

Original Research Article

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Molecular Assessment of Abiotic Stress Tolerance in Selected *Inula* Species Using PCR-Based Markers

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ABSTRACT

Keywords

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Abiotic stresses such as drought, salinity, and cold are major limiting factors for plant growth and productivity, particularly under the increasing pressures of climate change. This study investigates the molecular basis of stress tolerance in three *Inula* species—*Inula helenium*, *Inula grandis*, and *Inula glauca*—collected from diverse ecological zones in Uzbekistan. Genomic DNA was extracted using both CTAB and commercial kit-based methods, with the latter yielding higher quality and concentration. Sixteen stress-responsive gene markers associated with drought (e.g., NCED1, POD1), salinity (e.g., NHX2, PP2C8), and cold (e.g., CSP3) were amplified by PCR to evaluate gene presence and expression intensity. *I. helenium* showed the broadest tolerance, with amplification of 14 out of 16 markers, indicating strong generalist adaptability. *I. grandis* displayed high drought and salinity responses but lacked cold tolerance, while *I. glauca* exhibited moderate expression with an emphasis on cold response. These expression patterns align with the ecological distributions of the species and underscore genotype–environment interactions. The identified markers provide valuable tools for future conservation and marker-assisted breeding, with *I. helenium* emerging as a promising donor of multi-stress tolerance traits for crop improvement under environmental stress conditions.

Introduction

Abiotic stresses, including drought, salinity, and low temperature, represent some of the most severe constraints on plant growth, development, and productivity. Global agricultural systems are increasingly threatened by these stressors, which are intensified by climate change, desertification, and anthropogenic soil degradation (Kopecká *et al.*, 2023; Tarolli *et al.*, 2024).

For instance, drought stress alone is estimated to reduce crop yields more than any other environmental factor,

especially in arid and semi-arid regions where water availability is a key limiting factor (Muhammad *et al.*, 2024). Salinity stress, affecting over 20% of irrigated lands worldwide, disrupts osmotic balance, ion homeostasis, and redox regulation, ultimately leading to growth inhibition and yield loss (Atta *et al.*, 2023).

Similarly, cold stress restricts plant distribution in high-altitude or temperate environments by damaging membranes and altering gene expression networks, thereby limiting ecological fitness and agricultural output (Sudesh, 2010, Taïbi *et al.*, 2018).

Plants have evolved complex adaptive strategies to mitigate abiotic stress damage, ranging from physiological and biochemical adjustments to transcriptional reprogramming and molecular signaling cascades (Zhang *et al.*, 2023). Central to these processes are plant hormones, particularly abscisic acid (ABA), which orchestrates stomatal regulation and stress-induced gene expression through key biosynthetic genes such as *NCED1* and *NCED2*. Parallel to this, antioxidative enzymes including catalase (*CAT*), glutathione reductase (*GR*), and glutathione-S-transferase (*GST*) protect cells against reactive oxygen species generated under stress (Rajput *et al.*, 2021). Membrane transporters like *NHX2* play crucial roles in maintaining ion balance during salt stress, while regulatory proteins such as *PP2C* phosphatases and *SAPK2* kinases integrate environmental signals into downstream responses (Barragán *et al.*, 2012). Thus, molecular markers linked to these genes provide valuable tools for identifying genotypes with superior tolerance traits and guiding marker-assisted breeding (MAS).

Within this broader context, medicinal and wild plants from ecologically diverse regions serve as unique models for studying stress adaptation. The genus *Inula* (Asteraceae) comprises approximately 100–120 species distributed across Eurasia, ranging from lowland steppe habitats to mountainous subalpine zones (Seca *et al.*, 2014). Members of this genus are notable not only for their ecological plasticity but also for their pharmacological relevance: species such as *Inula helenium* produce sesquiterpene lactones (e.g., alantolactone, isoalantolactone) with anti-inflammatory, antimicrobial, and antioxidant properties (Buza, 2020). Previous studies have explored the physiology of stress responses in *Inula viscosa* and related taxa (Al-Hassan *et al.*, 2016; Araniti *et al.*, 2017), but comprehensive molecular investigations into abiotic stress tolerance across multiple *Inula* species remain limited.

