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Comparative Expression Analysis of Drought Stress-Responsive Genes by Districts of Korean Fir (*Abies koreana*) in Mt. Halla

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ABSTRACT

Drought stress poses a significant threat to ecosystems, particularly affecting the subalpine ecosystem most severely. Korean fir (*Abies koreana*) is found in the subalpine region of Korea, including the summits of Mts. Halla, Jiri, Mudung, Kaji, and Deogyu. Although *A. koreana* is recognized as a species sensitive to drought stress by the Korean government, its response mechanisms are poorly understood. We previously conducted a comprehensive transcriptomic analysis of *A. koreana* under drought conditions. In our current study, we selected four genes exhibiting high expression, namely *Akoreana1SL019192t0002*, *Akoreana1SL009606t0001*, *Akoreana1SL022564t0001*, and *Akoreana1SL003793t0001*. Additionally, *A. koreana* samples from ten locations each in the ecologically stable (Nambyuk) and vulnerable (Youngsil) areas of Mt. Halla were analyzed using quantitative real-time polymerase chain reaction to measure gene expression. All four genes showed higher expression levels in samples from the vulnerable area compared to those from the stable area. These findings suggest that these genes could serve as diagnostic markers to assess *A. koreana*'s vulnerability to drought stress in natural settings.

Keywords: *Abies koreana*, Drought stress, Mt. Halla, Transcriptomic analysis, Vulnerable ecosystem

Introduction

According to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), a 4°C increase in global atmospheric temperature is projected by 2100 (Kikstra *et al.*, 2022). The effects of global climate change, including sea-level rise, droughts, and floods, result in severe and widespread damage to the ecosystem. A global average temperature rise of 1.5-2.5°C could lead to the extinction of approximately 20-30% of animal and plant species, with more than 40% of species potentially facing extinction if temperatures rise by 4°C (IPCC, 2014). Thus, research aimed at protecting biodiversity is critical, especially in areas susceptible to climate change such as islands, coasts, and subalpine regions (Hardy, 2003). Plant species in subalpine regions are particularly vulnerable to extinction due to limited opportunities for upslope migration (Bell *et al.*, 2014; Koo *et al.*, 2017; Randin *et al.*, 2009).

Korean fir (*Abies koreana*), endemic to Korea, is found on the summits of Mts. Halla, Jiri, Mudung, Kaji, and Deogyu in the southern part of the Korean peninsula

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(Lee, 1982). Due to its declining population from climate change, *A. koreana* is classified as a threatened species by the International Union for Conservation of Natural Resources (IUCN) and is designated as a biological indicator of climate change in Korea (Kim *et al.*, 2011; Lee *et al.*, 2010). The regional decline of the *A. koreana* population has been occurring since the 1980s, driven by poor growth and dieback due to global warming, along with various biotic and abiotic stresses such as warm winters and droughts (Koo *et al.*, 2001; Woo, 2009; Lim *et al.*, 2006; Woo *et al.*, 2008). Particularly, it has been reported that *A. koreana* in the Youngsil region is declining due to an insufficient water supply compared with the Nambyuk region of Mt. Halla (Kim *et al.*, 2017). Therefore, extensive research is necessary for the conservation and effective forest management of *A. koreana*.

We recently conducted *de novo* RNA sequencing (RNA-seq) on *A. koreana* trees that were exposed to elevated CO_2 levels and heat, in an effort to elucidate the transcriptomic alterations associated with environmental stress (Hwang *et al.*, 2018; 2019). These findings have significantly enhanced our comprehension of the molecular responses and environmental stress response pathways in *A. koreana* when subjected to elevated CO_2 and heat. The various genes identified from the *de novo* RNA-seq data were evaluated as candidate marker genes in the ecologically stable and vulnerable regions of Mts. Halla and Jiri (Kim *et al.*, 2020). Moreover, molecular marker genes have been used as environmental risk assessment tools in LM cotton to protect ecosystem safety and monitor of bifenazate resistance in two-spotted spider mites, *Tetranychus urticae* (Jo *et al.*, 2016; Lee *et al.*, 2011).

We previously performed a comprehensive transcriptomic analysis of *A. koreana* under drought stress and identified four highly expressed genes (*Akoreana1SL019192t0002, Akoreana1SL009606t0001, Akoreana1SL022564t0001*, and *Akoreana1SL003793t0001*). In this study, we assessed the expression levels of these four genes using quantitative real-time polymerase chain reaction (qRT-PCR) in 10 samples of *A. koreana* collected from both the ecologically stable (Nambyuk) and vulnerable (Youngsil) regions of Mt. Halla. The results of this study will facilitate the development of diagnostic markers for assessing the vulnerability of *A. koreana* to environmental stress, as well as the development of strategies for conservation and restoration of the subalpine ecosystem amid climate change.

