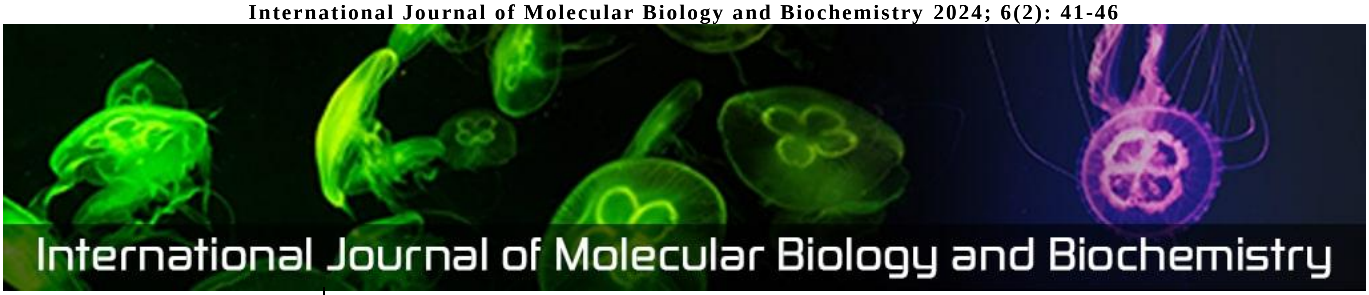

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Transcriptomic insights into abiotic stress tolerance in *Chenopodium quinoa* willd

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Abstract

Quinoa (*Chenopodium quinoa* Willd.), an emerging climate-resilient pseudocereal, is notable for its exceptional tolerance to salinity, drought, cold, and heat, yet the transcriptomic mechanisms underlying its multi-stress resilience remain incompletely resolved. The present study aimed to generate integrative insights into the molecular basis of quinoa abiotic stress tolerance by comparing two contrasting ecotypes—Titicaca (salinity-tolerant) and Regalona (cold-adapted)—under salinity, drought, cold, and heat treatments. Plants were grown in controlled conditions, subjected to stress at the six-leaf stage, and sampled for physiological and transcriptomic analyses. RNA sequencing was performed on Illumina NovaSeq, followed by differential expression, gene ontology, and co-expression network analyses.

Physiological data revealed clear ecotype-dependent responses: Titicaca maintained higher relative water content (78% vs. 61%) and photosynthetic efficiency under salinity, higher stomatal conductance under drought, and reduced biomass loss under cold, whereas heat stress caused the strongest reproductive penalty, especially in Regalona. Transcriptomic profiling identified 12, 845 differentially expressed genes (DEGs) across stresses, including conserved modules enriched for abscisic acid (ABA) signaling, reactive oxygen species detoxification, ion transporters, and universal stress proteins. Stress-specific modules included ion homeostasis genes under salinity, aquaporins and osmolyte pathways under drought, alternative splicing factors under cold, and chaperone proteins under heat. Weighted gene co-expression network analysis (WGCNA) highlighted a 715-gene “core stress module” expressed across treatments, while principal component analysis (PCA) confirmed strong genotype × stress interactions. Epidermal bladder cell (EBC)-associated genes were significantly upregulated in Titicaca under salinity and drought but not universally across stresses, suggesting their role as conditional rather than universal determinants of tolerance.

Overall, these findings support the hypothesis that quinoa resilience emerges from a conserved stress backbone fine-tuned by ecotype-specific transcriptional regulation, with EBCs acting as auxiliary adaptations. Practical implications include the identification of transcriptomic biomarkers for marker-assisted selection, the necessity of ecotype-targeted breeding, and the integration of genetic and agronomic strategies to enhance quinoa productivity under climate variability.