Understanding the genetic basis of stress adaptation in *Inula* species is particularly relevant in Central Asia, where diverse habitats range from drought-prone valleys to saline steppe soils and cold mountainous regions. Many *Inula* taxa native to Uzbekistan, such as *I. helenium*, *I. grandis*, and *I. glauca*, are adapted to specific ecological niches yet remain poorly characterized at the molecular level. Identifying stress-responsive genes in these species will not only clarify their ecological strategies but also contribute to conservation biology and the sustainable use of genetic

resources. Importantly, species with robust stress tolerance may serve as donors of resilience traits for crop improvement, aligning with global efforts to enhance agricultural sustainability under climate instability.

This study investigates the molecular responses of *I. helenium*, *I. grandis*, and *I. glauca* to drought, salinity, and cold stresses using a set of 16 stress-related molecular markers amplified by PCR. By correlating marker expression patterns with ecological distributions, the research aims to (1) compare the stress tolerance potential of the three species, (2) elucidate genotype–environment associations, and (3) highlight candidate genes for future breeding and conservation strategies.

Materials and Methods

Leaf tissues of three *Inula* species — *Inula helenium* subsp. *helenium*, *Inula grandis*, and *Inula glauca* — were collected from natural populations distributed across Uzbekistan. The sampling sites encompassed diverse ecological gradients, ranging from semi-arid valleys to mountainous habitats at altitudes of 1100–1800 m. Genomic DNA was isolated from 20–30 mg of fresh or dried leaf tissue using two extraction protocols: a classical CTAB method and a silica column–based commercial kit (GeneJET Plant Genomic DNA Purification Kit, Thermo Scientific). The CTAB protocol, a widely used method for plant DNA isolation (Doyle & Doyle, 1990), involved homogenization of leaf tissues in CTAB buffer, incubation at 65 °C, and organic extraction using chloroform: isoamyl alcohol (24:1). DNA was then precipitated with sodium acetate and isopropanol, washed with 70% ethanol, air-dried, and dissolved in TE buffer. In parallel, the commercial kit protocol employed lysis with proprietary buffers, centrifugation, and DNA binding to a silica membrane, followed by sequential washing and elution with 50 µl of elution buffer.

DNA concentration and purity were measured using a NanoDrop spectrophotometer (NanoPhotometer N60, Implen, Germany), with absorbance ratios at A260/A280 and A260/A230 serving as quality indicators. Pure DNA was defined as having an A260/A280 ratio between 1.8–2.0 and an A260/A230 ratio above 2.0 (Ahmad *et al.*, 2020). Electrophoresis on 1% agarose gels stained with ethidium bromide further confirmed DNA integrity. The CTAB method produced DNA yields ranging from 23 to 100 ng/µl, whereas the kit method consistently yielded higher concentrations of 147–583 ng/µl.

For the molecular evaluation of stress tolerance, sixteen stress-responsive gene markers were selected (Table 1). These included genes associated with drought tolerance (*NCED1*, *NCED2*, *CYP707A*, *GST*, *PYL4*, *BCH*, *POD1*, *POD2*), salinity tolerance (*CAT*, *GR*, *NHX2*, *PP2C78*, *PP2C8*, *SAPK2*), cold tolerance (*CSP3*), and pathogen-related responses (*RBOH*). Many of these genes are known to participate in abscisic acid (ABA) signaling pathways, antioxidative defense, ion transport, and stress-induced signal cascades (Urbanavičiūtė *et al.*, 2021).

