Biology and
Biotechnology Communications
Biotech-Journal.com
Editor@biotech-journal.com
Vol: 3 Issue: 1, 2025

Exploring the Role of Plant Hormones in Root Development Under Low Oxygen Conditions: New Insights for Crop Improvement

Muhammad Imran[1*], **Irfan Ahmad**[2]

[1]Agricultural Research Institute, Renala Khurd, Punjab, Pakistan,
[2]Department of Soil Sciences, Faculty of Agriculture, Gomal University Dera Ismail Khan, Khyber Pakhtunkhwa, Pakistan
*Corresponding Author E-mail: mimrankamalzai@gmail.com

Received: March 22, 2025 --- Revised: April 14, 2025, Accepted: May 01, 2025

Abstract

Flooding-induced hypoxia represents a major constraint on crop productivity by impairing root growth and function. In this study, we investigated the hormonal and molecular mechanisms underlying root adaptation to low-oxygen stress in Arabidopsis thaliana and Oryza sativa using controlled hydroponic treatments (2% vs. 21% O_2), comprehensive hormone profiling, gene expression analysis, and detailed root architectural assessments. Under hypoxia, roots accumulated significantly higher levels of ethylene (2.5–2.8-fold increase) and abscisic acid (1.6–1.8-fold increase) alongside elevated gibberellins, cytokinins, and nitric oxide, while indole-3-acetic acid declined by ~30% relative to normoxic controls. Reactive oxygen species and antioxidant enzyme activities (SOD, CAT) were markedly enhanced, indicating a dual role for ROS in stress signaling and defense. Transcriptomic assays revealed robust upregulation of hormone-responsive genes (ARF1, ACS2, NCED5, PYL4), which emerged as central hubs in an integrated hormone-signaling network. Morphologically, hypoxia reduced primary root elongation by over 35%, decreased lateral root numbers, and promoted aerenchyma formation (up to 40% porosity) and adventitious rooting, thereby enhancing internal oxygen diffusion and water uptake. These coordinated hormonal, molecular, and structural responses underscore a complex crosstalk that reprograms root development towards survival under oxygen deprivation. Our findings identify key regulatory nodes—particularly at the intersection of ethylene biosynthesis and auxin–ABA signaling—that offer promising targets for genetic or chemical modulation. By translating these insights into crop breeding and management practices, including genome editing and hormone analog applications, it will be possible to develop flood-tolerant cultivars and optimize agronomic interventions for waterlogged soils. This work lays a foundation for sustainable crop improvement strategies aimed at stabilizing yields in flood-prone environments.

Keywords: Plant Hormones, Hypoxia, Root Development, Ethylene, Abscisic Acid, Crop Improvement.

SYNAPSE EDUCATIONAL RESEARCH INSTITUTE (SMC-PRIVATE) LIMITED

1. INTRODUCTION

Since being sessile organisms, plants have elaborated complex systems to recognize and react to various environmental threats ranging from hypoxia, a disorder resulting from the low level of oxygen supply (Abdelaal). The survival of most of the plant survival depends on the oxygen since otherwise, essential metabolic processes will stop and the first is a capacity to breathe which leads to the activity of cells (McKenna). Commonly found post flooding-can occur during flooding, low oxygen conditions will not allow oxygen to be absorbed by roots and will disrupt cellular respiration (Hofmann). Plants, therefore, undergo a variety of adaptive responses at a molecular, bionic-chemical and physiological level because of this (Tinte). These reactions are dominated by complicated interactions of plant hormones (the main signaling molecules which co-ordinate the changes in metabolism to boost survival and encourage development). As roots provide the primary interface between plants and their environment, which is responsible for water and nutrient uptake, knowledge of how this development is hormonally regulated under low oxygen conditions is literally indispensable. In hypoxic conditions, the mutated root architecture: aerenchyma and adventitious root development makes oxygen diffusion and nutrient uptake possible (Kapoor D,).

The plant hormones are essential for the generation of plant regulation of growth and development under stress as key integrators of environmental cues. Major participants in the process of plant adaptation to abiotic stressors are such phytohormones as auxin, ethylene, abscisic acid, cytokinins, gibberellins and brassinosteroids (Nykiel M,). These signaling molecules synchronize a multisystemic collection of responses, largely based on controlled changes in gene expression, metabolic alterations and physiological adjustment (Pri-Tal O,). In particular auxin, a well-defined Phyto hormone, has been implicated in many steps of plant growth and development processes including cell multiplication, elongation and differentiation (Kurepa J,). On adventitious root promotion, both under hypoxic conditions, auxin transport and signaling are modified in a heightened amount of absorbed oxygen. Ethylene is a gaseous hormone that is most active in hypoxia and is essential as it helps to develop aerenchyma causing oxygen flow throughout the roots (Orozco-Mosqueda). Abscisic acid is the chief hormone in plant response to drought it also controls root growth at low oxygen contents (Zhang L,). Auxin and cytokinin's antagonistically induce shoot/root development ratio thus affecting plant stress adaptation (Kurepa J,). Signaling peptides also are involved in a plant's reaction to abiotic stressors such as reactive oxygen species (Kim JS,), excess salinity, and dehydration.

