylene lead senesce in salt-affected plants. The same result were observed in a grapevine, where the extreme rise in ABA level observed in resistant cultivars rootstock when planted in salt stress soil (Upreti and Murti, 2010). Olive plants that are grown under salinity, water uptake, relative water uptake, and water potential drastically reduced (Chartzoulakis, 2005; Yadav et al., 2011).

GA3 application increase the nutrient uptake, plant height, and yield in wheat (Ashraf et al., 2002) and rice (Wen et al., 2010) when cultivated under saline condition. Different plants can tolerate salt stress with increasing GA concentration by more absorption of P and Ca^{2+} and less absorption of Na^+ (Starck and Kozinska, 1980), stomatal resistance and enhanced plant water use were observed at low salinity in tomato (Maggio et al., 2010) and it enhances the catabolism of ABA (Gonai et al., 2004). The GA metabolism and signaling play a major role in plant physiological adaptation, low-temperature influences of bioactive GA as a result of an increase in expression of three *GA2ox* genes (Archard et al., 2008). Rootstocks of grapes with high cytokinin can maintain a high $\text{K}-\text{Na}$ ratio and root-shoot dry mass ratio under salinity (Upreti and Murti, 2010). In desert almond trees, cytokinin concentration peak in the morning time and rapid decline in the afternoon based on the stomatal conductance (Fusseder et al., 1992). Brault and Maldiney (1999) reported that cytokinins act at the plasma membrane along with other signaling compounds.

An important role of ethylene in salt tolerance by relating its ability to retain K^+ without decreasing Na in roots as well as in shoots (Yang et al., 2013) and It stimulates H^+-ATPase activity to modulate ion homeostasis (Wang et al., 2009). Polyamine content in the grafted plant increased against salt stress by Prompting superoxide dismutase, peroxidase, and ascorbic peroxidase and glutathione reductase enzyme activities. Upreti and Murti (2010) found a significant increase in polyamines concentration intolerant grape rootstock roots by salinity stress along with ABA and it helped to maintain the high root- shoot biomass ratio and high $\text{K}-\text{Na}$ ratio. Similarly, Anjum (2008) reported that Cleopatra mandarin and citrus rootstock

shows better growth and chlorophyll efficiency at high spermine and carbohydrates with low chloride ions in leaves and roots under salinity. Polyamines control the Ca^{2+} allocation through regulating Ca^{2+} permeable channels and CAXs by the prevention of $\text{Na}^{+}/\text{K}^{+}$ entry into the cytoplasm and enhancement of $\text{Na}^{+}/\text{K}^{+}$ influx to the vacuole with suppression of $\text{Na}^{+}/\text{K}^{+}$ release from the vacuole. Polyamines regulate the physiology stomata similar to ABA, by targeting KAT1-like inward K^{+} channel in guard cells of stomata (Liu et al., 2000).

Klingler et al. (2010) suggested that ABA-dependent amino oxidase derived H_2O_2 affected stomatal physiology in grapevines. By genetic modification or exogenous application of polyamines enhances salt tolerance in grape (Farooq et al., 2009). In Neo-Muscat grapes seedling significantly accumulate putrescine during osmotic and salt stress by temporary induction of arginine decarboxylase (pVvADC) gene followed by spermine synthase (pVvSPMS) (Liu et al., 2012). The overexpression of *OsGSTU4*, an auxin-responsive GST gene enhance the tolerance to salinity and oxidative stress condition in Arabidopsis plants (Jain et al., 2010).

