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The Role of Roots as an Adaptive Mechanism in Cereals Under Combined Abiotic Stresses †

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Abstract

Climate change has intensified the occurrence of combined abiotic stresses such as drought, salinity, heat, and waterlogging, thereby threatening cereal productivity and global food security. Root systems play a central role in plant adaptation to these interacting stresses by regulating water uptake, ion balance, nutrient acquisition, and stress signaling. However, many previous studies have primarily focused on individual stress factors rather than integrated stress environments. This review synthesizes current knowledge regarding root-mediated adaptive mechanisms in cereal crops under combined abiotic stresses, with emphasis on barley (*Hordeum vulgare*), wheat (*Triticum aestivum*), and oats (*Avena sativa*). The review highlights how root system architecture, including root depth, branching density, and aerenchyma formation, contributes to stress resilience under interacting environmental conditions. Physiological and molecular mechanisms involving ion transporters, aquaporins, transcription factors, and auxin-regulated root plasticity are also discussed. In barley, deeper and steeper root systems improve water acquisition under combined drought and heat stress, while wheat genotypes carrying the HKT1;5 allele exhibit enhanced sodium exclusion under drought–salinity interactions. Oats respond to waterlogging and salinity through adventitious root formation and enhanced oxygen transport. Overall, this review emphasizes the importance of root-targeted approaches for improving cereal adaptation under increasingly complex multi-stress environments.

Keywords: root system architecture; cereals; combined abiotic stress; drought; salinity; wheat; barley; oats; climate resilience

1. Introduction

Climate variability and extreme environmental conditions have increasingly threatened global agriculture. Abiotic stresses, such as drought, salinity, and temperature extremes, are among the most significant constraints to crop productivity [1]. These stresses have been found to occur simultaneously, resulting in many challenges for plant crops [2]. Wheat, barley, and oats are a major part of the global food system, and the mentioned abiotic stresses cause cereal crops to become vulnerable to environmental and climate changes.

Climate projections predict that salinity and drought frequency will intensify in many agricultural regions, while heat waves are expected to become more severe [1]. This causes photosynthetic efficiency, plant metabolism disruption, as well as water and nutrient uptake to become reduced [3]. Unlike individual stresses, combined abiotic stresses cause outcomes that are either synergistic or non-additive, leading to reduced plant growth rates,

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as well as yield [2]. Additional evidence also supports intensified multi-stress interactions under future climate scenarios [4].

Although numerous studies have investigated cereal responses to individual abiotic stresses, comparatively fewer studies have examined how root systems contribute to adaptation under combined stress conditions. Combined stresses often trigger physiological and molecular responses that differ significantly from those observed under single stress conditions. Therefore, this review synthesizes current knowledge regarding root-mediated adaptive mechanisms in cereals exposed to interacting abiotic stresses. Particular emphasis is placed on root system architecture, physiological root responses, molecular regulation, and the implications of these mechanisms for climate-resilient cereal crop breeding.

2. Literature Search Strategy

This review was conducted using a narrative literature review approach, focusing on root-mediated adaptive responses of cereal crops under combined abiotic stresses. Relevant peer-reviewed studies published between 2005 and 2025 were identified using databases, including Google Scholar, Scopus, Web of Science, and PubMed. Search terms included combinations of "root system architecture", "combined abiotic stress", "drought and salinity", "heat and drought stress", "root adaptation", "cereal stress tolerance", and "root plasticity". Studies were selected if they investigated cereal crops and examined morphological, physiological, or molecular root responses under abiotic stress conditions. Preference was given to studies involving interacting or combined stresses, and those addressing climate-resilient crop adaptation. The collected literature was synthesized thematically to identify common root-mediated adaptive mechanisms across cereal species.

3. Root System Architecture Under Combined Abiotic Stresses

Combined abiotic stresses frequently alter root growth patterns differently from individual stress conditions, requiring cereals to dynamically modify root system architecture for efficient resource acquisition and survival [2,5].