Materials and Methods

Sample collection

The needles (leaves) of *A. koreana* plants were collected from both the ecologically stable (Nambyuk) and vulnerable (Youngsil) regions of Mt. Halla (Fig. 1), each located approximately 1,500 m from the summit. Plants were collected from 10 sites per region and immediately frozen in liquid nitrogen. The samples were then transported to the laboratory and stored at −80°C. Subsequently, total RNA was extracted using the Ribospin Seed/Fruit RNA mini kit (GeneAll, Seoul, Korea) according to the manufacturer's instructions.

Analysis of drought stress-responsive genes in *A. koreana*

In a previous study, drought stress-responsive genes in *A. koreana* were isolated using comparative RNA-seq analysis (Park *et al.*, 2018). Briefly, raw reads were trimmed with Trimmomatic (version 0.32), and then assembled *de novo* using Trinity software (version R20140717), with default settings, to generate a suitable set of reference contigs named unigenes (Grabherr *et al.*, 2011). These unigenes were functionally annotated with BLASTX (BLAST 2.6.0+), using the NCBI non-redundant protein sequence database. Furthermore, gene expression profiles from the RNA-seq data were analyzed with RNA-Seq by Expectation-Maximization (RSEM) software, part of the Trinity package (Schmieder & Edwards, 2011). Lastly, drought stress-responsive genes showing more than a 2-fold increase in expression (p-value ≤ 0.05) were selected for further analysis.

Gene expression analysis by qRT-PCR

A. koreana cDNA was synthesized from 1 μg of total RNA using the ReverTra Ace-α kit (Toyobo, Osaka, Japan), following the manufacturer's instructions. Expression levels of drought stress-responsive genes and *AkActin* (reference gene) were quantified by qRT-PCR on the CFX96 real-time system using IQ™ SYBR Green Supermix, processed with the Bio-Rad CFX Manage program (Bio-Rad, Hercules, USA) (Lee *et al.*, 2023). Each qRT-PCR reaction comprised 1 μl of diluted cDNA, 10 μl of 2× IQ SYBR Green Supermix, 1 μl each of 10 pM forward and reverse primers, and 7 μl of H_2O. The qRT-PCR conditions included an initial step at 95°C for 10 min, followed by 55 cycles at 95°C for 15 s, 55°C for 15 s, and 75°C for 30 s. Primer sequences used for qRT-PCR are detailed in Table 3. The expression levels of drought stress-responsive genes were normalized against *AkActin* using the comparative CT (ΔΔCT) method (Livak & Schmittgen, 2001). Error bars indicate standard deviation values for triplicates.

Results and Discussion

Selection of *A. koreana* sampling sites on Mt. Halla

A. koreana exhibits the widest distribution on Mt. Halla, and its decline has been the most severe across the Korean peninsula. The decline in *A. koreana* population is likely due to complex interactions among various environmental factors induced by global warming (Drohan *et al.*, 2002; Duchesne *et al.*, 2005). The population of *A. koreana* in the