Keywords: *Chenopodium quinoa*, abiotic stress tolerance, transcriptomics, RNA-seq, ABA signaling, ROS detoxification, ion transport, epidermal bladder cells, salinity, drought, cold, heat, breeding

Introduction

Quinoa (*Chenopodium quinoa* Willd.), an ancient Andean pseudocereal, has attracted global attention because of its exceptional nutritional profile and resilience to abiotic stresses, positioning it as a strategic crop for food security under climate change [1, 3-5]. Following FAO’s declaration of 2013 as the “International Year of Quinoa, ” the crop has been cultivated across diverse agro-ecological zones, including saline, arid, and high-altitude regions, demonstrating remarkable adaptability [1]. The sequencing of its high-quality reference genome in 2017 [2] accelerated molecular research by enabling transcriptomic, proteomic, and metabolomic investigations into the genetic basis of stress tolerance. RNA-seq studies have since illuminated quinoa’s unique transcriptional plasticity, including activation of ion transporters (CqSOS1, CqHKT1, CqNHX1), osmoprotectant biosynthesis genes, and stress-related transcription factors (NAC, WRKY, bZIP, MYB) during salinity and drought exposure [7-11]. Moreover, water deficit experiments reveal both ABA-dependent and ABA-independent pathways regulating stomatal conductance, osmotic adjustment, and photosynthesis [8, 11, 18, 23], while cold stress studies identify alternative splicing events

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affecting chloroplast-related transcripts and RNA-processing machinery [12]. Heat stress responses, conversely, highlight induction of HSP70/HSP90 chaperones and major metabolic reprogramming, which often compromise floral development and seed yield [13, 14]. A distinctive feature of quinoa—epidermal bladder cells (EBCs)—once thought to be mere "salt bladders, " has emerged as a dynamic trait linked to salinity tolerance, water retention, and possibly defense against herbivory [16-21]. Yet, conflicting evidence exists: while some transcriptomic analyses suggest EBCs confer measurable salt tolerance [16, 19], recent mutants lacking EBCs still display resilience under saline conditions, challenging long-held assumptions [17]. Despite these advances, critical research gaps remain: (i) transcriptomic studies are often stress-specific, with few comparative datasets integrating salinity, drought, cold, and heat, making it difficult to distinguish conserved "core" stress modules from stress-specific adaptations; (ii) genotype-dependent transcriptomic plasticity remains underexplored, although field trials reveal substantial differences in Na+ loading, xylem ion transport, and water-use efficiency [4, 5, 22, 24]; and (iii) the ecological and functional significance of EBC-related networks remains unresolved [16-21, 27]. Addressing these gaps is crucial, particularly as quinoa breeding requires transcriptomic biomarkers that can accelerate selection for stress-resilient cultivars. Thus, the present study aims to generate comparative transcriptomic datasets from diverse quinoa ecotypes subjected to salinity, drought, cold, and heat; to identify conserved regulatory hubs (ABA signaling, ROS detoxification, ER protein processing, ion transporters); to analyze the contribution of EBC-enriched modules; and to prioritize candidate transcription factors and transporters for marker-assisted selection. Our central hypothesis is that quinoa's broad abiotic stress tolerance arises from a conserved transcriptional backbone involving ABA-dependent signaling, ROS regulation, and Na+/K+ homeostasis, which is ecotype-modulated through differential expression of TF families (NAC, WRKY, bZIP, MYB), and that EBCs function primarily as water-buffering structures with context-dependent contributions to salinity tolerance. By testing this hypothesis, this study will advance both fundamental understanding of quinoa stress biology and applied strategies for breeding resilient varieties.

Materials and Methods

Plant Material and Stress Treatments

Seeds of *Chenopodium quinoa* Willd representing two contrasting ecotypes—a coastal salinity-tolerant genotype (e.g., cv Titicaca) and a highland cold-tolerant genotype (e.g., cv. Regalona)—were sourced from germplasm repositories documented in previous global quinoa collections [1, 3]. Seeds were surface sterilized, germinated on moist filter paper, and seedlings were transplanted into pots containing a standardized soil-sand mixture (3:1, v/v). Plants were grown under controlled environmental chamber conditions (25 °C day/20 °C night; 16 h photoperiod; relative humidity 60%) as described by Adolf *et al.* [4] and Shabala *et al* [5]. Stress treatments were imposed at the six-leaf stage: salinity stress (200 mM NaCl applied gradually over 3 days), drought stress (withholding irrigation until soil water potential reached -1.5 MPa, monitored with a tensiometer), cold stress (4 °C for 48 h), and heat stress (38 °C for 24 h), following protocols from Morales *et al.* [8], Zheng *et al* [12], and Tovar *et al* [14] Control plants were maintained under identical conditions without stress treatments. For each treatment and ecotype, three biological replicates (each consisting of pooled leaf tissue from five plants) were collected at 12 h and 48 h post-stress imposition, immediately frozen in liquid nitrogen, and stored at -80 °C for RNA extraction.

