Popular Article

TRENDS IN AGRICULTURE SCIENCE

Vol.3 Issue 05 May 2024, Page: 1844-1851

Metabolic Pathways Regulation in Plants for the Development of Heat and Drought Tolerance

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https://doi.org/10.5281/zenodo.11399667

Summary

High temperature and water deficit conditions are the two major abiotic threats influencing proper growth and development of crop plants by imposing negative impact on the physiological and biochemical processes of the plants. Globally, continuous increase in temperature and drought decreases crop production and impacted per capita food availability. To ensure global food security in the era of climate change, development of new strategies may provide an opportunity for the development of stress-tolerant crop cultivars to ensure global food security. Several attempts including conventional breeding, molecular breeding, functional genomics, and transgenic approaches have been employed for the development of heat and drought-tolerant crop cultivars. Recently, metabolic pathway manipulations come into existence for strategic crop improvement for various biotic and abiotic threats. In this literature, we discuss the various approaches of metabolic pathway manipulation for the development of heat and drought tolerance in crop plants.

1. Introduction

Among the abiotic stresses, drought and heat are the most damaging, often causing harmful effects on the economic yield of the crops. Particularly, the occurrence of drought and heat stress is more devastating at the reproductive stage of the crops than at other phenological stages (Lamaoui, et al., 2018). Besides, the combinational effect of drought and heat is greater than the individual stress effect. Therefore, robust biotechnological approaches that emphasise the development of tolerance in crop plants will significantly accelerate the opportunity for introgression of stress tolerance in crop plants.

To date, several attempts have been made by the researchers for development of stress tolerance in plants through genetic manipulation of the plants including trait/gene introgression, gene manipulation, introgression of genes from one to other crop cultivars etc.

However, due to the polygenic nature of drought and heat stress, multiple gene or pathway manipulation may give robust responses in the development of long-term stress tolerance in the crop plants (Sinha, et al., 2021). Thus, the improvement of plants for drought and heat tolerance may require promising metabolic pathway manipulation (Tenorio Berrio, et al., 2022). In context

Published: 26 May 2024

ISSN: 2583-7850

to metabolic pathway manipulation for development of drought and heat tolerance, several candidate metabolic pathways including γ-aminobutyric acid (GABA) biosynthesis pathway, starch biosynthesis, phenylpropanoid biosynthesis and plant hormonal signalling pathways have been identified are involved in the heat and drought tolerance mechanism. We summarised the role of these metabolic pathways in the regulation of drought and heat stress in the plants.

2. γ- aminobutyric acid (GABA) pathway

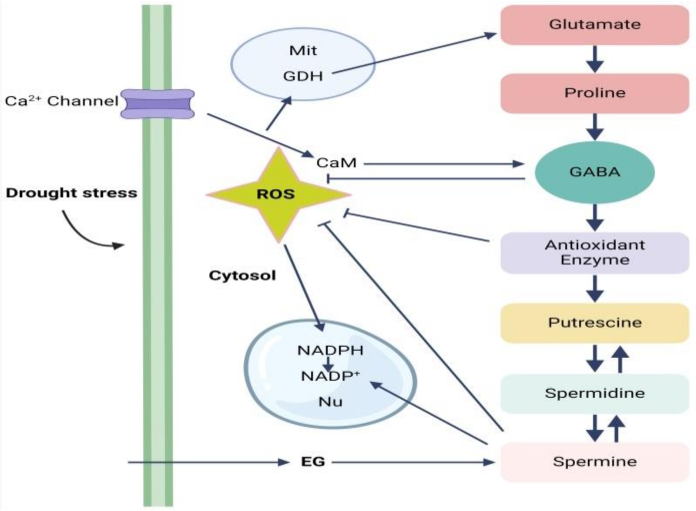
GABA is one of the important components of metabolite biosynthesis in plants. GABA pathway involved as intermediates in the amino acid biosynthesis and nitrogen metabolism. GABA is a non-protein part of the amino acid, which tends to accumulate as protective compounds against drought and heat stress. Under acute drought and heat stress, GABA increases osmolytes and leaf turgor pressure and reduces oxidative damage via oxidant regulation. It may also provide benefits in the stomatal closure, transpiration and regulating the release of tonoplast-localised anion transporter. Such type of alteration in the plant body may increase the water use efficiency and abiotic stress tolerance; particularly drought and heat tolerance. However, exogenous application of GABA may also increase the activity of antioxidant enzymes and the glyoxylate systems involved in the MG detoxification (Li, et al., 2021).