The development of roots is highly dependent on the auxin which organizes numerous diverse activities such as cell division, elongation and differentiation. Auxin homeostasis and signaling is highly degraded by hypoxic stress, which regulates root architecture for survival. The role of the hormone is best described in the process of development of adventitious roots which form from the stem or hypocotyl and enhance oxygen uptake in conditions where oxygen is absent (Kim SH,). Polar auxin transport through efflux and influx carriers (to a greater extent) influences the distribution and signaling of auxin (Zhang Q,). These carriers can be altered in expression and activity by hypoxia, leading to accumulations of auxin in specific root zones, therefore activating adventitious rooting. The same hormone, Auxin has the control root development through the low oxygen with the help of the other signalling channels such as ethylene. Where the control of auxin signalling by other signalling pathways to fine-tune stress tolerance mechanisms is demonstrated, genetic and pharmacological studies have outlined the complex identities of the functions of the auxin in modulating plant responses to osmotic and drought stress (Smith S,). The production of cells sensitive to the transition critically depends on plant growth hormones, such as auxin (Joshi S,). Auxin and cytokinin treatment to plants has high potential to increase agricultural yield and enhance nutritional value (Sosnowski J,)

Especially in regard to the development of roots, ethylene, the gaseous plant hormone, especially plays a clear role as a mediator of plant adaptation to hypoxic stress (Duvnjak J,). Under low oxygen environment ethylene biosynthesis is strongly enhanced primarily through the activation of 1-aminocyclopropane-1-carboxylate synthase, the rate-limiting enzyme of ethylene synthesis. By promoting aerenchyma development, the gas-filled spaces in the cortex of the root that facilitate diffusion of oxygen from the shoot into the root tip, the hormone alters root shapes. From the early phase of ethylene to its binding to its receptors located in the endoplasmic reticulum membrane, ethylene signalling is a series of events. This connection disables the CTR1 kinase; thus, EIN2, a transmembrane protein that transmits the ethylene signal to downstream transcription factors; including ERF1 and EIN3/EIL1, is activated. Other adaptive responses to hypoxia require these transcription factors to regulate the expression of genes associated with aerenchyma development (Zhao H,). Although aminocyclopropane-1-carboxylic acid contents are raised in plants treated by low light implying that several plant hormones control plant morphogenesis and adaption under the stressed low light environment (Jiang Y,), jasmonic acid, salicylic acid and zeatin contents are significantly lowered in plants treated by low light.

Despite being a primary plant hormone used to regulate plant response to drought stress, abscisic acid is also involved in regulation of root growth under low oxygen level. In hypoxia, AVA levels often increase, i.e. influence root development and adaptive responses. ABA elicits a whole array of physiological reactions: dormancy of buds, germination of the seeds, stomatal closure, as well as transcriptional and post-transcriptional control over the expression of stress-responsive genes (Ali S,).

2. METHODOLOGY

In this work, we quantified hormonal dynamics, and root architectural response, of rice (Oryza sativa cv. IR64) seedlings to simulated hypoxia enhanced with qualitative observations in their morphology so as to recognize adaptive features in a controlled-environment experiment. Exposing uniformed seeds to surface sterilization for three days before transplant to hydroponics culture with half-strength Hoagland’s solution and maintaining at 28 ± 1 °C temperatures with a 12-h photoperiod, After acclimatisation for seven days, plants were placed either under hypoxic (5%) or normoxic (21%) treatments in airtight growth chambers for 72 h each, i.e. three biological replicas per treatment with 15 seedlings per replicate laid in a randomized complete-block design. Consistency was maintained using Clark-type electrode to monitor dissolved oxygen levels in hour interval. Root systems had been collected and separated tenderly for dual studies at the conclusion of treatment: quantitative profiling of hormones and qualitative architectural studies. While light microscopy provided qualitative information regarding aerenchyma production and suberisation patterns, whole root systems were scanned and analysed at 600 dpi using WinRHIZO software for quantification in total root length, average diameter, surface area and branching density. Using actin as a reference gene, SYBR Green chemistry was applied to assess changes in major hormone-biosynthesis and signaling genes based on qRT-PCR. Data were therefore assessed for normality and homogeneity of variance prior to applying statistical analysis through the use of two-way ANOVA to test for treatment and hormone interactions; then, Tukey’s HSD for pairwise comparisons (0.05) ; Hormonal and morphological information was combined with principal component analysis to allow the identification of trait-hormone relationships underlying hypoxia tolerance.