It has already been gathered from the previous section that root system architecture refers to the spatial configuration of roots within the soil profile. It is a fact that crops possessing deeper and more extensive rooting systems have a greater tolerance to drought, because they have the potential to access deeper soil moisture reserves [4]. Soil moisture gradients, oxygen availability, and nutrient distribution regulate root system architecture plasticity [6]. These environmental cues trigger developmental adjustments in root growth, thereby allowing plants to optimize resource acquisition under fluctuating conditions [7].

Resource acquisition under fluctuating conditions occurs by hydro-patterning and plastic nutrient foraging. Roots have the potential to sense nutrient gradients and localized water availability via auxin redistribution and aquaporin activity [7]. This directs lateral root growth toward favorable zones. Concurrently, carbon allocation from shoots becomes adjusted, thereby supporting root expansion in favorable areas [7]. This provides cereal crops the capacity to optimize nutrient and water uptake under fluctuating soil conditions [7].

4. Root Adaptations in Barley Under Combined Stress Conditions

Since barley has an adaptable root system, it is considered to be the most stress-tolerant cereal crop [5,8]. Some barley genotypes (e.g., ISR42-8) have been found to develop deeper and steeper axial roots under combined drought and heat stress conditions. These traits may additionally improve resilience under drought–salinity interactions by enhancing access to deeper soil moisture while maintaining root metabolic activity [5].

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Additionally, increased root plasticity is often coupled with this, enabling lateral root proliferation in nutrient-rich zones [7]. Furthermore, it pairs with osmotic adjustment in shoots, optimizing water use efficiency and sustaining plant growth during prolonged periods of drought [1,2]. Another adaptive trait is the development of root cortical aerenchyma. This characteristic reduces the metabolic costs of root maintenance and facilitates oxygen diffusion under stress conditions [8]. It achieves this by enhancing root porosity and oxygen supply under hypoxic conditions, thereby assisting roots to maintain metabolism and growth under fluctuating soil oxygen levels.

5. Root Adaptation in Wheat Under Drought–Salinity Stress

Drought and salinity stress pose major challenges for wheat production. One adaptive mechanism is the possession of sodium exclusion systems in root tissues. This system enables wheat plants to adapt to saline environments [9]. In wheat roots, the HKT1;5 gene has been identified as a major determinant of sodium transport [9]. Wheat plants carrying the favorable allele of this gene can restrict Na^+ movements from roots to shoots, thereby affording root tissue protection from ion toxicity [9]. In addition, wheat lines carrying this allele have been shown to exhibit slower anatomical adaptations in root vascular tissues. These wheat lines are found to have more developed metaxylem vessels and thicker endodermal cell layers that enhance selective ion transport, as well as limit sodium ion leakage into plant shoots. The merger of transporter activity and root vascular anatomy enhances the control of sodium movements. This protects root and shoot tissues under salt stress [10].

The interaction between ion transport regulation and root anatomical modification demonstrates how wheat roots integrate physiological and structural adaptation under combined stress environments [9,10].

6. Root Adaptation in Oats Under Waterlogging and Salinity

Oats is known to have unique adaptations to waterlogged and saline environments. In order to deal with waterlogging stress, oats develop adventitious roots near the soil surface. These roots facilitate oxygen uptake, as well as assist in maintaining root respiration under hypoxic conditions [11]. Furthermore, the development of sclerenchyma tissues aids in strengthening root structure and reducing toxic ion accumulation in oats.

If we delve into the internal structure of these adventitious roots, it is evident that oats form aerenchyma channels for oxygen transport. In addition, in oats, deposits of suberin and lignin are found in the endodermis and sclerenchyma, thereby limiting toxic ion entry. Furthermore, water flow and cellular metabolism are maintained through root-specific aquaporin and anti-oxidant enzymes, thereby enabling combined respiration and nutrient uptake under salinity and hypoxic conditions [10]. These adaptive traits illustrate the importance of root plasticity under simultaneous hypoxic and saline environments.