2.1 GABA biosynthesis in plants: In plants, GABA is biosynthesized by the GABA shunt pathway. GABA shunt pathway is important for GABA production and maintenance of GABA level. GABA biosynthesis is catalysed by enzymes glutamic acid decarboxylase (GAD), succinic semi-aldehyde dehydrogenase (SSADH) and transaminase. GAD and SSADH are cytosolic enzymes while transaminase is a mitochondrial enzyme.

2.2 GABA induced drought and heat regulation in plants: When plants are subjected to heat and drought conditions, most of the cellular components of the plants are damaged due to overproduction of reactive oxygen species (ROS). Overproduction of ROS induces proline biosynthesis under drought conditions. All metabolites like proline, *Ala, Glu,* and GABA involved in the development of tolerance in plants against drought and heat stress are directly associated with GABA shunt pathway. These GABA shunt pathway synthesised metabolites are accumulated in the plants in response to reduce the over expression of ROS.

The role of GABA against drought stress induced oxidative damage has been experimented in many plant species. Application of GABA increased leaf area, dry shoot weight and shoots weight in plants under drought and heat stress. Therefore, manipulation of biosynthetic pathways associated with GABA shunt pathway for over expression of GABA may regulate drought and heat stress tolerance in plants (Figure–1).

Published: 26 May 2024
ISSN: 2583-7850



Figure–1: GABA pathways in drought stress regulation

3. Starch biosynthesis in response to drought and heat stress

Starch metabolism in plants may increase cellular carbohydrate and starch storage. In response to drought and high temperature, starch breakdown releases a range of sugars against stress exposure. The strategic breakdown of starch may also boost carbon flow into hexose phosphate in response to drought and heat stress. A number of investigations have shown that starch is synthesised during the day period and mobilised during the night periods in the plant organs, while photosynthesis is not possible (Figure–2).

3.1 Starch metabolism in plants: Starch metabolism is well studied in the model genetic plant *Arabidopsis thaliana* where starch is degraded via network of reactions employing multiple enzymes. During night time, hydrolytic enzymes β-amylase attack on the non-reducing end of the starch to release maltose in the leaf chloroplast. The starch degrading enzyme β-amylase (BAM3) is also involved in the hydrolysis of α-1,6- branches of starch into short soluble malto-oligosaccharides. Synergistically, debranching enzyme isoamylase (ISA3) is also involved in the hydrolysis of starch into soluble malto-oligosaccharides.

Therefore, the activity of BAM3 and ISA3 depends on the phosphorylation of the starch with the help of three enzymes- glucan water diskinase (GWD), phosphoglucan water diskinase (PWD), and phosphoglucan phosphatase starch excess 4 (SEX4). Hence, starch phosphorylation increases the hydration level and disrupts their crystallinity and facilitates the action of glucan-hydrolyzing enzymes. It is well studied that starch metabolism plays functional role to control water and CO_2 exchange and also helps to generate organic acids and sugars to increase the turgor of guard cells and promote stomatal conductance. This type of degradation of starch in plants plays pivotal role in the regulation of drought and heat tolerance.

3.2 Starch metabolism induced drought and heat regulation in plants: It is well documented in *Arabidopsis thaliana*, the transcripts of many enzymes of starch degradation in the leaf at light

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Published: 26 May 2024
ISSN: 2583-7850

hours co-ordinately peaked towards the end of the day and fell to low at the end of the night. Therefore, the associated gene expression does not correlate with the amount of enzyme activity.