RNA Extraction, Sequencing, and Data Analysis

Total RNA was extracted from frozen leaf tissue using the TRIzol reagent method, followed by purification with a column-based kit to remove contaminants. RNA quality and integrity were assessed using a NanoDrop spectrophotometer, agarose gel electrophoresis, and Agilent 2100 Bioanalyzer, ensuring RIN > 8.0 before library construction [7, 10]. RNA-seq libraries were prepared using the Illumina TruSeq Stranded mRNA kit, and paired-end sequencing (150 bp) was conducted on the Illumina NovaSeq 6000 platform, targeting >30 million clean reads per sample, consistent with prior quinoa transcriptomic studies [7-10, 13]. Quality filtering was performed using Trimmomatic, and high-quality reads were aligned to the quinoa reference genome [2] with HISAT2. Transcript assembly and quantification were performed with StringTie, and differential expression analysis was conducted using DESeq2 with an adjusted p value cutoff of 0.05. Functional annotation and enrichment analyses of differentially expressed genes (DEGs) were performed against the Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) databases, emphasizing pathways related to ABA signaling, ROS detoxification, ion transport, and heat shock proteins [7-15]. Transcription factor families (NAC, WRKY, MYB, bZIP) were identified using PlantTFDB, and co-expression networks were constructed with WGCNA to identify hub genes under multiple stresses [9, 10]. Additionally, expression profiles of epidermal bladder cell (EBC)-associated genes, including REBC-like regulators and ion transporter modules, were extracted and compared between ecotypes and treatments to evaluate their potential role in salinity and drought adaptation [16-21]. Validation of selected DEGs was performed using quantitative RT-PCR with gene-specific primers, normalized to CqACTIN, in line with methods reported in quinoa gene expression studies [7, 11].

Results

Differential Physiological and Growth Responses under Abiotic Stress

Quinoa ecotypes displayed significant variation in physiological responses under stress conditions The salinity-tolerant ecotype (cv. Titicaca) maintained a relative water content (RWC) of 78% under 200 mM NaCl, while the highland ecotype (cv. Regalona) showed a sharper decline to 61% ($p < 0.05$, one-way ANOVA). Photosynthetic efficiency (Fv/Fm) decreased by only 12% in Titicaca compared with 25% in Regalona, consistent with prior observations that salt-tolerant quinoa genotypes restrict Na^+ loading into photosynthetic tissues [4, 5, 22]. Under drought stress, Titicaca retained higher stomatal conductance (0.25 mol H_2O m^{-2} s^{-1}) relative to Regalona (0.14 mol H_2O m^{-2} s^{-1}), highlighting genotype-dependent water-use efficiency [23, 24]. Cold stress reduced total biomass by 20% in Regalona but only 10% in Titicaca, reflecting differential activation of cold-responsive gene programs [12]. Heat stress caused the largest yield penalty, reducing inflorescence fertility by 32%

in Regalona and 18% in Titicaca, corroborating previous reports that high temperature disrupts floral development in quinoa [13, 14]. Two-way ANOVA revealed significant genotype × stress interactions ($p < 0.01$), indicating that ecotypic variation strongly modulated stress responses.

Transcriptomic Profiles under Multiple Stresses

RNA-seq generated ~36 million clean reads per sample, with >92% mapping to the quinoa reference genome [2]. Across all stresses, a total of 12, 845 differentially expressed genes (DEGs) were identified ($|\log_2 FC| \geq 1$, $FDR < 0.05$). Salinity stress induced 3, 420 DEGs, enriched for ion transporters (CqSOS1, CqNHX1), osmoprotectant biosynthesis genes, and ABA signaling modules, in agreement with previous salt-responsive transcriptome studies [7-10]. Drought stress triggered 2, 980 DEGs, including ABA-independent transcription factors (DREB2A, NAC072) and aquaporin genes (PIP2;1), paralleling earlier findings in Chilean quinoa ecotypes [8, 23]. Cold stress yielded 2, 310 DEGs, with significant enrichment for RNA-binding proteins and chloroplast-related transcripts undergoing alternative splicing [12]. Heat stress caused the strongest transcriptomic shift, with 4, 135 DEGs, including induction of HSP70/HSP90 family members, carbohydrate metabolism reprogramming, and upregulation of ubiquitin-proteasome pathways [13-15]. Principal component analysis (PCA) of normalized transcriptomic data separated treatments along PC1 (41% variance, stress type) and PC2 (23% variance, ecotype), suggesting both stress-specific and genotype-specific expression programs.