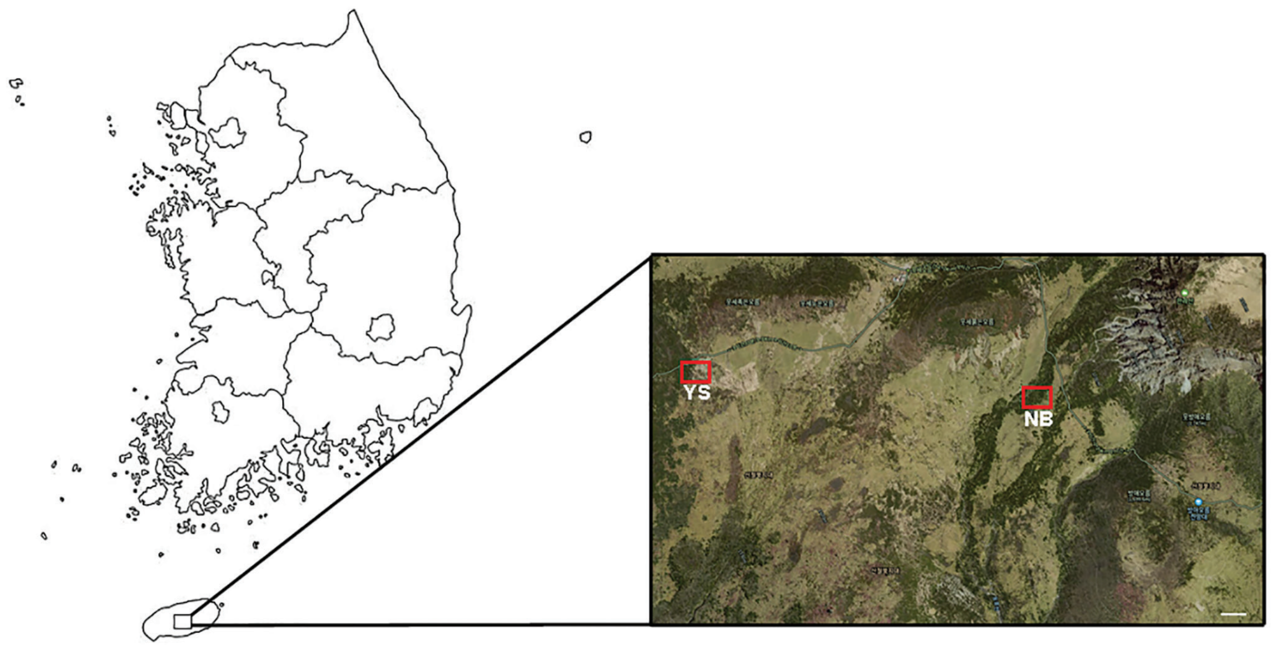

Fig. 1. Area of investigation of *Abies koreana* in the subalpine region of Mt. Halla in Korea. Red rectangles denote the ecologically stable region (Nambyuk, NB) and vulnerable region (Youngsil, YS), classified based on the growth of *A. koreana*. Scale bar = 100 m.