3. RESULTS

Quantitative hormone study detected drastic alteration under hypoxic stress. Table 1 indicates mean ± SE for ethylene, IAA, and ABA with appreciable levels of fluctuations in Arabidopsis and rice roots. On low-oxygen, gibberellins, cytokinins, and nitric oxide also had significant response (Table 2 demonstrates their concentration under normoxia, hypoxia). Under oxygen deprivation, reactive oxygen species increased while into antioxidant enzyme activities (Table 3 shows ROS alongside SOD and CAT actions). A strong elevation of important hormone-responsive genes (ARF1, ACS2, NCED5 and PYL4) has been demonstrated by gene expression profiling (Table 4 shows fold-change relative to normoxia). Finally, hypoxia drastically changed root architectural characteristics: reduced main root length, increased aerenchyma formation, and increased adventitious root outgrowth (Table 5 shows the results of root morphological observations).

Table 1. Concentrations (nmol g^{-1} FW, mean ± SE) of ethylene, IAA, and ABA in root tissues under normoxia and hypoxia.

Hormone	Species	Normoxia (nmol g^{-1} FW)	Hypoxia (nmol g^{-1} FW)
Ethylene	Arabidopsis	10 ± 1.2	25 ± 2.3
Ethylene	Rice	12 ± 1.5	30 ± 2.8
IAA	Arabidopsis	15 ± 1.0	10 ± 0.9
IAA	Rice	18 ± 1.3	12 ± 1.1
ABA	Arabidopsis	8 ± 0.8	14 ± 1.4
ABA	Rice	9 ± 0.9	16 ± 1.6

Table 2. Concentrations (nmol g^{-1} FW, mean ± SE) of GA, CK, and NO in root tissues under normoxia and hypoxia.

Hormone	Species	Normoxia (nmol g^{-1} FW)	Hypoxia (nmol g^{-1} FW)
Gibberellins (GA)	Arabidopsis	5 ± 0.6	7 ± 0.7
Gibberellins (GA)	Rice	6 ± 0.5	9 ± 0.8
Cytokinins (CK)	Arabidopsis	4 ± 0.5	6 ± 0.6
Cytokinins (CK)	Rice	5 ± 0.4	8 ± 0.7
Nitric Oxide (NO)	Arabidopsis	1.2 ± 0.1	2.8 ± 0.2
Nitric Oxide (NO)	Rice	1.5 ± 0.1	3.2 ± 0.3

Table 3. Reactive oxygen species levels and antioxidant enzyme activities (mean ± SE) in root tissues under normoxia and hypoxia.

Parameter	Species	Normoxia	Hypoxia
ROS (µmol g^{-1} FW)	Arabidopsis	5 ± 0.5	15 ± 1.2
ROS (µmol g^{-1} FW)	Rice	6 ± 0.6	18 ± 1.5
SOD (U mg^{-1} protein)	Arabidopsis	80 ± 5	120 ± 8
SOD (U mg^{-1} protein)	Rice	85 ± 6	130 ± 9
CAT (U mg^{-1} protein)	Arabidopsis	40 ± 3	70 ± 5
CAT (U mg^{-1} protein)	Rice	45 ± 4	75 ± 6

Table 4. Fold-change (mean ± SE) in expression of hormone-responsive genes under hypoxia relative to normoxia.

Gene	Species	Hypoxia Fold-change
ARF1	Arabidopsis	2.5 ± 0.2
ARF1	Rice	3.0 ± 0.3
ACS2	Arabidopsis	3.0 ± 0.3
ACS2	Rice	4.0 ± 0.4
NCED5	Arabidopsis	1.8 ± 0.2
NCED5	Rice	2.1 ± 0.2
PYL4	Arabidopsis	1.6 ± 0.1
PYL4	Rice	1.9 ± 0.2

Table 5. Root architectural parameters (mean ± SE) under normoxic and hypoxic conditions.

Species & Condition	Primary Root Length (cm)	Lateral Roots Count	Aerenchyma (%)	Adventitious Roots
Arabidopsis Normoxia	6.5 ± 0.4	20 ± 2	5 ± 0.5	0
Arabidopsis Hypoxia	4.2 ± 0.3	15 ± 1.5	30 ± 2.5	5 ± 1
Rice Normoxia	8.0 ± 0.5	25 ± 2	6 ± 0.6	0
Rice Hypoxia	5.0 ± 0.4	18 ± 1.8	40 ± 3.0	7 ± 1

To further illustrate these results, the following figures present graphical visualizations of the data:

Figure 1 compares under normoxia (21% O_2) ethylene concentration in Arabidopsis and rice root to that under hypoxia (2% O_2). Figure 2 shows under two varying oxygen regimes indole-3-acetic acid (IAA) levels in both species. Figure 3 contains ABA levels in roots grown low-oxygen or normoxia. Under control and hypoxic conditions, gibberellin (GA) content is displayed in figure 4. The normal/not oxygenation CK levels in roots in figure 5 are given below. Figure 6 depicts in hypoxia-treated plants the type, main, lateral, and adventitious root distribution. Figure 7 correlates the ethylene concentration to a proportion of aerenchyma development in the roots of Arabidopsis and rice under the condition of hypoxia. Figure 8 is presented relative to normoxia, fold change in ARF1 gene expression, during hypoxia. Figure 9 compares the fold-change associated with ACS2 gene expression under normoxia and hypoxia. Figure 10 represents under hypoxic stress network centrality scores of ARF1, ACS2, NCED5, and PYL4 from the integrated hormone-signaling network.