PCR amplification was carried out in a 20 µl reaction mixture containing 10 µl of 2× PCR Master Mix (Taq polymerase, dNTPs, and MgCl₂), 1 µl of genomic DNA template (~10–20 ng), 1 µl of primer pair (0.5 µl each forward and reverse primer, 10 pmol), and 8 µl of nuclease-free water. Amplification was performed using a thermocycler programmed for an initial denaturation at 94 °C for 2 minutes, followed by 35 cycles of denaturation at 94 °C for 20 seconds, annealing at 55 °C for 30 seconds, and extension at 72 °C for 30 seconds, with a final extension step of 72 °C for 7 minutes and storage at 10 °C.

PCR products were separated by electrophoresis on 1.5% agarose gels prepared in 1× TBE buffer, run at 90 V for 45–60 minutes, and stained with ethidium bromide (0.5 µg/ml). DNA fragments were visualized under UV light using a GenoSens documentation system, and fragment sizes were compared with a 100 bp DNA ladder. Amplification was recorded as the presence or absence of specific bands, while band intensity was used as an indicator of relative gene expression.

The amplification profiles obtained for each species were compared to determine the number and type of stress-related markers expressed. The presence of specific stress-responsive genes was then correlated with the ecological distribution and habitat characteristics of each *Inula* species, thereby linking molecular responses to environmental adaptation strategies (Fig. 3).

Results and Discussion

The quality of extracted DNA was consistently high across all three *Inula* species, with clear differences observed between extraction protocols. The CTAB method yielded DNA concentrations ranging from 23 to 100 ng/µl, whereas the commercial kit method produced significantly higher values, from 147 to 583 ng/µl. The

A260/A280 absorbance ratios of 1.87–1.99 confirmed minimal protein contamination, while A260/A230 values above 2.0 indicated that polysaccharide and phenolic impurities were largely absent. Agarose gel electrophoresis further demonstrated intact, high-molecular-weight DNA suitable for PCR amplification.

PCR amplification of sixteen stress-responsive markers revealed clear interspecific variation in stress tolerance profiles. *Inula helenium* showed the highest level of amplification, with bands observed for 14 of the 16 markers. These included genes associated with drought stress (*NCED1*, *POD1*, *POD2*, *CYP707A*, *GST*, *PYL4*, *BCH*), salinity tolerance (*NHX2*, *GR*, *CAT*, *PP2C78*, *PP2C8*, *SAPK2*), and cold tolerance (*CSP3*). By contrast, *Inula grandis* exhibited amplification for 9 of the 16 markers. Most notably, markers related to drought tolerance (*NCED1*, *NCED2*, *POD1*, *POD2*, *CYP707A*, *GST*) and salinity tolerance (*PP2C78*, *SAPK2*) were strongly expressed, whereas cold-responsive markers were absent. *Inula glauca* also showed amplification for 9 markers, though band intensity was generally weaker than in the other two species. Amplified markers included drought-responsive genes (*NCED1*, *POD2*, *CYP707A*), salinity-responsive genes (*PP2C78*, *PP2C8*), and the cold-responsive gene *CSP3*. Unlike *I. glauca* expressed at least one cold-tolerance marker, reflecting its natural distribution in relatively moist, high-altitude habitats with moderate to low temperatures. Nevertheless, the limited number of active drought and salinity markers indicates a narrower stress tolerance compared with *I. helenium*.

A comparative analysis of the three species revealed that *I. helenium* was the most genetically versatile, responding to nearly all stress categories tested. *I. grandis* demonstrated high drought and salinity tolerance but lacked cold adaptation, while *I. glauca* displayed moderate tolerance across all stress types, with a bias toward salinity and cold response.

The comparative molecular analysis of *Inula helenium*, *Inula grandis*, and *Inula glauca* reveals that species within the same genus can adopt distinct genetic strategies to cope with environmental stresses. The amplification of 14 out of 16 stress-responsive markers in *I. helenium* indicates a broad-spectrum stress tolerance, whereas *I. grandis* and *I. glauca* each amplified nine markers, showing narrower but ecologically specialized tolerance profiles. These findings highlight the evolutionary plasticity of the genus *Inula*, which has

colonized diverse ecological niches across Eurasia (Gutiérrez-Larruscain *et al.*, 2018).