Starch metabolism plays a key role in mediating abiotic stress response particularly in drought, high temperature, and high soil salinity. During abiotic stresses, starch acts as a signalling molecule employing ABA-dependent signalling pathway to activate downstream components in the stress responsive cascade. Several transcriptional regulations of starch metabolism have been reported are associated with ABA-dependent genes directly involved in the primary carbohydrate metabolism. Meanwhile, accelerated biosynthesis of ABA plays a pivotal role in heat and drought tolerances in plants are associated with the alteration of starch metabolism. Exogenous ABA induced starch degradation increases freezing tolerance in plants (Keskin, et al., 2010). So, manipulation of the starch degradation pathway rapidly accelerates the drought and heat stress regulation in plants for development of tolerance. However, transcriptional modification plays a critical role in the abiotic stress management in plants.

4. Phenylpropanoid biosynthetic pathway in regulation of heat and drought stress

Phenylpropanoid is the phenolic compound, naturally synthesised in the plant and plays crucial role in several physiological and biochemical processes. The biosynthesis of phenylpropanoid generally activated in the plants under abiotic stressed condition like drought, high temperature, and salinity. Phenylpropanoid have potential to scavenge harmful reactive oxygen species under stress conditions.

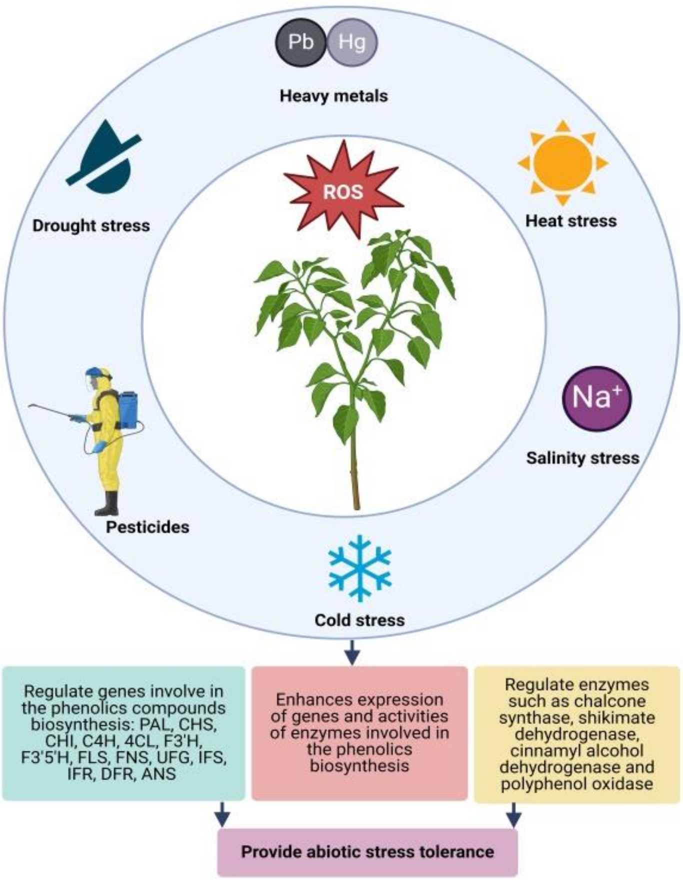
4.1 Phenylpropanoid biosynthetic pathway in plants: Phenylpropanoid are secondary plant products composed of aromatic rings and phenolic in nature. Biosynthesis of phenylpropanoid initiated from phenylalanine. Due to phenolic in nature, biosynthesis of phenylpropanoid, initiated through phenylpropanoid pathway, and through shikimate pathway. Phenolic compound is biosynthesized by erythrose-1-phosphatase and phosphoenolpyruvate to phenylalanine. In the next step, phenylalanine is converted into trans-cinnamic acid in presence of enzyme phenylalanine ammonia lyase (PAL). Several compounds including phenylpropanoid, lignans, tannins, coumarins, etc. are from through this biosynthetic pathway (Hasan, et al., 2018). This pathway is commonly known as the phenylpropanoid pathway.

