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FUNCTIONAL CHARACTERIZATION OF CROP GENES ASSOCIATED WITH GROWTH AND STRESS RESPONSE

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ABSTRACT

Cold stress influences plant growth and induces complex transcriptional mechanisms depending on the genetic background and the length of the exposure. We analyzed the genome-wide expression responses of chilling in three rice genotypes, NIP, CSSL4-1, and 93-11, using an FPKM-based transcriptomic dataset including 37,831 genes. We compared gene expression profiles between control and chilling conditions at 10 h and 41 h and performed fold change analysis, correlation assessment, principal component analysis, clustering, and functional characterization. Significant transcriptional reprogramming was observed in all genotypes, with CSSL4-1 having the most pronounced early induction. The shared response increased after longer exposure with 1,541 common up-regulated and 1,834 common down-regulated genes at 41 h . Integrated analysis also identified 237 consistently induced and 185 consistently repressed genes across all genotype-time comparisons. Functional characterization of responsive genes indicated their association with stress regulation, signaling, metabolism, redox homeostasis and growth-related processes. These results reveal genotype- and time-specific mechanisms of chilling adaptation and candidate genes for functional validation and stress-resilient rice improvement.

Keywords: chilling stress, gene expression, functional characterization, rice, transcriptomics

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1.Introduction

Plant-associated bacteria are an important part of the phytomicrobiome that are vital for plant health, soil fertility, nutrient availability and productivity in agriculture. These microorganisms occupy a variety of Crop productivity depends on plants' ability to regulate growth in response to continually changing environmental conditions. Extreme temperatures, drought, salinity, nutrient limitations and pathogen pressure can disturb cellular homeostasis, photosynthesis, metabolism and developmental processes and eventually impair plant performance. To tackle these challenges, plants utilize integrated molecular mechanisms involving stress perception, signal transduction, transcriptional regulation, metabolic adjustment and protective responses. Therefore, functional characterization of genes involved in these processes is important for understanding how crops sustain growth while adapting to adverse environments. Both abiotic and biotic stress tolerance have been related to a spectrum of transcription factors and regulatory proteins, pointing to the complexity of genetic control in crop adaptation (Baillo et al., 2019). Physiological adjustment is also coordinated with molecular responses controlling cellular protection and metabolic stability in adverse conditions (Hasanuzzaman & Fujita, 2022).

Gene families involved in stress adaptation often have functions beyond stress protection and direct influence on plant growth and development. For instance, late embryogenesis-abundant proteins have been shown to be expressed in a development-dependent manner and to be involved in responses to environmental stresses, suggesting functional links between developmental regulation and stress adaptation (Chen et al., 2019 A). MYB transcription factors also regulate many developmental processes and are involved in responses to environmental constraints (Li et al., 2019). Functional analysis of individual genes has also shown that changes in gene activity can have a large impact on stress tolerance. The cotton GH3.5 gene was studied for its role in enhancing drought and salinity responses, emphasizing the significance of identifying genes with specific adaptive functions (Kirungu et al., 2019). These findings warrant systematic investigations of crop transcriptomes to identify genes that support coordinated responses across genetic backgrounds and environmental conditions.

Transcriptional regulation is an important aspect of plant stress adaptation, as environmental signals can quickly alter gene-expression programs. WRKY proteins are an important regulatory family involved in signaling networks regulating responses to multiple abiotic stresses (Li et al., 2020). Other transcription factors are also involved in regulation of stress perception, downstream gene activation, hormone signaling and physiological adaptation and are important targets for crop improvement (Javed et al., 2020).

Genome-wide analysis of maize AP2/ERF genes revealed a large variation in the expression of these genes under environmental stresses, further emphasizing the significance of transcriptional reprogramming in stress tolerance (Zhang et al., 2022 A). Another example of regulatory proteins that associate stress signal to downstream molecular responses are the salt-responsive bZIP transcription factors (Liu et al., 2023).