Drought emerged as the most consistently targeted stress response across all three species, with strong amplification of ABA-related genes (*NCED1*, *NCED2*, *CYP707A*, *PYL4*) in *I. helenium* and *I. grandis*. The ABA biosynthetic genes *NCED1* and *NCED2* are central regulators of stomatal closure and water use efficiency (Wu *et al.*, 2018), while *CYP707A* modulates ABA catabolism to fine-tune stress responses. Similarly, amplification of *POD1* and *POD2* suggests enhanced peroxidase activity, which mitigates oxidative damage caused by water deficit, a response also noted in other Asteraceae species (Lee *et al.*, 2009; Akram *et al.*, 2025). In contrast, *I. glauca* displayed fewer drought-responsive markers, consistent with its ecological preference for wetter habitats. Although *CYP707A* and *NCED1* were amplified, the weaker band intensities imply lower baseline expression levels. This reduced drought specialization parallels findings in other high-altitude plants, which often rely more on cold and moderate salinity responses than on drought mechanisms (Bartels *et al.*, 2005).

Salinity tolerance was strongly represented in both *I. helenium* and *I. grandis*, evidenced by amplification of *PP2C8*, and *SAPK2*. Amplification of *PP2C8* and *SAPK2* further underscores the role of protein phosphatases and kinases in integrating osmotic stress signals into adaptive responses. These results agree with previous studies (Singh *et al.*, 2015), which suggest that some plants accumulate proline and maintain chlorophyll stability under saline conditions, key physiological markers of salt tolerance. Interestingly, *I. glauca* also expressed *PP2C78* and *PP2C8*, despite being adapted to relatively moist environments. This suggests that even species not typically associated with saline habitats may retain molecular mechanisms for salt stress, likely as an evolutionary safeguard.

Cold stress markers were primarily expressed in *I. helenium* and *I. glauca*, with amplification of *CSP3*. This gene encodes a cold-shock protein involved in maintaining RNA stability and transcriptional activity under low temperatures. The presence of *CSP3* in *I. helenium* corresponds with its distribution in high-altitude regions (1200–1800 m), where seasonal cold is a significant environmental pressure. Likewise, its

detection in *I. glauca* reflects adaptation to upland habitats with moderate-to-cold climates. Conversely, its absence in *I. grandis* indicates limited cold tolerance, in agreement with the species' restriction to drier, warmer lowland slopes. This ecological-genetic alignment mirrors broader patterns, where cold tolerance genes correlate with elevational gradients (Halbritter *et al.*, 2018). From an evolutionary perspective, the variation in stress-responsive gene expression among the three *Inula* species reflects niche differentiation and adaptive radiation within Central Asia. *I. helenium* exemplifies ecological generalism, possessing a wide genetic toolkit that enables survival across diverse conditions. In contrast, *I. grandis* is an ecological specialist, with strong drought and salinity tolerance but reduced cold adaptation. *I. glauca* occupies an intermediate niche, with modest tolerance across stress types but particularly notable cold response. This genotype–environment alignment illustrates how natural selection shapes stress tolerance traits to match ecological distributions (Coşgun *et al.*, 2025). Practically, these findings have significant applications for plant breeding and conservation. Stress-resilient markers such as *NCED1/2*, *CYP707A*, *NHX2*, and *PP2C8* represent potential targets for marker-assisted selection (MAS) in crop improvement programs (He *et al.*, 2025). *I. helenium*, with its broad tolerance profile, emerges as a valuable donor species for stress resilience traits. At the same time, *I. glauca* provide unique gene pools for drought and cold tolerance, respectively. Conserving these wild relatives is thus essential not only for biodiversity but also for future agricultural resilience under climate change.

In conclusion, this study presents a comprehensive molecular assessment of abiotic stress tolerance in three *Inula* species—*I. helenium*, *I. grandis*, and *I. glauca*—native to the ecologically diverse regions of Uzbekistan. By employing sixteen stress-responsive molecular markers linked to drought, salinity, and cold resistance, we reveal distinct interspecific variation in gene expression patterns that correlate with the species' natural habitats and ecological preferences. *Inula helenium* demonstrated the broadest genetic response, amplifying 14 of 16 markers and showing strong expression in all three stress categories. This broad-spectrum adaptability suggests that *I. helenium* functions as an ecological generalist with high resilience to environmental fluctuations.