5. Role of phenolics in response to drought and heat tolerance

Biosynthesis of polyphenols in plants confers the higher degree tolerance against various abiotic stresses like drought, salinity, high and low temperature. When plants are subjected to stressful conditions, they synthesise more phenolic compounds and other secondary metabolites in comparison to normal environmental conditions. The polyphenols/ phenylpropanoid rapidly synthesised in the plants under acute environmental conditions scavenging free radicals, ROS, and reducing cell membrane peroxidation (Kumar, et al., 2019). These enzymes also up regulate transcript level of genes encoding key biosynthetic enzymes like PAL, cinnamate-4-hydroxylase 4-coumarate and CoA ligase, chalcone isomerase, flavonoid 3'-hydroxylase, isoflavone synthase, flavonol synthase, etc.

Drought stress is regulated by accumulation of phenolic compounds in plants. The drought- induced accumulation of phenolic compounds is the modulation of phenylpropanoid biosynthetic pathway. Several key genes encoding enzymes associated with phenylpropanoid result in the stimulation of phenolic compound biosynthesis. Therefore, strategic manipulation of the biosynthetic pathway of the phenolic compounds and flavonoid accelerates the drought tolerance mechanism by reducing the effect of ROS and other membrane related phenomena (Smirnov, et al., 2015).

Global warming due to high temperature also influences proper growth and development of plants. Increase in temperature stimulates endogenous phenolic biosynthesis in plants and provides strength to develop tolerance against toxic effects caused due to high temperature, increased accumulation of anthocyanin, flavonoids, flavonols, and phenolic acid confers tolerance to survive against high temperature. So, alteration of associated pathway for excess biosynthesis of these compounds may also accelerate the tolerance rate in plants by protecting cells under both low and high temperature conditions.



Figure–2: Plant Phenolics in regulation of abiotic stresses

Published: 26 May 2024
ISSN: 2583-7850

6. Phytohormonal regulation in heat and drought regulation

Phytohormones are naturally biosynthesised in very low concentrations in the plants and play pivotal roles in the growth and development under normal environmental conditions. Some phytohormones play a key role and coordinate signal transduction pathways in response to abiotic stresses like drought, heat, chilling, salinity, and metal toxicity. Apart from the phytohormones, ABA has been identified as stress responsive hormones in the plant system. ABA plays a crucial role in the plant development processes such as inhibition of germination, growth regulation, stomatal conductance, and abscission in response to abiotic stresses (Hasan, et al., 2021).

6.1 Abscisic acid: The abscisic acid biosynthesized in the plant is one of the essential messengers to regulate abiotic stress and accelerate tolerance level. In response to abiotic stress like heat and drought/ salinity, ABA level increases rapidly in plants for activating signalling pathways in context to modifying gene expression (Sreenivasulu, et al., 2010). It has been reported that ABA transcriptionally regulates up to 10 per cent protein encoding genes and acts as an internal signalling for the plants to survive under adverse environmental conditions (Nemhauser, et al., 2006). Furthermore, ABA regulates numerous stress-responsive genes and in synthesis of LEA proteins, dehydrin and other protective proteins (Shahzad, et al., 2018). They also regulate the cell turgor maintenance, synthesis of osmo-protenctants, antioxidants, enzymes, etc.

6.2 Cytokinin: Cytokinin (CK) has been identified to enhance their endogenous level under water-stressed conditions in plants. Reduced CK content leads to ABA accumulation for increasing ABA/ CK ratio to regulate water deficit stress. However, decreased CK level enhances apical dominance which together with ABA regulates stomatal conductance as water scavenger in adaptation to drought stress (Zalabak, et al., 2013).

6.3 Ethylene: Ethylene (ET) levels in plants are altered by the abiotic stress. Enhancing high concentrations of ET plays a major role in the regulation of heat and drought stress. Furthermore, modulation of gene expression associated with high concentration of ET plays an important role in the regulation of heat and drought stress. Moreover, the combination of ET with jasmonate (JA) and salicylic acid (SA) play a major role in the regulation of biotic stress like defence against pests and insects (Shi, et al., 2012).

