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Unlocking Auxin's Potential: How Plants Use Auxin Transport to Beat Drought

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ABSTRACT

Drought stress is a major environmental challenge that adversely affects plant growth and development. Auxin, a vital plant hormone, plays a crucial role in various aspects of plant development and morphogenesis, ranging from embryogenesis to senescence. Acting as internal growth regulators, auxinic compounds coordinate plant responses to their ever-changing environment. Stressing conditions, such as high or low temperature, salinity, drought or flooding, impact auxin biosynthesis, transport and signaling. Among these stresses, accumulating evidence indicate important roles of auxin upon drought and submergence. In Arabidopsis, crops and trees, auxin upon drought modifies the fine architecture and tropisms of plant organs to tolerate or escape stress. However, there is limited information on the modulation of auxin distribution, abundance, and localization of auxin transporters during drought stress. In this mini review, we discuss the impact of drought stress on modulation of auxin distribution or gradients, also the abundance of auxin transporters upon drought, and the involvement of auxin carriers in mediating drought stress responses.

Keywords: Arabidopsis; Auxin; Drought Stress; Trafficking; Polarity; Activity Regulation; Protein Interaction

Introduction

Plants are resilient species that can adapt to a wide range of environmental conditions and cope with various biotic and abiotic stresses. Drought stress is one of the most challenging conditions for plants and has significant negative impacts on their growth, survival, and productivity. Abiotic stress causes immediate changes in plant tissue architecture by inhibiting meristematic activities, reducing cell elongation rhythms, and decreasing root cell radial expansion. In the long term, drought stress alters plant architecture, especially the length of roots or/and the number of lateral roots [1-4]. Nevertheless, plants attempt to mitigate the negative effects of through various molecular and physiological responses. Understanding these key molecular and physiological pathways is the focus of studies aimed at developing drought-tolerant crops. An understudied aspect of plant responses to drought stress that has recently gained importance is how hormones are modulated by and involved in plant response to drought stress. Phytohormones are endogenous plant chemicals involved in regulating almost all aspects of growth, development, and response to environmental stimuli. It is therefore not surprising that recent research has focused on understanding the involvement of hormones in plant responses to gravity, light, nutrients, and biotic stresses. Recent evidence points to phytohormones including auxin in coordinating plant adaptive responses to drought.

This has been demonstrated by studies showing that auxin content in aboveground tissues decreases, while its accumulation in root cortical tissues increases during drought stress. In addition, drought-induced or ectopically expressed auxin biosynthesis genes (*GH3.13*, *YUCCA*) have been detected in drought-resistant plants [5-7]. Possibly due to the positive regulation of auxin on drought resistant genes such as RDs, DREB2s [7]. Conversely, DREB2s also link drought and auxin signaling by directly regulating the transcriptional auxin repressors *IAA5* and *IAA19* [8]. This suggests that auxin biosynthesis, transport, and signaling are modulated early after the onset of drought stress to fine-tune and coordinate plant responses. In this

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mini review, we will briefly discuss the modulation of auxin biosynthesis and transport by drought and the implications of these modulations for plant adaptation strategies to this stress.

Drought-Induced Modulation of Auxin Biosynthesis

Drought stress leads to changes in auxin homeostasis and biosynthesis, which in turn leads to changes in the distribution and content of auxin in the plant [6,7]. Studies in *Arabidopsis* have shown that drought stress leads to both local and systemic changes in auxin levels [9,10]. Drought-induced reduction of water potential in roots and subsequent systemic signaling from root to shoot lead to auxin redistribution, which affects various developmental and adaptive processes [11,12]. Drought stress has been shown to affect the expression of the auxin biosynthesis genes *YUCCA* and *TAA*. The transcription factor DREB2B, which is strongly induced by drought and salt stress [7,8], directly represses the expression of *YUCCA* and *TAA1* in the shoot. This reduction in shoot auxin levels stimulates ABA-induced stomatal closure, minimizing water loss by transpiration. Moreover, the *YUCCA* genes are induced in the root upon/during drought in *Arabidopsis*, maize, and rice and are related to the promotion of root growth that seeks new water resources in the soil to alleviate drought stress. The *YUC7* gene is induced by drought primarily in the roots, and elevated levels of free auxin in Arabidopsis activation-tagged mutant *yuc7-1D* promotes root growth and enhances root architecture. Accordingly, *yuc7-1D* plants are resistant to drought and show upregulation of drought-responsive genes [13].