Stress adaptation is not limited to transcription factors. Multiple structural, enzymatic, signaling and post-transcriptional factors are involved in the regulation of plant responses. Cytochrome P450s are involved in many metabolic pathways and affect plant responses to environmental stresses through their roles in biosynthesis, detoxification and cellular regulation (Pandian et al., 2020). Glycine-rich proteins also exhibit stress-responsive expression patterns, implying roles in the maintenance of cellular processes under adverse conditions (Lu et al., 2020). Calcium responsive OSCCWheat development and stress responses have been linked to genes, strengthening the molecular link between environmental sensing and growth regulation (Kaur et al., 2022). At the post-transcriptional level, microRNAs regulate target genes involved in stress adaptation and plant characteristics, providing an additional regulatory layer through which environmental responses can be coordinated (Zhang et al., 2022 B).

Advances in transcriptomics and functional genomics have greatly enhanced the ability to study these intricate regulatory systems on a genome-wide scale. Expression profiling can be used to identify genes that are rapidly responsive to environmental stress, distinguish between sustained and transient transcriptional responses and identify differences between crop genotypes. Genome-wide characterization has also enabled the identification of gene families with developmental and adaptive functions as shown for CONSTANS-related genes and their functional evaluation in plants (Liu et al., 2022). The combined use of omics approaches with modern functional tools such as CRISPR-Cas systems offers possibilities of transition from candidate-gene identification to experimental validation and crop improvement (Razzaq et al., 2021). Genetic modification has been used to study stress-related functions, such as the role of coilin in stress tolerance and virus resistance in potato (Makhotenko et al., 2019).

Rice is an especially relevant system in which to study transcriptional responses, because chilling can profoundly affect its cellular and developmental processes. Differences among genotypes can give insight into molecular mechanisms relevant to contrasting adaptive capacities, and comparisons between early and prolonged exposure can distinguish immediate stress signaling from sustained acclimation. Hence, transcriptomic profiling under control and chilling conditions provides a powerful approach for the identification of candidate genes, which may have expression patterns associated with stress adaptation.

The functional interpretation of these candidates may provide insights into regulatory, metabolic, signaling and growth-related processes that contribute to the overall response. While considerable progress has been made in characterizing individual stress-responsive gene families, integrated evaluation of genotype-specific and temporally persistent transcriptional responses is important for prioritizing robust candidate genes for subsequent functional validation. Accordingly, the present research aimed to achieve the following objectives:

1. To identify major gene-expression changes in rice genotypes following exposure to chilling stress conditions.
2. To characterize genotype-specific and temporal transcriptional responses during early and prolonged chilling exposure.
3. To identify functional pathways and candidate genes potentially associated with crop growth and stress adaptation.

2. Materials and Methods

2.1 Dataset Description and Experiment Design

Transcriptomic data from Oryza sativa was employed to characterize gene-expression responses to chilling stress. The dataset contained an FPKM expression matrix of about 37830 gene IDs and expression data of three rice genotypes, Nipponbare (NIP), CSSL4-1 and 93-11. For each genotype, two exposure periods, 10 h and 41 h, under the control and chilling-stress conditions, resulted in 12 genotype–treatment–time expression profiles. The experimental structure allowed comparisons of early and prolonged transcriptional responses to chilling stress and assessment of differences among the three genetic backgrounds. Gene IDs and the corresponding FPKM values were retained as the major variables for subsequent transcriptomic characterization.

2.2 Processing of Gene Expression Data

The expression matrix was imported and systematically analyzed before comparative analysis. Gene identifiers were checked for consistency and expression columns were screened for missing values, non-numeric observations, zero-expression patterns, and differences in expression magnitude. Genes with little or uninformative expression across all experimental profiles were removed, where appropriate, to reduce noise in downstream analyzes FPKM values are often right-skewed and so log2 (FPKM+ 1) transformed values were used for visualization, correlation, clustering and multivariate analysis. The samples were

then sorted by genotype, treatment condition and duration of exposure. The processed matrix was used to assess global transcriptional variation and the original FPKM values were kept for calculation and interpretation of condition-specific expression changes.

