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Physiological and Transcriptomic Responses of Grafted Citrus Rootstocks under Combined Drought and Salinity Stress

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Citriculture globally faces severe threats from environmental stressors, particularly the concurrent occurrence of drought and soil salinity. While individual stress responses in *Citrus* species are well-documented, combined stress factors trigger unique, interactive physiological and transcriptomic dynamics. Rootstocks play a crucial role in mediating abiotic stress tolerance by regulating water transport, ion homeostasis, hormone signaling, and scion transcriptomic reprogramming. This review examines the physiological adaptations (osmotic adjustment, ROS scavenging, and stomatal control) and transcriptomic networks (ion transporters, transcription factors, and hormone pathways) activated in grafted citrus combinations under combined drought and salinity stress.

Keywords: Citrus rootstocks, Grafting, Drought stress, Salinity stress, Transcriptomics, Osmoregulation, ROS scavenging.

Introduction

Citrus species are economically vital fruit crops cultivated in sub-tropical and Mediterranean climate zones. However, these regions are increasingly subjected to soil salinization and prolonged water scarcity driven by climate change (Rafie-Rad et al., 2023). Because most cultivated citrus cultivars are grown as scions grafted onto specific rootstock species, the rootstock serves as the primary interface between the plant and the soil matrix, making it critical for sensing soil-borne abiotic stresses. When drought and soil salinity co-occur, plants experience a compound stress environment. Drought restricts soil water potential, while high concentrations of dissolved ions induce osmotic stress and ion toxicity (Duan et al., 2022). Unraveling the physiological and transcriptomic mechanisms that govern rootstock-mediated stress tolerance is essential for breeding resilient citrus rootstock-scion combinations.

Physiological and Morphological Adaptations

Osmotic Adjustment and Water Relations

Under osmotic pressure caused by salinity and water deficits, rootstock roots lose hydraulic conductivity. To maintain cell turgor, rootstocks synthesize and accumulate compatible osmolytes, including:

- **Proline** (mediated by *P5CS* gene upregulation)
- **Glycine betaine** (mediated by *CMO* gene expression)
- **Soluble sugars and proteins**

These osmolytes lower internal osmotic potential, allowing continued water uptake without accumulating toxic levels of sodium or chloride in leaves (Snoussi et al., 2022).

ROS Scavenging and Antioxidant Defense

Combined stress accelerates the generation of reactive oxygen species (ROS), such as hydrogen peroxide and superoxide radicals, leading to lipid peroxidation as measured by malondialdehyde (MDA) accumulation (He et al., 2023; Rafie-Rad et al., 2023). Tolerant rootstocks retain cellular integrity by upregulating enzymatic antioxidants:

- **Peroxidase (POD)**
- **Catalase (CAT)**
- **Superoxide Dismutase (SOD)**

Non-enzymatic antioxidants, particularly flavonoids and phenolic compounds, further assist in ROS detoxification during osmotic and ionic shock.

Transcriptomic Networks and Gene Expression Regulators

Recent high-throughput RNA sequencing (RNA-seq) studies have uncovered distinct transcriptional profiles in citrus under osmotic and ionic stress (Snoussi et al., 2022).

Ion Transporter and Homeostasis Genes

Maintaining ion balance is crucial under saline conditions. Transcriptomic analyses reveal key expression shifts in:

- High-Affinity Potassium Transporters (*HKT1*)
- Sodium/Hydrogen Antiporters (*NHX1*)
- Cation-Chloride Cotransporters (*CCC1*)

Phytohormone Cross-Talk and Signaling Pathways

Abscisic acid (ABA) acts as the primary systemic signal regulating stomatal closure and stress-responsive gene expression. Key genes identified include:

- *ABSCISIC ACID-INSENSITIVE 5 (ABI5)* and *ABA-responsive element binding factors (ABF)*, which regulate stress-adapted gene transcription (He et al., 2023).
- Auxin-responsive genes (*Aux/IAA*, *SAUR*) and cytokinin regulators, which fine-tune root architecture and shoot growth during prolonged stress (He et al., 2023).

Transcription Factor (TF) Families

Transcription factors coordinate widespread transcriptomic reconfiguration under abiotic stress. Major upregulated TF families in citrus include:

- **MYB and NAC:** Modulate secondary metabolism and flavonoid biosynthesis.
- **AP2/ERF:** Regulate hormone-mediated stress pathways and hypoxia/osmotic responses (He et al., 2023).
- **bHLH, HSF, and HD-ZIP:** Fine-tune antioxidant and heat-shock responses.

Rootstock-Scion Interactions and Systemic Signaling

The rootstock controls scion physiological performance through systemic vascular signaling. Stress signals generated in the root system—including mobile peptide hormones, micro RNAs, and ABA - travel via xylem pathways to trigger transcriptomic changes in scion leaves (Duan et al., 2022).

Rootstock Variety	Relative Salt/Drought Tolerance	Key Physiological/Transcriptomic Feature
Rangpur Lime (*C. limonia*)	High	Superior osmoregulation; strong induction of *P5CS* and *NHX1*
Volkamer Lemon (*C. volkameriana*)	Moderate-High	High root vigor; robust antioxidant enzyme upregulation
Cleopatra Mandarin (*C. reshni*)	High (Salinity)	Steady stomatal control
Carrizo Citrange (*C. sinensis* $\times$ *P. trifoliata*)	Moderate	Moderate drought tolerance via stomatal regulation
Trifoliate Orange (*Poncirus trifoliata*)	Low (Salinity) / Moderate (Drought)	High cold hardiness, but sensitive to salt accumulation

Conclusion and Future Directions

The integration of physiological evaluations and transcriptomic profiling demonstrates that combined drought and salinity stress requires a co-coordinated cellular response. Grafted rootstocks confer scion stress tolerance by:

1. Activating osmotic adjustment mechanisms and ROS-scavenging enzymatic defense systems.
2. Inducing transcriptomic shifts in ion transporters (*HKT1*, *NHX1*) and transcription factors (*MYB*, *NAC*, *AP2/ERF*).
3. Generating mobile systemic signals that reconfigure leaf-level transcriptomes for optimized transpiration and photosynthesis.

Future breeding strategies should leverage multi-omics approaches (integrating transcriptomics, metabolomics, and phenomics) to select rootstocks capable of surviving complex, real-world environmental stress scenarios.

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