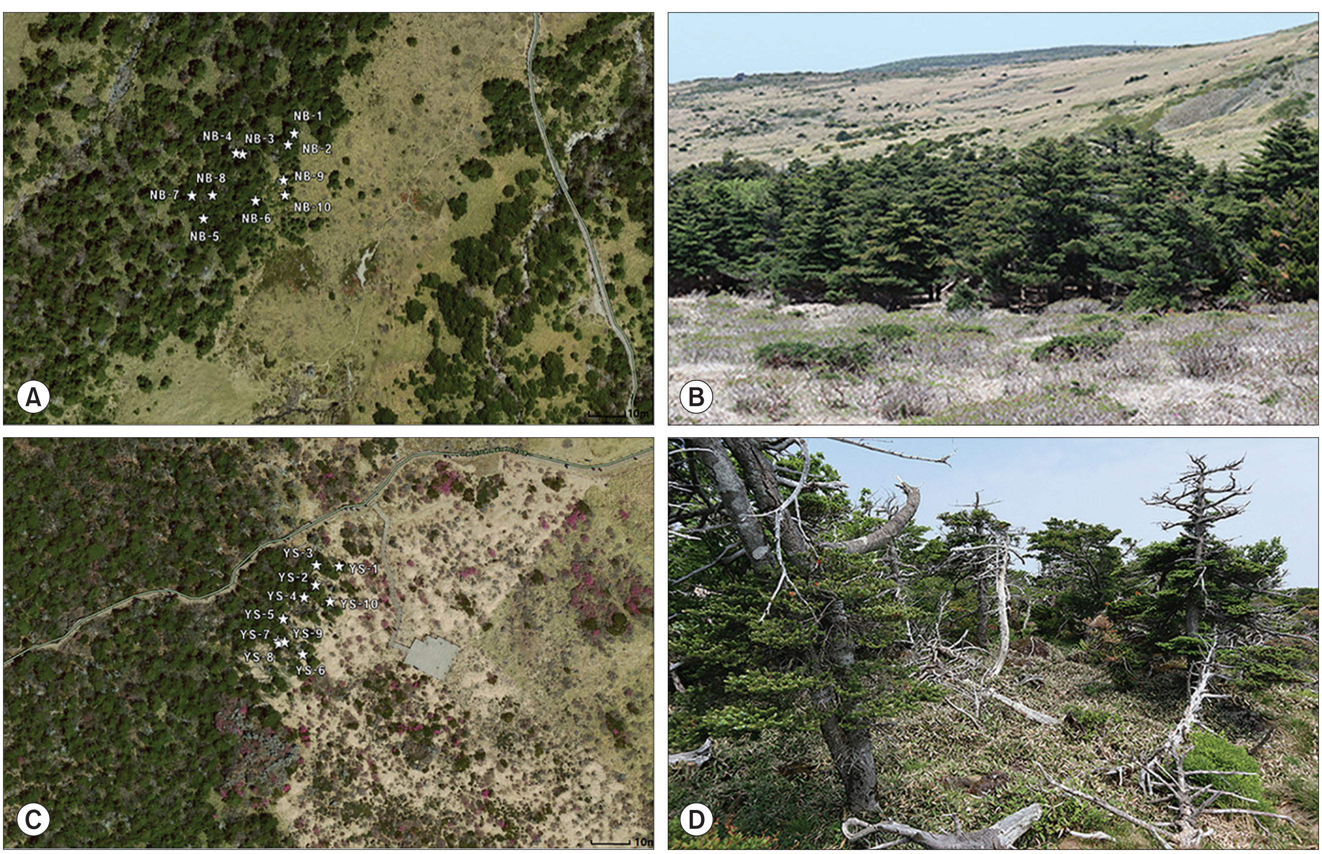

Fig. 2. Sampling sites of *A. koreana* in the ecologically stable region (Nambyuk, NB) and the vulnerable region (Youngsil, YS) of Mt. Halla. (A) Depicts the locations of 10 sampling sites in NB. (B) Shows a photograph of NB. (C) Illustrates the locations of 10 sampling sites in YS. (D) Displays a photograph of YS. Scale bars represent 10 m.

Youngsil region of Mt. Halla decreased by 21.5% (25.3 ha) compared to 2006 (Kim *et al.*, 2017). For this study, two regions on Mt. Halla were selected for sample collection: Nambyuk (NB) and Youngsil (YS) (Fig. 1). NB, situated south of the peak of Mt. Halla, supports ecologically stable growth of *A. koreana*. In contrast, YS is located southwest of the Mt. Halla peak and designated as an ecologically vulnerable region because of the declining *A. koreana* population. Ten *A. koreana* plants were sampled from each region (Fig. 2), with the geographic coordinates as follows: NB: 33.358731-33.358936 (latitude) and 126.508706-126.508871 (longitude); YS: 33.357776-33.357923 (latitude) and 126.523485-126.523713 (longitude) (Table 1). These plants were then subjected to gene expression analysis to identify the ecologically stable and vulnerable regions of *A. koreana* in Mt. Halla.

Isolation and characterization of drought stress-responsive genes in *A. koreana*

A. koreana, an endangered species sensitive to drought, is experiencing severe decline due to global warming. Therefore, it is crucial to uncover the adaptive molecular mechanisms utilized by *A. koreana* in response to drought stress. We previously conducted a comprehensive transcriptomic analysis on *A. koreana* exposed to varying periods of drought stress and identified genes that were upregulated and downregulated in comparison with untreated (control) plants (Park *et al.*, 2018). In this study, we focused on genes whose expression increased by more than 2-fold under drought stress. Among these, four genes (*Akoreana1SL019192t0002*, *Akoreana1SL009606t0001*, *Akoreana1SL022564t0001*, and *Akoreana1SL003793t0001*) were selected for further analysis. Gene annotation with BLASTX (BLAST 2.6.0+) showed that *Akoreana1SL019192t0002* codes for Myb domain protein 21, which contributes to salt tolerance in *Arabidopsis thaliana* (Zhang *et al.*, 2021) and Myb-related protein 305 in *Populus trichocarpa*; *Akoreana1SL009606t0001* encodes ATP-binding cassette 14, which strengthens the abscisic acid signaling in guard cells and enhances water use efficiency in *Arabidopsis* (Kuromori *et al.*, 2016) and ABC transporter G family member 21 isoform X1 in *Populus*; *Akoreana1SL022564t0001* encodes ethylene-responsive element binding factor 3 (ERF3), associated with drought stress responses in *Arabidopsis* (Song *et al.*, 2005) and ERF9 in *Populus*; and *Akoreana1SL003793t0001* encodes a basic helix-loop-helix (bHLH) DNA-binding superfamily protein, activated by the presence of NaCl or glucose in *Arabidopsis* (Ikeya *et al.*, 2020) and a bHLH family protein in *Picea sitchensis* (Table 2). Subsequently, the expression levels of these four genes were validated in the sampled *A koreana* plants through qRT-PCR using gene-specific primers (Table 3).