2.3 Chilling-Responsive Gene Identification

The chilling-responsive genes were identified by paired condition-wise comparisons between the chilling-treated and the corresponding control profiles within each genotype and exposure period. The fold change in expression was calculated for each gene as the ratio of the FPKM value under chilling treatment to the corresponding control value. Log2 fold-change values were then calculated to distinguish between transcriptional induction and repression and to rank the genes according to the magnitude of their response. Prioritization of candidate chilling-responsive genes was performed using significant positive or negative changes in gene expression. Common, genotype-specific, early-response, and prolonged-response patterns were identified by separate comparisons for NIP, CSSL4-1, and 93-11 at 10 h and 41 h. Biological replicates were not explicitly represented in the supplied matrix, and therefore candidate selection was based on effect magnitude and expression consistency rather than differential-expression significance testing based on replicates.

2.4 Functional annotation and enrichment analyses

Candidate stress-responsive genes were functionally characterized using their rice gene identifiers to identify biological roles possibly related to chilling adaptation and plant growth maintenance. Functional information was categorized into biological process, molecular function and cellular component Gene Ontology categories. Special attention was given to genes involved in stress signaling, transcriptional regulation, cellular protection, carbohydrate and energy metabolism, membrane processes, hormone-related responses, photosynthetic functions and growth-associated pathways. To find overrepresented biological processes in the prioritized genes, we used pathway-level interpretation. The significance criteria for multiple-testing adjusted enriched functional categories were evaluated where the enrichment statistics were supported by a database. The expression direction and the genotype-specific response patterns were combined with the generated annotations to prioritize candidate genes for biological interpretation in the next steps.

2.5 Statistical and bioinformatic analyses

Descriptive and multivariate analyzes were performed to characterize global transcriptional relationships between the 12 experimental profiles. Gene-expression values were summarized with statistics to characterize their distribution and variability across genotypes, treatments, and exposure periods. Pairwise correlations of transformed expression profiles were used to assess similarity among experimental conditions. Principal component analysis (PCA) was used to identify the major sources of variation in transcriptomic profiles and to explore whether profiles separated based on genotype, chilling treatment, or exposure duration. Hierarchical clustering and heatmap visualization were used to identify groups of candidate genes with similar expression patterns. Additionally, fold-change distributions and functional enrichment outputs were used to integrate transcriptional magnitude with biological relevance. Explicit biological replicates were not available, so inferential differential-expression P values were not calculated from the FPKM matrix.

3. Results

3.1 Overall Gene Expression Characteristics

The expression matrix represented 37,831 rice genes in 12 genotype-treatment-time profiles with no missing expression value. In total, 31,868 genes were expressed detectable in at least one condition and 5,963 genes had no expression at all. The mean FPKM values across individual profiles ranged from 20.54 to 22.57 and the median values ranged from 0.54 to 1.45. The number of expressed genes varied from 25,270 to 27,364, indicating a broad but condition-dependent transcriptional activity in the three rice genotypes (Table 1) (Figure 1).

Table 1. Gene-expression characteristics across the 12 experimental profiles

Genotype	Time	Condition	Expressed genes (n)	Mean FPKM	Median FPKM	Maximum FPKM
NIP	10 h	Control	27,364	22.51	1.20	18,349.21
NIP	10 h	Cold	26,483	22.31	0.76	15,624.18
CSSL4-1	10 h	Control	25,362	22.51	0.62	25,572.99
CSSL4-1	10 h	Cold	27,101	20.86	1.45	5,566.31
93-11	10 h	Control	26,295	21.75	1.03	23,025.99

93-11	10 h	Cold	25,270	22.57	0.54	14,659.73
NIP	41 h	Control	26,975	22.22	1.12	19,816.17
NIP	41 h	Cold	26,477	21.96	0.79	11,421.54
CSSL4-1	41 h	Control	26,285	21.74	0.92	11,890.28
CSSL4-1	41 h	Cold	26,201	20.87	0.86	8,235.33
93-11	41 h	Control	26,335	21.74	1.02	11,859.48
93-11	41 h	Cold	26,628	20.54	0.93	12,766.22