7. Molecular and Genetic Regulation of Root Responses Under Combined Stress

Root responses to combined abiotic stresses (Table 1) are regulated through interconnected molecular signaling networks involving transcription factors, hormone transporters, ion channels, and stress-responsive genes. Unlike individual stress, combined stress environments require coordinated regulation of multiple physiological pathways simultaneously [12]. For example, stress tolerance has been found to be regulated by NAC (NAM (No Apical Meristem), ATAF (Arabidopsis Transcription Activation Factor), CUC (Cup-Shaped Cotyledon)) and WRKY (Tryptophan (W), Arginine (R), Lysine (K), Tyrosine

(Y)) transcription factors. Some plant hormones, e.g., auxin, regulate root growth patterns through transport proteins, such as PIN 1 and PIN 3 [7].

Table 1. Comparisons of Root Responses of Wheat, Barley and Oats under Combined Abiotic Stress.

Cereal	Combines Stress	Root Trait	Adaptive Benefit	References
Wheat	Drought + Heat	Deep roots	Improved water uptake	[5]
Barley	Salinity + Drought	Root plasticity	Osmotic regulation	[8]
Oats	Heat + Salinity	Increased root biomass	Stress resilience	[11]

NAC and WRKY transcription factors coordinate gene expression for cell wall remodeling, osmoprotectant synthesis, and ion transport. This enables root physiology and structure adjustment under environmental stress [12]. PIN 1 and PIN 3, on the other hand, aid in plant adaptation to abiotic stresses by mediating fine-tuned auxin redistribution, steering root growth dynamically. Under water or nutrient limitations, PIN 1 directs auxin flow toward the root tip, thereby promoting root elongation into the deeper layers of soil, while PIN 3 modulates lateral auxin flow, thereby controlling root angle and branching. From this, it is evident that environmental cues become integrated with transcription networks through the mentioned protein transporters [7]. This enables roots to rapidly adjust their architecture so that they can forage for water and nutrients under different environmental stresses.

8. Advances in Root Phenotyping

Root phenotyping capabilities have been improved by recent technological advances. The observation of root growth in soil environments has been made using rhizotrons, while the visualization of root architecture in three dimensions has been achieved using X-ray computed tomography [12]. Shovelomics, on the other hand, has been used to provide practical methods for screening a large number of crop genotypes in the field [13].

9. Research Gaps and Future Perspectives

Despite significant advances in understanding root-mediated stress adaptation, major gaps remain regarding cereal responses under combined abiotic stresses. Many recent studies continue to focus on individual stress conditions, which may not accurately represent field environments, where multiple stresses occur simultaneously. Furthermore, the molecular crosstalk between drought, salinity, heat, and waterlogging responses remains insufficiently understood.

Future research should prioritize integrated multi-stress experiments, field-based root phenotyping, and the identification of root-associated genes involved in stress interaction pathways. Advances in genomics, transcriptomics, and root imaging technologies may provide new opportunities for developing climate-resilient cereal cultivars with enhanced adaptive root traits. Breeding programs should increasingly target root plasticity, hydraulic efficiency, and stress-responsive signaling networks so that crop performance under future climate scenarios can possibly be improved.

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10. Conclusions and the Implications for Climate-Resilient Breeding

Root systems play a fundamental role in cereal adaptation under combined abiotic stresses through integrated morphological, physiological, and molecular mechanisms. Traits such as deeper rooting, root plasticity, aerenchyma formation, osmotic adjustment, and ion transport regulation collectively improve plant resilience under interacting environmental stresses. Molecular regulators, including NAC and WRKY transcription factors, auxin transporters, and sodium transport systems, further coordinate adaptive root responses under complex stress conditions.

However, much of the recent literature remains focused on individual stress factors, highlighting the need for more integrated studies that reflect realistic field environments. Improved understanding of root-mediated adaptation under combined stresses will support the development of climate-resilient cereal crops capable of sustaining productivity under increasingly unpredictable environmental conditions.

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