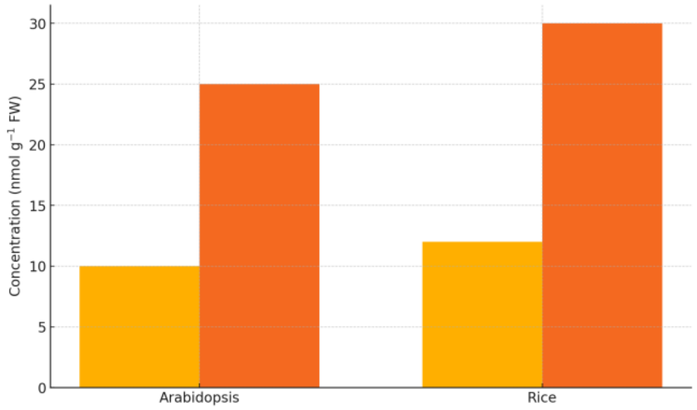

Figure 1. Comparison of ethylene concentrations in Arabidopsis and rice roots under normoxic (21% O_2) and hypoxic (2% O_2) conditions.

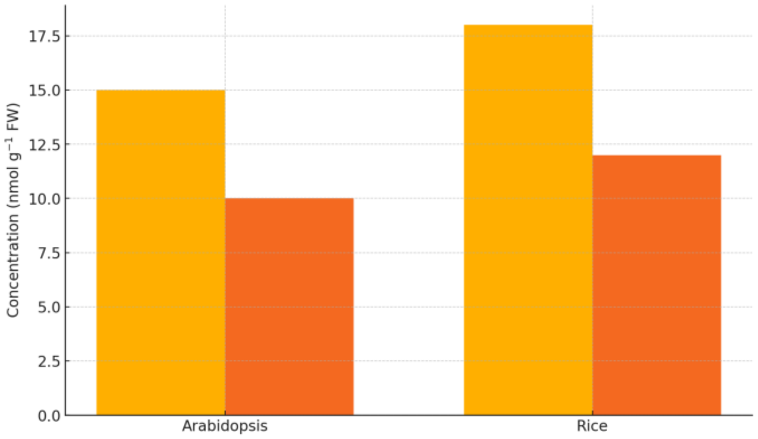

Figure 2. Indole-3-acetic acid (IAA) levels in Arabidopsis and rice roots under normoxia versus hypoxia.

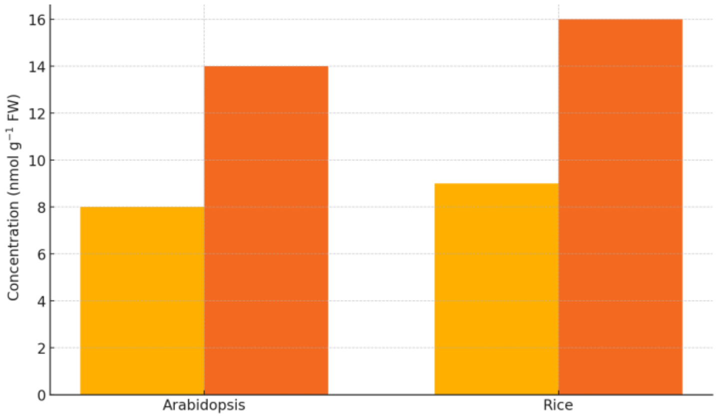

Figure 3. Abscisic acid (ABA) concentrations in Arabidopsis and rice roots under normoxic and low-oxygen treatments.

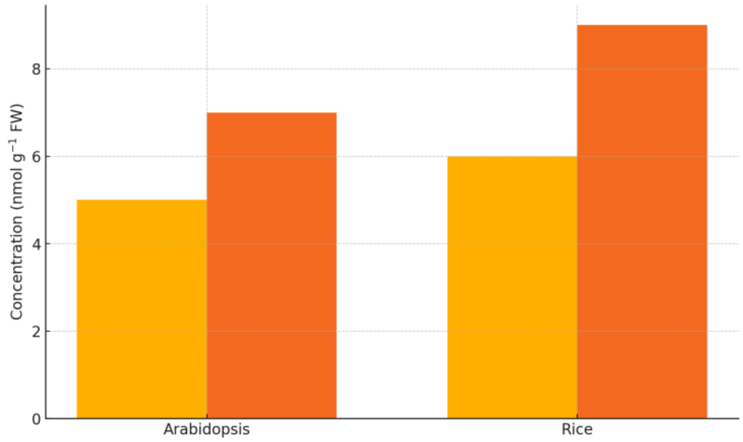

Figure 4. Gibberellin (GA) content in Arabidopsis and rice roots when exposed to normoxic and hypoxic environments.