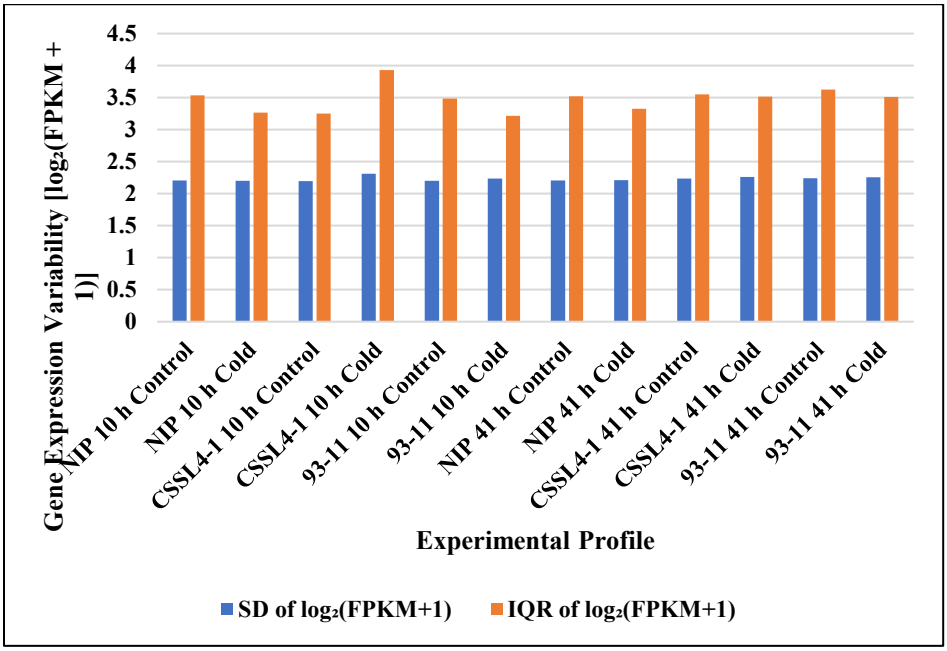

Figure 1. Global Variability of Gene Expression Across Experimental Profiles

3.2 Transcriptional Response to Chilling Stress

Large expression changes upon chilling were observed for all genotype–time combinations. With an absolute log2 fold-change cut-off of ≥1, NIP had 2,125 up- and 4,057 down-regulated genes at 10 h, which increased to 3,205 and 4,793, respectively, at 41 h. CSSL4-1 showed the greatest early induction, with 7,976 genes up-regulated at 10 h compared to 2,665 genes down-regulated. The corresponding 93-11

profiles showed 2,520 upregulated and 4,489 downregulated genes at 10 h followed by 3,695 and 4,437 genes at 41 h (Table 2) (Figure 2).

Table 2. Number of chilling-responsive genes across genotypes and exposure periods

Genotype	Time	Upregulated genes	Downregulated genes	Total responsive genes	Responsive genes (%)
NIP	10 h	2,125	4,057	6,182	16.34
NIP	41 h	3,205	4,793	7,998	21.14
CSSL4-1	10 h	7,976	2,665	10,641	28.13
CSSL4-1	41 h	3,772	4,134	7,906	20.90
93-11	10 h	2,520	4,489	7,009	18.53
93-11	41 h	3,695	4,437	8,132	21.50