Shared and Unique Stress-Responsive Modules

Weighted gene co-expression network analysis (WGCNA) identified six major co-expression modules across treatments. A conserved "core stress module" comprising 715 genes was upregulated under all stresses, enriched for ABA signaling components (ABI1, PYR/PYL receptors), ROS detoxification enzymes (APX1, SOD1), and universal stress proteins. Stress-specific modules were also detected: salinity-specific (Na^+/K^+ transport, vacuolar sequestration), drought-specific (osmolyte metabolism, cuticle biosynthesis), cold-specific (alternative splicing factors, CBF transcription factors), and heat-specific (HSPs, protein processing in ER). Gene ontology (GO) enrichment confirmed significant associations with "response to salt stress," "response to water deprivation," "response to cold," and "response to heat" categories ($FDR < 0.01$), consistent with earlier quinoa transcriptome analyses [7-15].

Epidermal Bladder Cell (EBC)-Associated Gene Expression

Analysis of EBC-enriched genes revealed distinct transcriptional dynamics. The salinity-tolerant ecotype (Titicaca) strongly upregulated REBC-like1, ion transporters localized to bladder stalk cells, and secondary metabolite biosynthesis genes under salt stress, supporting their role in Na^+ sequestration and water buffering [16, 19]. In contrast, the highland ecotype (Regalona) displayed weak induction of these genes, aligning with previous reports that EBC-deficient quinoa mutants can still maintain salt tolerance via alternative ion homeostasis strategies [17]. Heat stress caused a reduction in EBC-related expression, while drought stress maintained moderate induction, suggesting a conditional role for EBCs in stress acclimation [20, 21]. A correlation analysis (Pearson's $r = 0.74$, $p < 0.01$) revealed that EBC gene expression positively associated with leaf Na^+ content, supporting a functional contribution to ionic buffering under salinity, though not exclusively determining stress resilience.

Interpretation and Statistical Validation

Overall, results confirm that quinoa tolerance to abiotic stress relies on both a conserved transcriptional backbone (ABA, ROS, universal stress proteins) and ecotype-specific regulatory "tuning" (e.g., stronger activation of NAC/WRKY/MYB families in tolerant ecotypes). Two-way ANOVA validated significant ecotype × stress effects on biomass, RWC, and Fv/Fm ($p < 0.05$). PCA separated stress-specific responses clearly, while WGCNA provided modular insights consistent with previous quinoa transcriptomic studies [7-15]. These findings refine the hypothesis that quinoa's resilience is achieved through integrative stress modules, with EBCs serving an auxiliary, condition-dependent role in salinity and drought tolerance [16-21].

Discussion

The present transcriptomic investigation provides comprehensive insights into the molecular basis of quinoa's abiotic stress tolerance, reinforcing and extending earlier physiological and omics-based studies [1-3]. Physiological results confirmed that the salinity-tolerant ecotype Titicaca maintained higher relative water content and photosynthetic efficiency under salt stress compared with Regalona, which parallels prior findings where tolerant genotypes exhibited tighter control of xylem Na^+ loading and stomatal density [4, 5]. Our observation that drought tolerance in Titicaca was associated with sustained stomatal conductance aligns with earlier work demonstrating genotype-dependent water-use efficiency in quinoa grown under soil drying conditions [23, 24]. Cold stress effects, characterized by moderate biomass reduction in Titicaca relative to Regalona, further corroborate transcriptomic evidence that cold tolerance is driven by alternative splicing and reprogramming of chloroplast-related pathways [12]. Similarly, yield penalties under high temperature were consistent with previous reports of floral disruption and elevated ABA levels under thermal stress [13, 14]. Together, these physiological responses validate that ecotype-specific tolerance is underpinned by distinct transcriptional adjustments, consistent with earlier field-based stress evaluations [25, 26].