Figure.1 The name and the characteristics of the sixteen stress-responsive gene markers.



Figure.2 PCR amplification stages and thermal cycling conditions.

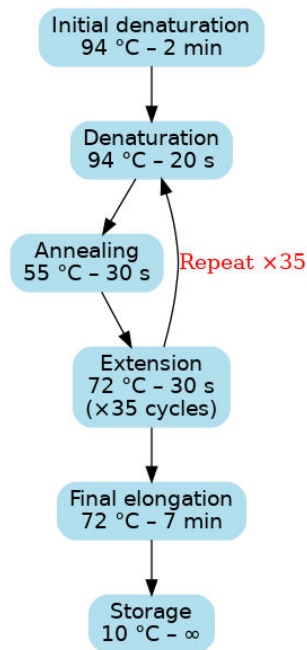


Figure.3 The overall method of the evaluation of stress-responsive gene activity in *Inula* species.

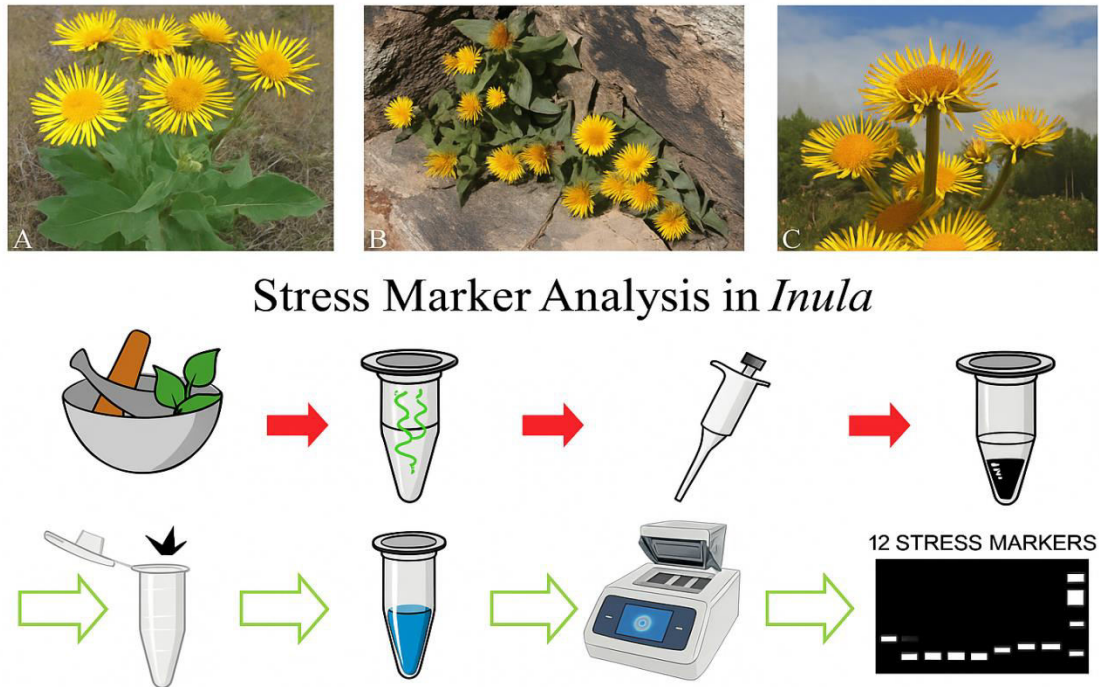


Figure.4 Nanodrop absorbance spectra of DNA samples isolated by Method 1 (left) and Method 2 (right).