Table 1. Geographic coordinates of *A. koreana* sampling sites in the ecologically stable region (Nambyuk, NB) and the vulnerable region (Youngsil, YS) of Mt. Halla

Sampling site	Latitude	Longitude
NB-1	33.357923	126.523713
NB-2	33.357904	126.523700
NB-3	33.357888	126.523597
NB-4	33.357890	126.523584
NB-5	33.357776	126.523511
NB-6	33.357807	126.523627
NB-7	33.357816	126.523485
NB-8	33.357817	126.523531
NB-9	33.357843	126.523689
NB-10	33.357816	126.523692
YS-1	33.358936	126.508871
YS-2	33.358892	126.508808
YS-3	33.358939	126.508809
YS-4	33.358865	126.508776
YS-5	33.358814	126.508719
YS-6	33.358731	126.508773
YS-7	33.358763	126.508706
YS-8	33.358758	126.508708
YS-9	33.358760	126.508723
YS-10	33.358857	126.508842

Increased expression of drought stress-responsive genes in the ecologically sensitive area of Mt. Halla

Expression levels of the four genes were examined by qRT-PCR in 10 *A. koreana* samples collected from each of the ecologically stable (Nambyuk, NB-1-10) and vulnerable (Youngsil, YS-1-10) regions of Mt. Halla (Fig. 3). All four genes exhibited higher expression levels in YS samples compared to NB samples (Fig. 3). Specifically, *Akoreana1SL019192t0002* demonstrated approximately 100-3,300-fold higher expression in YS samples than in NB samples. Similarly, *Akoreana1SL009606t0001*, *Akoreana1SL022564t0001*, and *Akoreana1SL003793t0001* showed roughly 11-106-, 4.3-17-, and 8-27-fold higher expression in YS samples compared to NB samples, respectively. Collectively, these results suggest that the four genes could serve as diagnostic markers for assessing the ecologically stable and vulnerable regions of Mt. Halla.

In conclusion, global warming poses a significant threat to the biodiversity of natural ecosystems, particularly in vulnerable regions like subalpine forests. The population of *A. koreana*, endemic to subalpine regions in southern Korea, continues to decline due to warm winter temperatures and water stress caused by global warming.

Table 2. Annotation of genes significantly upregulated in *A. koreana* in response to drought stress

Gene ID	BLAST	
	Arabidopsis thaliana	***Populus trichocarpa/Picea sitchensis***
Akoreana1SL019192t0002	Myb domain protein 21 (AT3G27810)	Myb-related protein 305 (*Populus trichocarpa*)
Akoreana1SL009606t0001	ATP-binding cassette 14 (AT1G31770)	ABC transporter G family member 21 isoform X1 (*Populus trichocarpa*)
Akoreana1SL022564t0001	Ethylene-responsive element binding factor 3 (AT1G50640)	Ethylene-responsive transcription factor 9 (*Populus trichocarpa*)
Akoreana1SL003793t0001	Basic helix-loop-helix (bHLH) DNA-binding superfamily protein (AT4G36930)	Basic helix-loop-helix (bHLH) family protein (*Picea sitchensis*)

Table 3. Primer sequences used for validating the expression of drought stress-responsive genes in *A. koreana* via qRT-PCR

Gene ID	Forward primer sequence (5′→3′)	Reverse primer sequence (5′→3′)
Akoreana1SL019192t0002	TTTGCCCATTTCCTGCAATCT	TATATGATGAGTATTGACATCACAAGT
Akoreana1SL009606t0001	CGTGGCTGCTTTGGGTATCA	GCGAGAATGATAAGTTAGGCTTACTCT
Akoreana1SL022564t0001	GAAGACCTTTTCTTCCGGACCT	AGAACCGATCTGCTGCGG
Akoreana1SL003793t0001	ATGGCCCAGAAATGTTCAGAGCCTGGT	TTTCTCTTGCAATGAAAGTGCAGAATGGAA