Recent findings have shown that the tremendous potential of brassinosteroids (BRs) mitigate abiotic stresses such as high temperatures, chilling, soil salinity, drought, etc. through modulating antioxidant defence systems (Janeczko, et al., 2011). However, there is tremendous scope of BRs in plants to regulate and mitigate abiotic stress. Therefore, phytohormone engineering for the manipulation of biosynthetic pathways and signalling could be a robust platform from improving tolerance levels against the abiotic stresses like drought, heat, salinity and metal toxicity (Figure–3).

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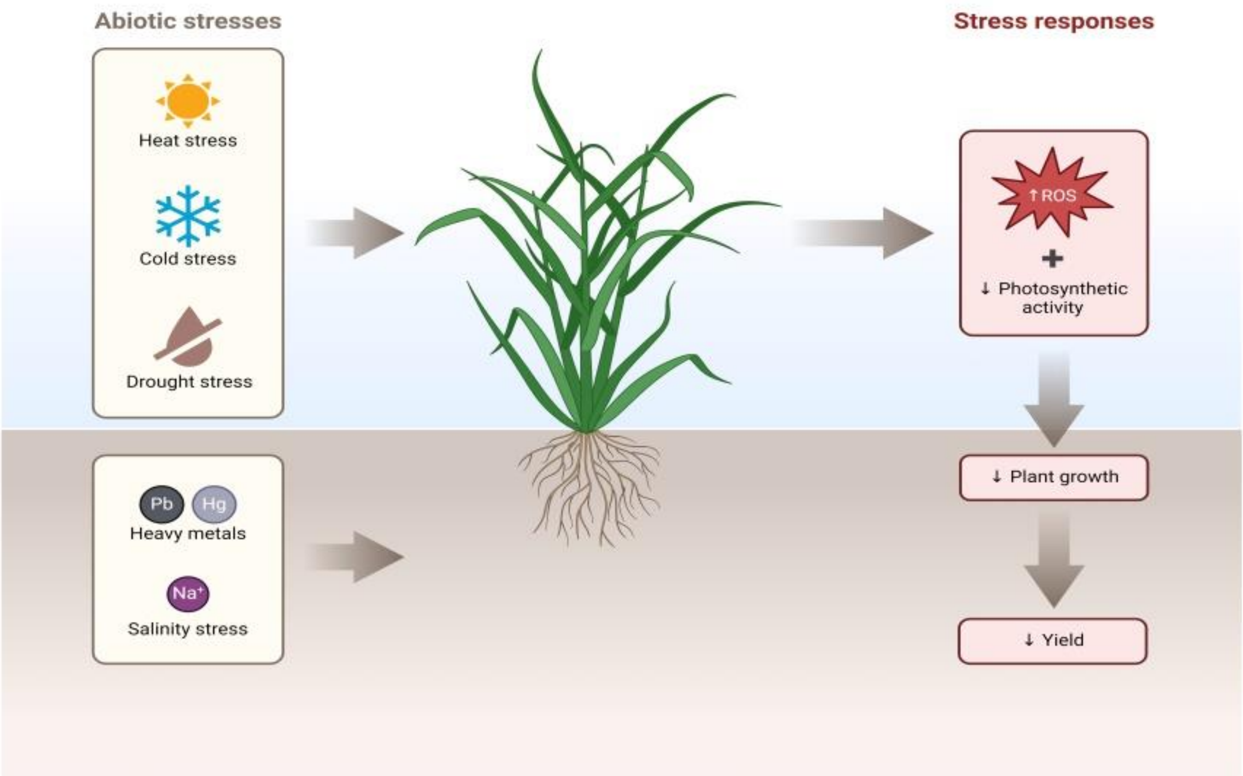

Figure–3: Photosynthetic activity and ROS in abiotic stress regulation

7. Conclusion

Secondary plant products naturally biosynthesised in the plants have several kinds of signalling attitude in the regulation of abiotic stress. Future research needs to manipulate the biosynthesis and signalling for the development of tolerance mechanisms to mitigate said abiotic threats. Furthermore, manipulation in the transcriptome to enhance the gene expression of those metabolites may also accelerate stress mitigation in plants to complete their life cycle under acute environmental conditions.

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