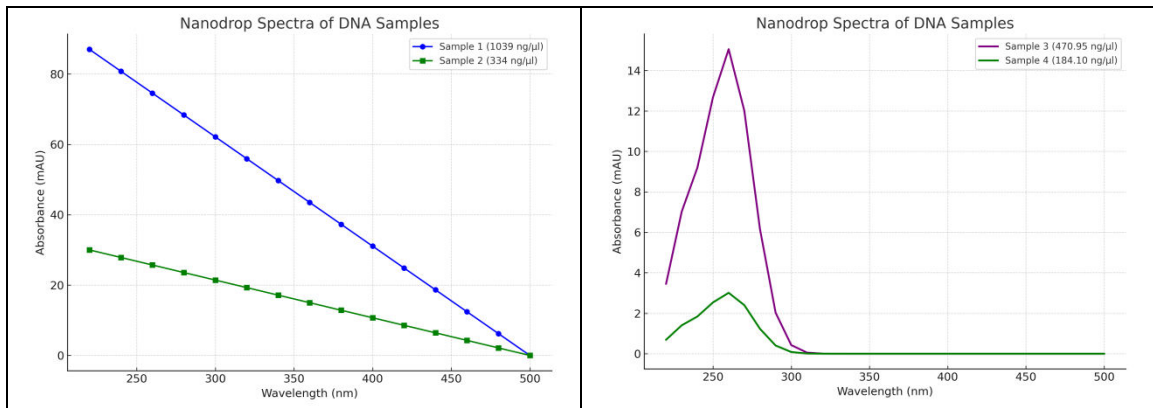


Figure.5 Results of Electrophoresis obtained using abiotic stress markers in *Inula* species.

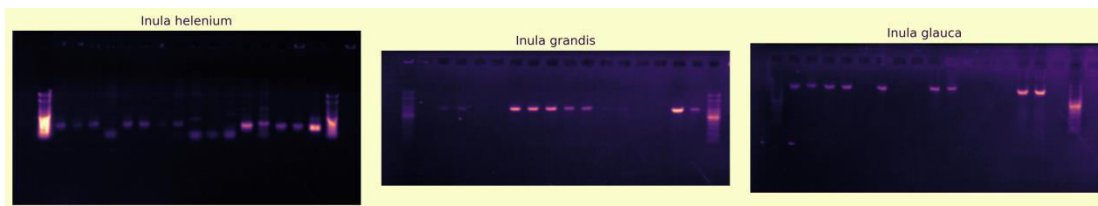


Figure.6 Distribution of stress-related gene markers in *Inula helenium*, *Inula grandis*, and *Inula glauca*