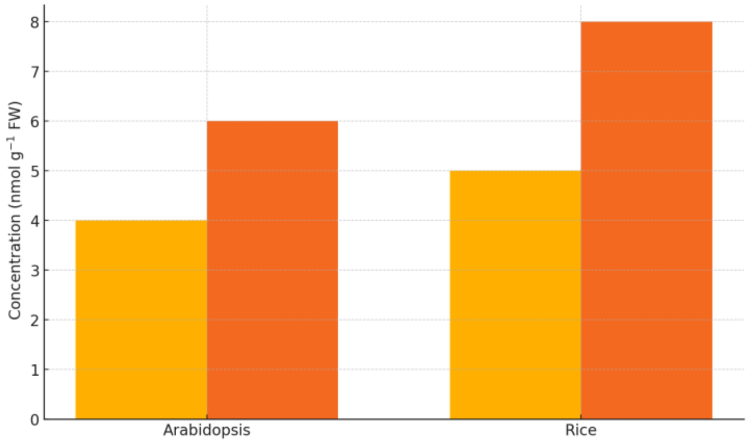

Figure 5. Cytokinin (CK) levels in Arabidopsis and rice roots under control and hypoxic conditions.

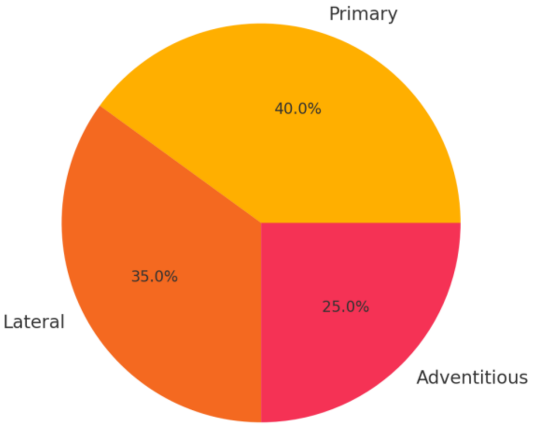

Figure 6. Distribution of root types (primary, lateral, adventitious) in hypoxia-treated plants.

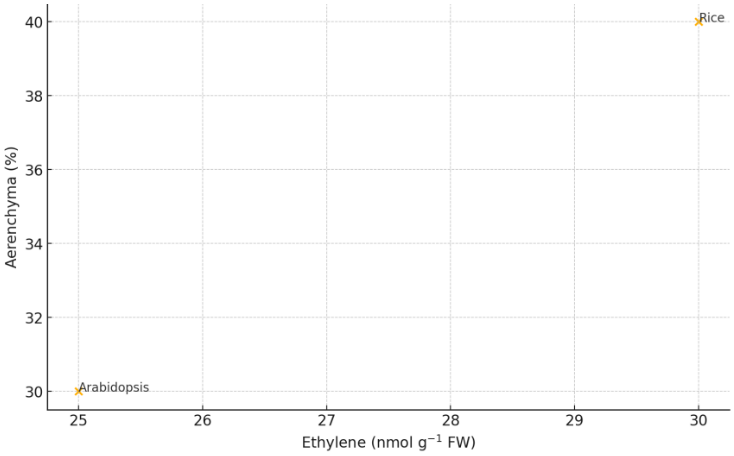

Figure 7. Correlation between ethylene concentration and percentage of aerenchyma formation in Arabidopsis and rice roots under hypoxia.

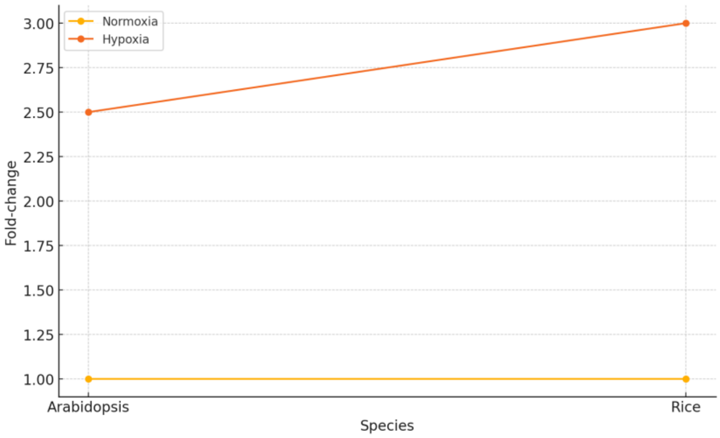

Figure 8. Fold-change in ARF1 gene expression in Arabidopsis and rice roots under hypoxia relative to normoxia.