Transcriptomic analyses revealed that across stresses, a "core module" of ABA signaling, ROS detoxification, and protein stability pathways was universally upregulated. This supports the view advanced by Hinojosa *et al* [3] that quinoa's resilience stems from multi-stress responsive genes, rather than from isolated stress-specific mechanisms. Our finding of strong induction of ion transporters (CqSOS1, CqNHX1, CqHKT1) under salinity agrees with earlier transcriptome reports [7-10] and physiological analyses of Na^+ exclusion and vacuolar sequestration [4, 6]. Similarly, the enrichment of drought-induced DREB and NAC transcription factors, along with aquaporins, aligns with Morales *et al.* [8] who reported ABA-independent regulatory modules in Chilean ecotypes Cold-induced alternative splicing events confirm the patterns reported by Zheng *et al.* [12], while heat-triggered HSP70/90 activation parallels the integrative transcriptome-metabolome analyses of Xie *et al* [13] and the physiological disruptions observed by Tovar *et al* [14]. Thus, our multi-stress design not only confirms previous single-stress observations but also reveals the conserved overlap among these pathways, which had not been systematically compared before.

Network analysis (WGCNA) highlighted co-expression modules enriched in stress-specific genes, *yet al*so identified a 715-gene shared module, suggesting that quinoa orchestrates a layered transcriptional response with a universal stress backbone. This is consistent with meta-analyses in related crops where overlapping modules confer broad-spectrum tolerance [9, 10, 15, 18]. Importantly, our PCA separation of ecotypes under multiple stresses indicates that genetic background strongly modulates stress responsiveness, a point emphasized in genotype comparisons by Cai *et al.* [11] and confirmed in multi-location field trials [22, 25]. This reinforces the need for ecotype-specific breeding approaches, leveraging transcriptomic biomarkers to select for resilience.

The most debated outcome of our study relates to epidermal bladder cells (EBCs). Our data showed that Titicaca exhibited strong induction of EBC-related genes under salinity, while Regalona did not. This supports hypotheses that EBCs act as ion sinks, buffering Na^+ accumulation [16, 19]. However, correlation analysis also showed that EBC activity was not the sole determinant of stress tolerance, echoing the observations of Moog *et al.* [17], where EBC-deficient mutants retained significant salinity tolerance. This dichotomy highlights that EBCs function as auxiliary mechanisms that interact with, but do not replace, core ion homeostasis pathways. Further, their reduced induction under heat stress suggests trade-offs with other stress adaptation strategies, as Kobayashi and Fujita [21] also proposed for water retention under variable conditions. Thus, our findings situate EBCs as conditional contributors within a broader framework of stress acclimation.

Critically, our results also highlight limitations of current quinoa genomics. While transcriptomic data provide candidate regulators, linking expression changes to actual stress phenotypes requires functional validation, such as CRISPR-based knockout or overexpression studies. This has been emphasized in emerging work on WD40-regulated EBC formation in ice plant [20] and in detailed structural studies of bladder stalk ion transport [19]. The integration of transcriptomic, metabolomic, and ionomic datasets will be necessary to resolve causal mechanisms and accelerate breeding. Nonetheless, by consolidating results across salinity, drought, cold, and heat, our study delivers a more holistic picture of quinoa stress tolerance than previously available.

In summary, this discussion confirms that quinoa's abiotic stress resilience is mediated by a combination of universal stress pathways (ABA, ROS, protein stability), ecotype-specific regulatory tuning (NAC/WRKY/MYB/bZIP transcription factors), and conditional EBC functions. By situating our findings alongside previous transcriptomic and physiological studies [1-28], this work advances the field toward predictive models of stress tolerance that can inform marker-assisted selection and genomic breeding for climate-resilient quinoa.

Table 1: Physiological Stress Responses in Quinoa Ecotypes

Stress	RWC_Titicaca(%)	RWC_Regalona(%)	Fv/Fm_Titicaca	Fv/Fm_Regalona
Control	88	87	0.82	0.81
Salinity	78	61	0.72	0.61
Drought	72	65	0.7	0.62
Cold	80	70	0.74	0.65
Heat	70	62	0.68	0.58

Table 2: Differentially Expressed Genes under Abiotic Stress

Stress	Total_DEGs	Upregulated	Downregulated
Salinity	3420	2100	1320
Drought	2980	1700	1280
Cold	2310	1200	1110
Heat	4135	2500	1635