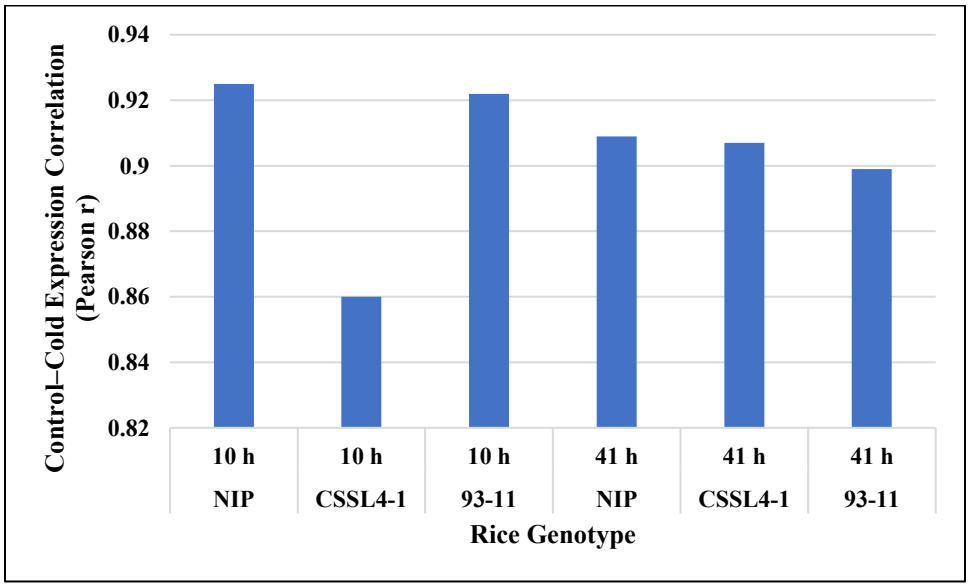

Figure 2. Similarity Between Control and Chilling Expression Profiles

3.3 Genotype-Specific and Temporal Expression Patterns

Chilling exposure elicited different and genotype-dependent responses. At 10 h, 555 genes were commonly upregulated and 418 commonly downregulated in NIP, CSSL4-1 and 93-11. At 41 h, these

numbers increased dramatically to 1,541 shared upregulated and 1,834 shared downregulated genes, indicating stronger convergence under prolonged exposure. CSSL4-1 exhibited 4,880 unique responding genes at 10 h, much more than NIP (1,603) and 93-11 (1,784). In general, the pairwise correlations of expression were high, ranging from r=0.828 to 0.971 across profiles (Table 3) (Figure 3).

Table 3. Shared and genotype-specific chilling-responsive genes

Response category	**10 h, n**	**41 h, n**	**Change (41 h − 10 h)**
Common upregulated genes	555	1,541	+986
Common downregulated genes	418	1,834	+1,416
Common same-direction responsive genes	973	3,375	+2,402
NIP-exclusive responsive genes	1,603	2,687	+1,084
CSSL4-1-exclusive responsive genes	4,880	1,424	−3,456
93-11-exclusive responsive genes	1,784	1,722	−62