Involvement of Auxin Transporters in Drought Stress Response

Auxin gradients and dynamics of auxin flux in plants vary drastically under both drought and salinity stresses [14-16]. Auxin carriers, including influx and efflux transporters, play a central role in regulating auxin transport and distribution in the plant. Drought stress affects the expression and activity of these auxin transporters, thus influencing the spatiotemporal distribution of auxin.

PIN (PIN-FORMED) Proteins

These are auxin efflux carriers localized at the plasma membrane and play a critical role in controlling the direction and extent of auxin flux and generating the auxin gradient in plants. Drought stress has been shown to modulate the expression of PINs in the shoot and root. *PIN1* and *PIN2* were down regulated by drought whereas *PIN3*, *PIN4*, and *PIN7* were up regulated in the root of plant subjected to drought (Figure 1). Rapid posttranslational modification has been shown to coordinate the allocation and redistribution of PINs at the plasma membrane. Consequently, changes in the polar localization of PINs in response to various developmental or environmental signals can dynamically alter auxin flow, thereby affecting plant physiological and morphological processes [17-21]. PIN1, PIN2, and PIN3 have been confirmed to be phosphorylated in drought-stressed plants. This modulation of PINs expression, stability, activity, and membrane localization is considered part of the plant adaptation responses to drought stress.

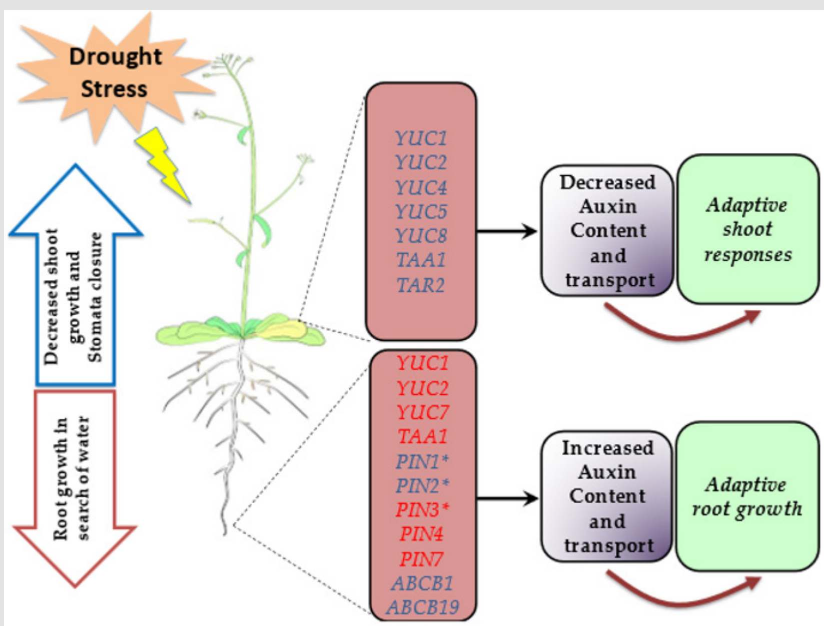

Figure 1: Regulation of Auxin Transporters and Biosynthetic Genes: Impact on Plant Response to Drought Stress.

Note: This figure illustrates an overview of the involvement of auxin transporters and biosynthetic genes in different regulatory states [up-regulated (Red) or down-regulated (Blue) in shoots and roots, and their impact on plant response to drought stress. It highlights the key genes involved and showcases the resulting plant physiological responses. Asterisks indicate proteins that have been shown to be phosphorylated in drought-stressed plants.