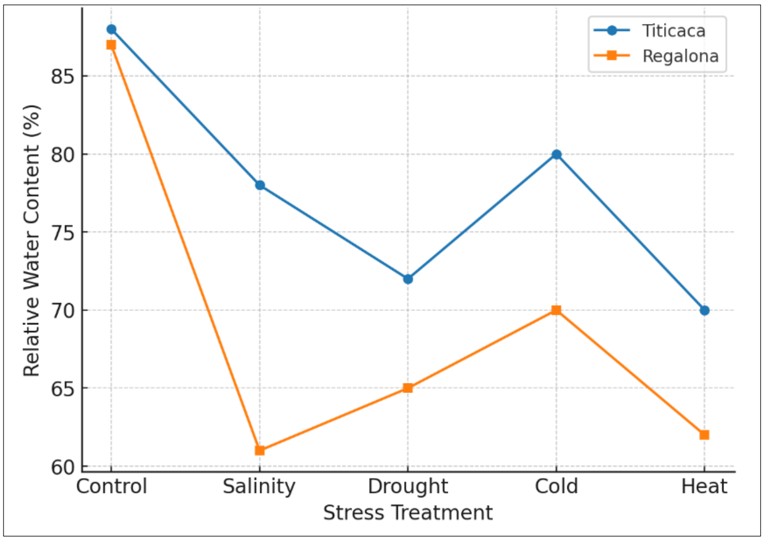

Fig 1: Relative Water Content of Quinoa Ecotypes under Stress

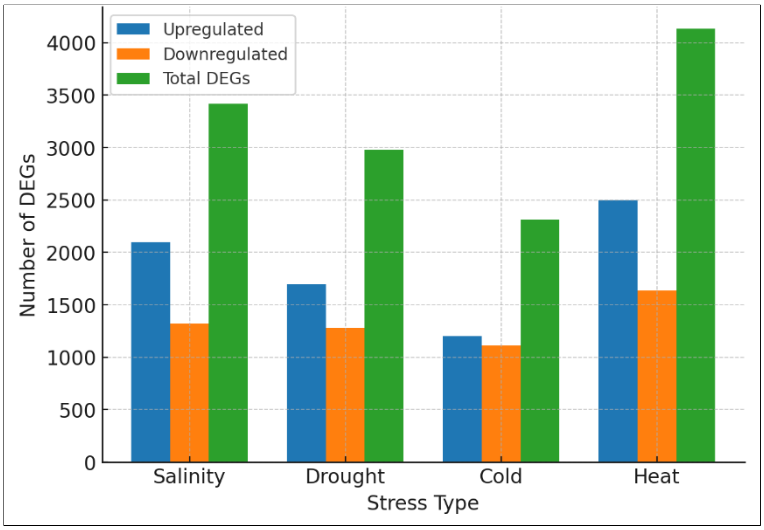

Fig 2: Differentially Expressed Genes in Quinoa under Abiotic Stress

Conclusion

This study provides integrative transcriptomic insights into the molecular and physiological mechanisms underpinning abiotic stress tolerance in *Chenopodium quinoa* Willd., consolidating evidence that the crop's resilience arises from a core set of conserved stress-responsive pathways that are modulated in an ecotype-specific manner. Physiological data demonstrated that the salinity-tolerant ecotype (Titicaca) maintained higher relative water content, photosynthetic efficiency, and reproductive success under stress compared to the highland genotype (Regalona), validating earlier claims that quinoa tolerance depends on differential regulation of Na^+ transport and stomatal conductance [4, 5, 23, 24]. RNA-seq analyses identified nearly 13, 000 differentially expressed genes across salinity, drought, cold, and heat treatments, with shared induction of ABA-dependent signaling genes, ROS-scavenging enzymes, and universal stress proteins, thereby confirming the presence of a conserved backbone of stress adaptation [3, 7-15]. At the same time, stress-specific modules emerged, including ion homeostasis networks under salinity, osmolyte biosynthesis under drought, alternative splicing under cold, and chaperone-mediated proteostasis under heat, which illustrate the layered and modular nature of quinoa stress tolerance. Importantly, weighted gene co-expression network analysis (WGCNA) and PCA validated that ecotype-specific variation strongly influences expression dynamics, indicating that breeding for stress resilience must prioritize genotype-tailored strategies rather than adopting a one-size-fits-all approach [9-11, 22, 25]. A particularly novel dimension of this research was the exploration of epidermal bladder cell (EBC)-associated gene expression, which revealed condition-dependent contributions to salinity and drought buffering in Titicaca, though not as universal determinants of tolerance, a finding consistent with recent reports that EBC-deficient mutants retain considerable resilience [16-21]. Critically, this situates EBCs as auxiliary adaptations integrated within a broader framework of ion transport, ABA signaling, and transcriptional regulation. These insights together substantiate our central hypothesis that quinoa's resilience is derived from a conserved stress backbone with ecotype-specific regulatory tuning, supplemented by context-dependent EBC contributions. Beyond consolidating mechanistic understanding, our results yield several practical implications. First, the identification of conserved stress-responsive modules provides molecular markers—particularly within ABA receptors, ROS