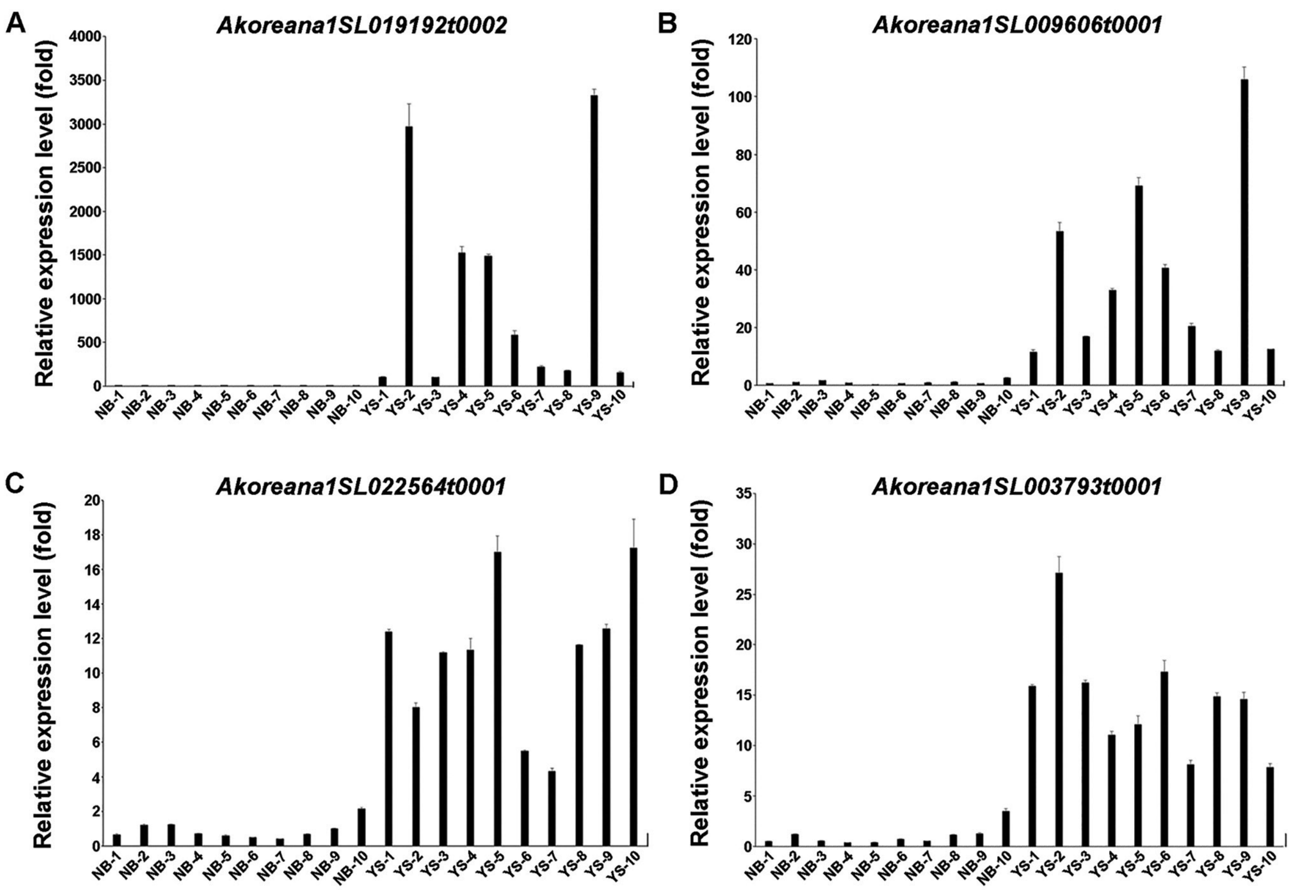

Fig. 3. Expression analysis of four genes in the ecologically stable (Nambyuk, NB-1-10) and vulnerable (Youngsil, YS-1-10) regions of *A. koreana* in Mt. Halla Samples were taken from 10 sites each in the ecologically stable (Nambyuk, NB) and vulnerable (Youngsil, YS) regions of Mt. Halla. (A-D) Show the expression levels of *Akoreana1SL019192t0002* (A), *Akoreana1SL009606t0001* (B), *Akoreana1SL022564t0001* (C), and *Akoreana1SL003793t0001* (D).

Therefore, it's crucial to investigate the mechanisms of environmental stress resistance in *A. koreana* under field conditions. Our findings indicate that the diagnostic genes can effectively assess the ecological vulnerability of *A. koreana* under various environmental stresses and aid in conservation efforts in subalpine ecosystems. Additionally, this study lays a strong foundation for further molecular studies and the development of conservation and restoration strategies for these ecosystems.

Author Contributions

H.C.P. designed the experiments. H.C.P., D.Y.P and D.Y.L. conducted the experiments and analyzed the data. H.C.P. drafted the manuscript and maintained the plant materials. H.C.P and D.Y.P discussed the results and finalized the manuscript. All authors have read and agreed to the published version of the manuscript.

Conflict of Interest

The authors declare that they have no competing interests.

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