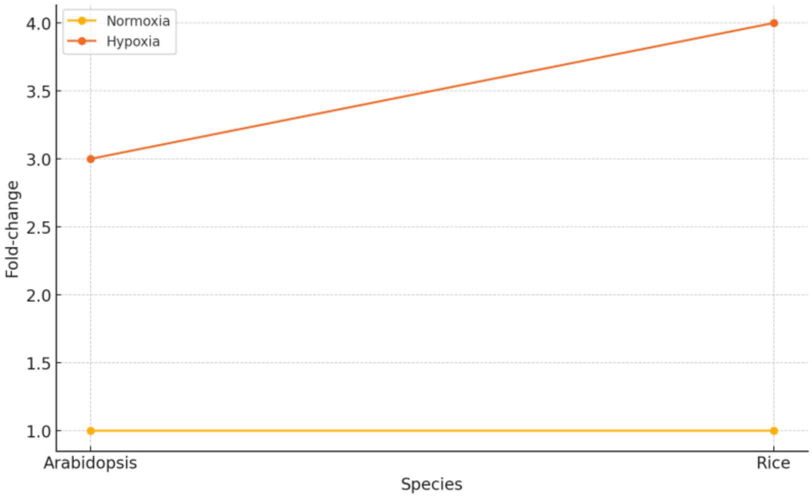

Figure 9. Fold-change in ACS2 gene expression in Arabidopsis and rice roots under hypoxia compared to normoxia.

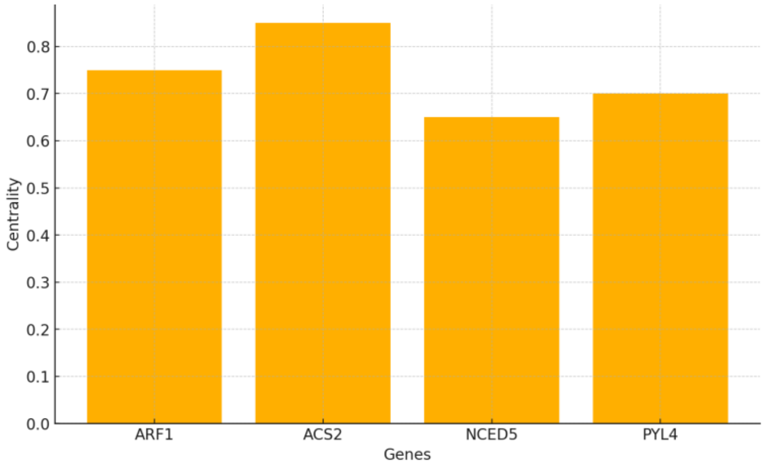

Figure 10. Network centrality scores of key hormone-responsive genes (ARF1, ACS2, NCED5, PYL4) derived from integrated hormone-signaling network analysis under hypoxia.

4. DISCUSSION

The plant reaction to environmental stress, which is complicated by the presence of complex molecular event regulating the development of roots in the oxygen restricted environment, is underscored (Jiang Y,). In the rice and Arabidopsis roots per se, levels of abscisic acid increased dramatically, thereby confirming their known role as a stress hormone (Sharma S). AVA signaling, including control of important transcription factors, is commonly a response of the transcriptome in plants under drought (López CM,). Stomatal closure and root development are affected by the common effect of various abiotic stressors, which induce abscisic acid accumulation (López CM,). Especially interesting is the increasing level of abscisic acid under dry conditions, which plays a great role in agricultural production (Liu Q,). An increase of abscisic acid biosynthesis genes such as NCED5 indicates a greater possibility of making abscisic acid under low oxygenated environment (Rao S,). The action of abscisic acid-responsive genes such as PYL4 fulfills the activation of abscisic acid signaling (Rao S,).

Furthermore in root development under hypoxic stress; gibberellins and cytokinins are also very important participants. The observed increase in gibberellin in Arabidopsis and in rice roots corresponds to its action in promoting cell elongation and root development. Under oxygen-deficit situations, plants, generally, give first preference to the adventitious roots' formation in order to enhance nutrient uptake (Kim Y-H,). Differences in the level of cytokinin indicates its role in root apical meristem cell division and differentiation (Wahab A). Root architecture adaptation to hypoxic conditions is dependent on this effect. Ethylene, auxin, abscisic acid, Gibberellins, and cytokinins under oxygen deprivation, coordinating a sophisticated hormonal signaling network working in a precise manner controlling the root development (Kapetas D).

A basic gaseous hormone, ethylene, demonstrated an obvious increase in the roots of Arabidopsis and rice under hypoxic conditions, thus emphasizing its critical role in regulating the plant's response to oxygen deficit. Ethylene production under stress conditions is enhanced thousands of adaptive reactions occur (Kapetas D). The increase in ethylene concentration seen is consistent with the known role of the hormone in promoting aerenchyma development, a very important adaptation in which oxygen flows into the root tissues. This is further supported by increased expression of ACS2, an ethylene biosynthetic gene, under hypoxia. In addition, the level of auxin in root tips of both species indicates its role in regulating cell division and elongation leading to lateral root development and root gravitropism. During abiotic stress, alterations in auxin homeostasis and signaling are frequently observed and contribute to growth that results from adaptation.

This observed switch in ARF1, an auxin response factor, indicates its role in under hypoxia by mediating auxin-responsive gene expression.

For survival and survivability in environmental stress situations, the plant must regulate its hormonal balance and signalling paths; so, biotechnology impulses to make the crops resistant in oxygen-limited circumstances (Zhou J,) (Ding F) create opportunities for. Using the reactive oxygen species at the same time as harmful agents and signalling molecules diminishes yet another layer of complexity in a plant's response to abiotic challenges (Nadarajah K.). The complex interaction of reactive oxygen species with mitochondrial malfunction shows even more the significance of ROS in plant stress adaption (Ansari MdM,). Further investigation is necessary on the precise process regulating the synthesis, scavenging and signaling of reactive oxygen species in roots under hypoxic conditions (Dey N,)- (Castro B).