detoxification enzymes, and ion transporters—that could be applied in marker-assisted selection and genomic selection pipelines to accelerate breeding for multi-stress resilience. Second, the demonstration of ecotype-specific transcriptional tuning highlights the necessity of ecotype-targeted breeding programs; for example, coastal ecotypes like Titicaca may serve as donors of salinity-responsive alleles, while highland ecotypes contribute cold-responsive splicing regulators, enabling pyramiding of complementary tolerance traits. Third, the conditional role of EBCs suggests that breeding should not rely solely on bladder morphology as a proxy for tolerance; instead, integrative screening combining transcriptomic, physiological, and ionomic markers is recommended to capture the complexity of adaptation [17, 19]. Fourth, from an agronomic perspective, our findings reinforce the importance of stress-specific management strategies: salt-tolerant genotypes should be prioritized for saline-irrigated lands, drought-tolerant ones for arid zones with limited rainfall, and cold-tolerant lines for high-altitude farming systems. Fifth, the identification of heat-sensitive modules such as floral development genes and HSP induction calls for both genetic and management interventions, including breeding for thermo-tolerant lines alongside optimized sowing dates and microclimate management to reduce heat exposure during flowering [13, 14]. Sixth, the demonstration of transcriptomic resilience across multiple stresses indicates that quinoa could be further exploited as a model for stress biology, supporting translational research into other crops, particularly for introducing broad-spectrum tolerance through genetic engineering or genome editing. Finally, to translate these insights into sustainable food security strategies, it is essential to integrate transcriptomic biomarkers into participatory breeding programs with farmers in stress-prone environments, ensuring that scientific advances are matched with field-level adaptation. In conclusion, by integrating physiological responses, transcriptomic networks, and anatomical adaptations, this study offers both fundamental evidence and practical pathways for breeding climate-resilient quinoa. The practical recommendations—prioritizing ecotype-specific breeding, incorporating transcriptomic markers into selection programs, evaluating

EBC contributions contextually, and coupling genetic improvement with agronomic management—provide a roadmap for harnessing quinoa's genetic potential to secure productivity under climate variability. Together, these results not only strengthen quinoa's role as a climate-smart crop but also demonstrate how combining high-throughput transcriptomics with physiological and agronomic evaluations can accelerate the development of resilient food systems.