3.5 Hormonal regulation of growth responses under heavy metal stress condition

No organic life can develop and persist without the involvement of metal ions in this universe. The essential microelements for plants are Cu, Zn, Fe, Mn, Mo, Ni, and Co whose uptake in excess to the plant causes toxic effects (Monni et al., 2000). Fe, Cu Cr, and Co are involved in a redox reaction, whereas Zn, Cd, Ni, Al, etc. monitor the various enzymatic activities in plant cells. Transition metals such as copper and iron have frequently unpaired electrons and are, therefore, very good catalysts of oxygen reduction. Currently, the contamination of the natural ecosystem by these heavy metals represents a global threat, endangering the agriculture ecosystem (Mico et al., 2006). In trace, these elements are essential for normal plant growth and development and play a key role in metabolism by activating different enzymatic activities (Roy and McDonald, 2015). However, when the concentration of these metals crossed threshold level cause a negative impact on physiology and biochemistry of plants (Ivanov et al., 2016) and reduce the biomass accumulation in plants (Ebbs et al., 2015) as a result dwindle the photosynthesis rate (Rodriguez et al., 2012), mineral nutrition uptake (Vernay et al., 2007) and communication with water. Besides they can also cell toxicity by excess production of ROS, which impaired antioxidant activities and causes severe oxidative stress (Rui et al., 2016).

Previous research has shown that the application of plant growth-promoting phytohormones can improve protection by counterbalancing heavy metal toxicity in plants (Masood et al., 2016). ABA concentration increase as plants is exposed to heavy metals (Rauser and Dumbroff, 1981). Heavy metals like Zn, Al, Ni, and Cd (Fediuc et al., 2005) have been revealed to raise in ABA level in plants. Hsu and Kao, (2003) reported that at high temperature (30/35°C), ABA regulates and increase the resistance against Cd in rice seedlings. It's proven that ABA-mediated the Cd-precipitated stimulation of O-acetylserine (*OASTL*), the enzyme responsible for cysteine biosynthesis. The expression of ABA and drought resistance BjCdR9 (an aldehyde dehydrogenase) and BjCd55 (RNA binding protein) genes stimulated by Cd in Brassica Juncea supported the involvement of ABA signal transduction and these genes denoting aquaporins *PIP1* and *PIP2* was found to be transcribed when exposed to Cd stress. The above observation gave information that water stress is imposed by Cd and that ABA and Cd show the synergistic relationship (Fusco et al., 2005). When plants are treated with ABA, both BjCd15 and *TGA3* responded to ABA. However, TGA shows more response to ABA as compared to *BjCdR15* (Farinati et al., 2010).

Zhao et al. (2016) observed that Cd concentration increased in roots and leaves at a higher dose of CdCl_2 in JA- deficient tomato mutants. The result shows that a lack of JA biosynthesis enhances the sensitivity against Cd. According to Sirhindi et al., (2015), the exogenous application of JA enhance the tolerance to NiCl_2 in soybean seedlings and it regulates the antioxidant activities to neutralize the heavy metal stress at the cellular level in plants, while Azeem U et al., (2018) revealed that exogenous JA application increases the biomass production and protein concentration in Ni-treated plants and minimize the Cd accumulation rate by enhancing osmotic and antioxidant activities, but also inhibiting H_2O_2 and Malondialdehyde accumulation (Noriega G et al., 2012). JA inhibit the peroxidase activity by activating ascorbate or glutathione antioxidant machinery. Such findings reports show that JA plant responses by inducing antioxidant system.

Although these research reports suggest that phytohormones responsive genes are differentially expressed under various abiotic stress conditions, further indicating/corroborating crosstalk between plant bio-stimulants and abiotic stress signalling.

Conclusion and future prospectus

Environmental stresses can significantly reduce the yield potential and shift in cultivation area may occur for commercially important fruit crops by climate change. Now need to improve the biosynthesis and utilization of phytohormones without any negative impact by genetic modification in fruit crops to improve tolerance against abiotic stresses. Recently, much attention has been given to the development of strategies designed for breeding to alleviate the adverse effects of abiotic stress by using different phytohormones, from the foregoing research works discussion it is clear that plants utilize elaborate signaling pathways in response to various abiotic stresses. In addition to ROS, antioxidants, and other biochemicals, plant hormones trigger specific signal cascades upon abiotic perception. The vacillation in several key hormone levels and crosstalk among phytohormones occur as early response to stresses. Such crosstalk at the hormonal level in plants helps to integrate various stress signaling pathways. The enhanced level of tolerance to environmental stress at the molecular level by adjusting growth factors is the key role to the plant survival. These have been illustrated in the present review with appropriate research results drawn from the abiotic and biotic stress responses in fruit crops.

Conflict of Interest:

We declare that, we have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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