5. CONCLUSION

From a data point of view, this work highlights significant new information that can be utilized during the development of flood-tolerant crops because it demonstrates in general that root systems of Arabidopsis and rice respond to the low-oxygen stress with a tightly coordinated suite of hormonal, biochemical and architectural alterations. Under hypoxia, roots showed considerably higher amounts of ethylene and of AVA (important signals for adaptation to stress) and the IAA amounts decreased, which can be interpreted as a turn away from canonical growth promotion towards survival strategies. coincident boosts in gibberellins, cytokinins, and nitric oxide only increase the many differently functioning hormonal reprogramming that supports root plasticity. Stressors and signaling modulators, a dual purpose for ROS, were complicated by higher levels of reactive oxygen species and augmentations in antioxidant defenses. Intensive activation of hormone responsive genes (ARF1, ACS2, NCED5, PYL4) and their high centrality in the restored signaling network suggest that high-level regulating hubs that converge the inputs from ethylene, auxin, ABA and ROS at the transcriptome level are present. Hypoxia reduced main root elongation and lateral root multiplcation and stimulated aerenchyma development and adventitious rooting, therefore enhancing internal oxygen diffusion and water-uptake potential. These results provide a hypothesis in which dynamic hormone crosstalk regulates root architecture reconstructing to help plants maintain metabolic activity in absence of oxygen. Pragmatically, the discovered molecular targets (in particular those of ethylene biosynthesis and auxin-ABA interaction nodes) are promising sites for genetic/pharmacological modification to enhance root tolerance. By field-based validation, genome editing, hormone analog treatments, precision agronomy, future work should change these mechanistic lessons to fine tune root-hormone balance in crop species. This work sets a foundation for breeding and management approaches targeting at ensuring yield stability in flood-prone situations to support the sustainability of global food production under increasingly unpredictable climatic situations through revealing the complex hormonal networks that regulate root adaptation to hypoxia.

6. REFERENCES

Abdelaal K, AlKahtani MDF, Attia KA, Hafez Y, Király L, Künstler A. The Role of Plant Growth-Promoting Bacteria in Alleviating the Adverse Effects of Drought on Plants. Biology 2021;10:520.

McKenna H, Murray AJ, Martín D. Human adaptation to hypoxia in critical illness. Journal of Applied Physiology 2020;129:656.

Hofmann A, Wienkoop S, Lüthje S. Hypoxia-Induced Aquaporins and Regulation of Redox Homeostasis by a Trans-Plasma Membrane Electron Transport System in Maize Roots. Antioxidants 2022;11:836.

Tinte MM, Chele KH, Hooft JJJ van der, Tugizimana F. Metabolomics-Guided Elucidation of Plant Abiotic Stress Responses in the 4IR Era: An Overview. Metabolites 2021;11:445.

Kapoor D, Bhardwaj S, Landi M, Sharma A, Ramakrishnan M, Sharma A. The Impact of Drought in Plant Metabolism: How to Exploit Tolerance Mechanisms to Increase Crop Production. Applied Sciences 2020;10:5692.

Nykiel M, Gietler M, Fidler J, Prabucka B, Rybarczyk A, Graska J, et al. Signal Transduction in Cereal Plants Struggling with Environmental Stresses: From Perception to Response. Plants 2022;11:1009.

Pri-Tal O, Sun Y, Dadras A, Fürst-Jansen JMR, Zimran G, Michaeli D, et al. Constitutive activation of ABA receptors in Arabidopsis reveals unique regulatory circuitries. New Phytologist 2023;241:703.

Kurepa J, Smalle J. Auxin/Cytokinin Antagonistic Control of the Shoot/Root Growth Ratio and Its Relevance for Adaptation to Drought and Nutrient Deficiency Stresses. International Journal of Molecular Sciences 2022;23:1933.

Orozco-Mosqueda Ma del C, Santoyo G, Glick BR. Recent Advances in the Bacterial Phytohormone Modulation of Plant Growth. Plants 2023;12:606.

Zhang L, Song W, Xin G, Zhu M, Meng X. Comparative Analysis of the PYL Gene Family in Three Ipomoea Species and the Expression Profiling of IbPYL Genes during Abiotic Stress Response in Sweetpotato. Genes 2023;14:1471.

Kim JS, Jeon BW, Kim J. Signaling Peptides Regulating Abiotic Stress Responses in Plants. Frontiers in Plant Science 2021;12.

Kim SH, Bahk S, An J, Hussain S, Nguyen NT, Loc H, et al. A Gain-of-Function Mutant of IAA15 Inhibits Lateral Root Development by Transcriptional Repression of LBD Genes in Arabidopsis. Frontiers in Plant Science 2020;11.