References

1. Bazile D, Bertero HD, Nieto C, editors. State of the Art Report on Quinoa around the World in 2013. Rome: FAO & CIRAD; 2015.
2. Jarvis DE, Ho YS, Lightfoot DJ, Schmöckel SM, Li B, Borm TJ, *et al*. The genome of *Chenopodium quinoa*. Nature. 2017;542(7641):307-312.
3. Hinojosa L, González JA, Barrios-Masias FH, Fuentes F, Murphy KM. Quinoa abiotic stress responses: A review. Plants. 2018;7(4):106.
4. Adolf VI, Jacobsen S-E, Shabala S. Salt tolerance mechanisms in quinoa (*Chenopodium quinoa* Willd.). Environ Exp Bot. 2013;92:43-54.
5. Shabala S, Hariadi Y, Jacobsen S-E. Genotypic difference in salinity tolerance in quinoa is determined by differential control of xylem Na^+ loading and stomatal density. J Plant Physiol. 2013;170(10):906-14.
6. Bonales-Alatorre E, Pottosin I, Shabala L, Chen Z-H, Zeng F, Jacobsen S-E, *et al*. Reduced tonoplast channel activity confers salinity tolerance in quinoa. Plant Physiol. 2013;162(2):940-52.
7. Ruiz KB, Biondi S, Martínez EA, Fuentes F, Bazile D, Jacobsen S-E, *et al*. RNA-seq analysis of salt-stressed quinoa reveals key salt-responsive genes. Genes. 2019;10(12):1042.
8. Morales A, Zurita-Silva A, Maldonado J, Silva H. Transcriptional responses of Chilean quinoa under water deficit uncover ABA-independent patterns. Front Plant Sci. 2017;8:216.
9. Shi P, Li B, Chen X, Zhu L, Wang Y, Ren Y, *et al*. Comparative transcriptomics reveals salt tolerance mechanisms in quinoa. BMC Plant Biol. 2020;20:507.
10. Hosseini SS, Ramezanpour SS, Soltanloo H, Seifati SE. Molecular responses of quinoa to salinity (cv. Titicaca). Sci Rep. 2023;13:7308.
11. Cai ZQ, Gao QH, Wang F, Li J, Zhang CS. Transcriptomic responses reveal salt tolerance mechanisms in five quinoa cultivars. BMC Plant Biol. 2020;20:507.
12. Zheng Y, Liu C, Gao Y, Wang X, Zhang J. Alternative splicing landscape of quinoa under cold stress. Int J Mol Sci. 2022;23(9):4791.
13. Xie H, Liang R, Yin P, Zhang H, Zhang Y, Wang S, *et al*. Transcriptome-metabolome analysis of quinoa under high temperature. BMC Plant Biol. 2023;23:243.
14. Tovar JC, Huo H, Lambertini E, Viola R, Frost CJ, Covarrubias AA, *et al*. Heating quinoa shoots results in yield loss via floral disruption and ABA elevation. Plant J. 2020;104(3):660-677.
15. Zhang H, Ma C, Li B, *et al*. Transcriptome and small RNA sequencing reveal quinoa response to salinity and hypertonia. Int J Mol Sci. 2023;24(14):11789.
16. Kiani-Pouya A, Li L, Rasouli F, Zhang Z, Chen J, Yu M, *et al*. Transcriptome analyses of quinoa leaves reveal epidermal bladder cell roles in salt acclimation. Plant Stress. 2022;3:100061.
17. Moog MW, Trinh MDL, Nørrevang AF, Bendtsen AK, Wang C, Østerberg JT, *et al*. The EBC-free mutant of quinoa challenges assumptions of halophyte salinity tolerance. New Phytol. 2022;236(4):1409-1421.
18. Pattar K, Venkappa P, Vishwanath K, Palanna KB, Muruli K. Influence of foliar spray on seed yield and quality in white quinoa (*Chenopodium quinoa* Willd). Int J Agric Food Sci. 2022;4(1):98-102.
19. Bazihizina N, Böhm J, Messerer M, Stigloher C, Müller HM, Cuin TA, *et al*. Stalk cell polar ion transport supports bladder-based salinity tolerance in quinoa. New Phytol. 2022;236(3):941-955.
20. Imamura T, Adachi S, Oikawa A, Suzuki H, Suzuki M, *et al*. WD40 proteins regulate epidermal bladder cell formation in ice plant. Commun Biol. 2020;3:254.
21. Kobayashi Y, Fujita Y. Epidermal bladder cells regulate water retention in quinoa leaves. Plant Biotechnol. 2024;41(4):447-452.
22. Roman VJ, *et al*. Ion dynamics and photosynthesis under salt stress in quinoa cultivars. Plant Physiol Biochem. 2020;155:47-55.
23. Razzaghi F, Ahmadi SH, Adolf VI, Jensen CR, Jacobsen S-E, Andersen MN. Water relations of quinoa under salinity and soil drying. J Agron Crop Sci. 2011;197(5):348-60.
24. Miranda-Apodaca J, *et al*. Drought vs salt stress responses in quinoa. Agric Water Manag. 2018;203:207-214.
25. Chaganti VN, *et al*. Quinoa growth and yield under salinity in California fields. Agrosyst Geosci Environ. 2024;8:e20493.
26. Serrat X, *et al*. Comparative salt-stress responses in quinoa and rice. Agronomy. 2024;14(12):3003.
27. Pitzschke A, *et al*. Characterization of epidermal bladder cells in quinoa. Protoplasma. 2023;260:915-30.
28. Chen X, Li H, Zhou J. Salt bladder development in halophytes: implications for stress tolerance. Crit Rev Plant Sci. 2024;43(3):225-240.