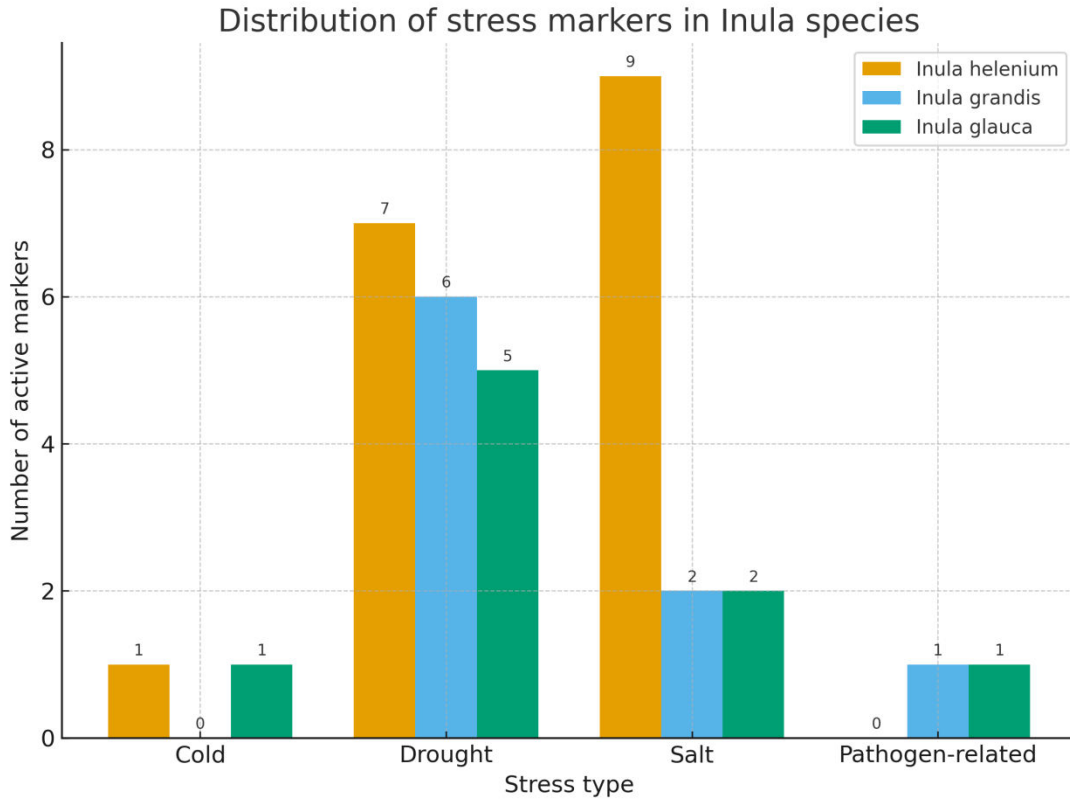


Table.1 Spectrophotometric characteristics of DNA samples (CTAB vs KIT).

Species	CTAB: DNA Conc. (ng/μl)	CTAB A260/A280	CTAB A260/A230	KIT: DNA Conc. (ng/μl)	KIT A260/A280	KIT A260/A230
<i>I. grandis</i>	45.65	1.878	2.197	216.60	1.957	2.055
<i>I. helenium</i>	100.65	1.878	2.197	184.10	1.957	2.055
<i>I. glauca</i>	212.00	1.824	2.016	470.95	1.999	2.065

Table.2 Habitat Distribution, Environmental Conditions, and Tolerance Profiles of Selected *Inula* Species

Species Name	Distribution Region	Ecological Conditions	Tolerance Level
<i>Inula helenium</i>	Southeastern mountains	Skeletal-gypsum soils, moderate precipitation	High
<i>Inula grandis</i>	Southern gypsum regions	Arid, saline, low precipitation	High
<i>Inula glauca</i>	Northeastern mountains	More humid, gypsum-rich areas	Low

I. grandis exhibited strong drought and salinity responses but lacked cold-responsive markers, reflecting adaptation to warm, arid conditions. Conversely, *I. glauca* showed moderate salinity and cold tolerance, aligning with its presence in moist, upland environments. The presence of key regulatory and

enzymatic markers such as NCED1, CYP707A, NHX2, CAT, PP2C8, and CSP3 confirms the involvement of ABA-mediated signaling, ion homeostasis, and oxidative stress defense in shaping abiotic stress resilience. These findings reinforce the evolutionary role of molecular plasticity in enabling *Inula* species to occupy diverse

ecological niches. From an applied perspective, these results highlight valuable candidate genes for marker-assisted selection (MAS) and crop improvement, particularly under the looming challenges of climate instability. *I. helenium*, with its robust gene profile, may serve as a genetic reservoir for breeding stress-tolerant crops, while *I. glauca* provide specialized traits for drought and cold adaptation, respectively. Ultimately, integrating molecular insights with ecological knowledge enhances our understanding of plant adaptation and supports conservation strategies aimed at preserving both genetic diversity and ecosystem functionality in vulnerable regions such as Central Asia.

Author Contributions

Ermatova Gulzoda Zakirdjanovna: Investigation, formal analysis, writing—original draft. Sharobiddinov Dilshod Azamatjonovich: Validation, methodology, writing—reviewing.

Data Availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethical Approval Not applicable.

Consent to Participate Not applicable.

Consent to Publish Not applicable.

Conflict of Interest The authors declare no competing interests.

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