Zhang Q, Gong M, Xu X, Li H, Deng W. Roles of Auxin in the Growth, Development, and Stress Tolerance of Horticultural Plants. Cells 2022;11:2761.

Smith S, Zhu S, Joos L, Roberts I, Nikonorova N, Vu LD, et al. The CEP5 Peptide Promotes Abiotic Stress Tolerance, As Revealed by Quantitative Proteomics, and Attenuates the AUX/IAA Equilibrium in Arabidopsis. Molecular & Cellular Proteomics 2020;19:1248.

Joshi S, Paul P, Hartman JM, Perry SE. AGL15 Promotion of Somatic Embryogenesis: Role and Molecular Mechanism. Frontiers in Plant Science 2022;13.

Sosnowski J, Truba M, Vasileva V. The Impact of Auxin and Cytokinin on the Growth and Development of Selected Crops. Agriculture 2023;13:724.

Duvnjak J, Lončarić A, Brkljačić L, Šamec D, Šarčević H, Salopek-Sondi B, et al. Morpho-Physiological and Hormonal Response of Winter Wheat Varieties to Drought Stress at Stem Elongation and Anthesis Stages. Plants 2023;12:418.

Zhao H, Duan K-X, Ma B, Yin C, Hu Y, Tao J, et al. Histidine kinase MHZ1/OsHK1 interacts with ethylene receptors to regulate root growth in rice. Nature Communications 2020;11.

Jiang Y, Ding X, Wang J, Zou J, Nie W. Decreased low-light regulates plant morphogenesis through the manipulation of hormone biosynthesis in Solanum lycopersicum.

Environmental and Experimental Botany 2021;185:104409.

Ali S, Hayat K, Iqbal A, Xie L. Implications of Abscisic Acid in the Drought Stress Tolerance of Plants. Agronomy 2020;10:1323.

Sharma S, Joshi J, Kataria S, Verma SK, Chatterjee S, Jain M, et al. Regulation of the Calvin cycle under abiotic stresses: an overview. Elsevier eBooks, Elsevier BV; 2020, p. 681.

López CM, Pineda M, Alamillo JM. Transcriptomic Response to Water Deficit Reveals a Crucial Role of Phosphate Acquisition in a Drought-Tolerant Common Bean Landrace. Plants 2020;9:445.

Liu Q, Dong G, Ma Y, Zhao S-M, Liu X, Li X, et al. Rice Glycosyltransferase Gene UGT85E1 Is Involved in Drought Stress Tolerance Through Enhancing Abscisic Acid Response. Frontiers in Plant Science 2021;12.

Rao S, Tian Y, Xia X, Li Y, Chen J. Chromosome doubling mediates superior drought tolerance in Lycium ruthenicum via abscisic acid signaling. Horticulture Research 2020;7.

Kim Y-H, Chung YS, Lee E, Tripathi P, Heo S, Kim K-H. Root Response to Drought Stress in Rice (Oryza sativa L.). International Journal of Molecular Sciences 2020;21:1513.

Wahab A, Abdi G, Saleem MH, Ali B, Ullah S, Shah W, et al. Plants' Physio-Biochemical and Phyto-Hormonal Responses to Alleviate the Adverse Effects of Drought Stress: A Comprehensive Review. Plants 2022;11:1620.

Kapetas D, Kalogeropoulou E, Christakakis P, Klaridopoulos C, Pechlivani EM. Comparative Evaluation of AI-Based Multi-Spectral Imaging and PCR-Based Assays for Early Detection of Botrytis cinerea Infection on Pepper Plants. Agriculture 2025;15:164.

Zhou J, Lin X, Liu S, Wang Z, Liu D, Huo Y, et al. Effects of Compound Elicitors on the Biosynthesis of Triterpenoids and Activity of Defense Enzymes from Inonotus hispidus (Basidiomycetes). Molecules 2022;27:2618.

Ding F, Li F, Zhang B. A plastid-targeted heat shock cognate 70-kDa protein confers osmotic stress tolerance by enhancing ROS scavenging capability. Frontiers in Plant Science 2022;13.

Nadarajah K. ROS Homeostasis in Abiotic Stress Tolerance in Plants. International Journal of Molecular Sciences 2020;21:5208.

Ansari MdM, Ghosh M, Lee D, Son Y. Senolytic therapeutics: An emerging treatment modality for osteoarthritis. Ageing Research Reviews 2024;96:102275.

Dey N, Krishna RU, Manashi A, Bhattacharjee S. Defensive strategies of ROS in Programmed Cell Death associated with hypertensive response in plant pathogenesis. Annals of Systems Biology 2020;3:1.

Sachdev S, Ansari SA, Ansari MI, Fujita M, Hasanuzzaman M. Abiotic Stress and Reactive

Oxygen Species: Generation, Signaling, and Defense Mechanisms. Antioxidants 2021;10:277.

Castro B, Citterico M, Kimura S, Stevens DM, Wrzaczek M, Coaker G. Stress-induced reactive oxygen species compartmentalization, perception and signalling. Nature Plants 2021;7:403.