Recent evidence indicates that osmotic perturbations affect the balance between endocytosis and exocytosis in the root meristem. Acute hyperosmotic stress attenuates exocytosis by promoting clathrin-mediated endocytosis, whereas the opposite effect is observed during hypo-osmotic stress [22]. Furthermore, salt-induced endocytosis of PIN2 as an adaptive mechanism triggers changes in auxin redistribution in root tips, enabling directional bending of the root away from the stressor [23]. However, our understanding of the molecular mechanisms involved in membrane trafficking of polar-localized PINs during stress is still limited. To gain a more comprehensive understanding of how auxin flux is adjusted in response to stress, further focused studies are required to elucidate the cellular regulation of membrane trafficking under stress conditions.

ABCB (ATP-BINDING CASSETTE B) Transporters

These are ATP-dependent auxin efflux carriers involved in auxin long-distance transport. Drought stress reduces the expression and activity of ABCB transporters in roots. ATP Binding Cassette (ABC) transporters, and putative auxin transporters PILS (PIN-LIKES) play vital roles in inter- and intra-cellular auxin transport. In maize, transcriptional analysis has shown that the stress-responsive genes *ZmLAX, ZmPIN, ZmPILS*, and *ZmABCB* exhibit contrasting expression patterns in shoots and roots under salinity, drought, or cold conditions. The expression of *ABCB1* and *ABCB19* was reduced in Arabidopsis roots under drought stress. The upstream regulators of these transporters during drought stress remain to be elucidated [24].

AUX / LAX (AUXIN RESISTANT / LIKE AUX1) Transporters

These transporters are auxin influx carriers localized in the plasma membrane and are responsible for the uptake of auxin into cells. Therefore, the effects of drought stress on these transporters are thought to influence canonical auxin signaling. In the root, the expression of AUX/LAX is modulated in response to the level of drought stress to either maximize root growth in search of water resources or generally arrest growth to ensure survival. Mutations in *AUX1/LAX* genes impact vital plant processes including root development, gravitropism, vascular patterning, seed germination, phyllotactic patterning, female gametophyte development and embryo development [25].

Towards Crop Resilience and Sustainable Agriculture

Insights gained from studying auxin biosynthesis, transport, and signaling under drought stress in *Arabidopsis thaliana* have far-reaching implications for crop improvement and sustainable agriculture. By understanding the molecular and biochemical makeup of auxin transport under drought stress, researchers can identify genetic targets and develop innovative strategies to enhance crop resilience to water scarcity. Manipulation of auxin transporters, transcription factors, and signaling pathways offers promising opportunities for the development of drought-tolerant crops. One potential application is the development of transgenic crops with improved water use efficiency by altering auxin transport. By enhancing the ability of crops to regulate auxin distribution under drought stress, researchers can optimize water uptake, root growth, and thus soil foraging strategies, and stress responses.

The advent of advanced genomics technologies such as CRISPR-Cas9 gene editing and high-throughput phenotyping has accelerated progress in this field, providing researchers with powerful tools to unravel the molecular basis of auxin transport regulation and explore its potential for crop improvement. The insights gained from studying auxin transport in Arabidopsis thaliana have broad applications in other crop species. While regulatory mechanisms may differ, the fundamental principles of auxin transport remains consistent across plants. Therefore, leveraging knowledge gained from Arabidopsis research holds significant potential for improving drought resistance in economically important crops. Furthermore, understanding auxin transport in the context of drought stress may pave the way for the development of environmentally friendly and sustainable agricultural practices. By manipulating auxin transport and associated regulatory pathways, it may be possible to promote plant growth and productivity under limited water availability, minimize the need for excessive irrigation, and reduce environmental impacts.

Conclusion

Molecular and biochemical analysis of auxin transport during drought stress in Arabidopsis thaliana has enhanced our understanding of plant responses to water scarcity. It unravels intricate regulatory networks and hormone interactions. Looking ahead, these findings offer promising avenues to improve plant resistance to drought and develop sustainable agricultural practices. By harnessing the power of genetic engineering, precision breeding and advanced molecular techniques, we can pave the way for resilient crops that ensure food security and environmental sustainability even under water-limited conditions.

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