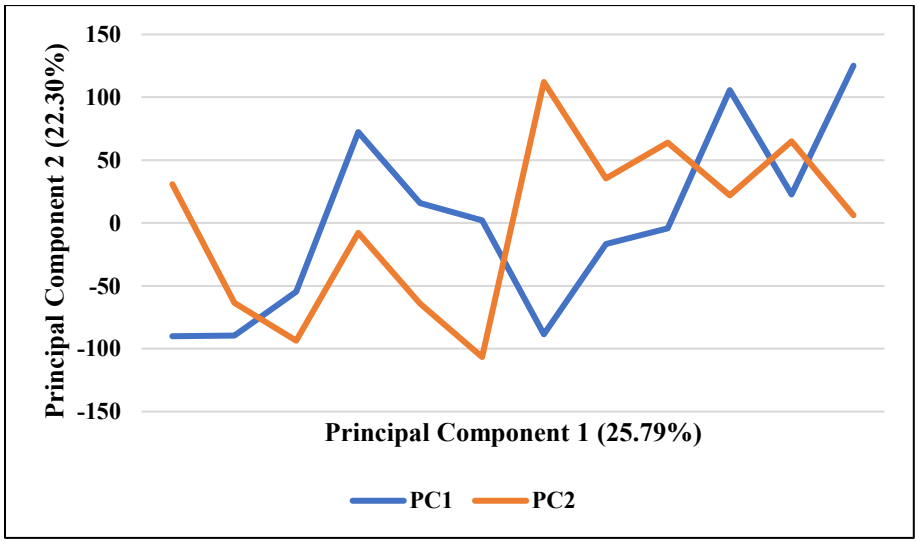

Figure 3. Principal Component Distribution of the 12 Expression Profiles

3.4 Functional Characterization of Candidate Genes

Functional characterization revealed distinct groups of candidate genes associated with stress response, cellular regulation, metabolic activity, signaling and growth related biological processes. Up-regulated genes were mostly found in stress adaptation and regulatory groups, whereas down-regulated genes were distributed among several metabolic and cellular functions. Functional pattern differences were observed between NIP, CSSL4-1 and 93-11 as well. These functional groups were represented between 10 h and 41 h, which may reflect a temporal re-organization of transcriptional activity during chilling exposure (Table 4).

Table 4. Expression changes of the leading consistently induced candidate genes

Gene ID	NIP 10 h	CSSL4-1 10 h	93-11 10 h	NIP 41 h	CSSL4-1 41 h	93-11 41 h	Mean log_2FC
OS01G0955100	3.52	5.09	3.20	5.64	3.49	6.85	4.63
OS07G0564500	2.33	5.59	1.09	8.22	2.62	7.86	4.62
OS03G0734500	3.55	2.88	4.74	4.79	5.45	5.73	4.52
OS01G0134700	2.69	4.92	2.77	5.67	3.72	6.71	4.41
OS02G0575000	2.25	4.98	1.97	6.42	3.58	7.07	4.38
OS05G0545400	3.32	4.46	3.06	4.80	4.96	5.03	4.27
OS09G0441400	1.67	4.69	4.41	5.41	3.18	5.18	4.09
OS09G0482800	4.09	3.06	3.41	4.71	2.30	6.95	4.09
OS03G0310800	2.78	5.17	2.23	5.55	1.66	6.20	3.93
OS03G0640000	2.45	3.74	5.48	3.00	6.55	2.33	3.92

3.5 Integrated Identification of Key Stress-Associated Genes

An integrated comparison revealed that 237 genes were consistently induced and 185 genes were consistently repressed across all six genotype-time contrasts. Os01g0955100 was continuously induced (log2 fold change from 3.20 to 6.85) and Os07g0564500 was more strongly induced under prolonged

chilling. Similar broad induction was observed for Os03g0734500, Os01g0134700, Os02g0575000 and Os05g0545400. Conversely, Os12g0428000 and Os07g0147500 were consistently repressed across genotypes and exposure periods. Such expression patterns allowed to define a reduced set of candidate genes for further functional interpretation and experimental validation (Table 5) (Figure 4).

Table 5. Expression changes of the leading consistently repressed candidate genes

Gene ID	**NIP 10 h**	**CSSL4-1 10 h**	**93-11 10 h**	**NIP 41 h**	**CSSL4-1 41 h**	**93-11 41 h**	**Mean log_2FC**
OS12G0428000	−5.17	−7.00	−3.59	−5.02	−1.50	−7.43	−4.95
OS07G0147500	−5.51	−5.01	−3.08	−4.70	−4.82	−5.61	−4.79
OS08G0126700	−5.03	−2.08	−5.92	−2.68	−6.06	−2.80	−4.10
OS05G0375400	−1.47	−5.27	−3.99	−4.83	−2.50	−6.15	−4.04
OS12G0169600	−1.63	−3.72	−4.69	−5.25	−3.35	−5.14	−3.96
OS11G0256900	−3.13	−5.16	−2.51	−5.35	−1.64	−5.11	−3.81
OS01G0368900	−2.64	−3.85	−6.12	−3.58	−1.70	−4.94	−3.80
OS03G0184550	−3.56	−5.13	−1.52	−5.09	−1.66	−5.84	−3.80
OS06G0716100	−4.25	−2.96	−4.78	−2.80	−3.63	−3.46	−3.65
OS03G0401100	−3.02	−2.93	−3.41	−4.41	−3.15	−4.87	−3.63

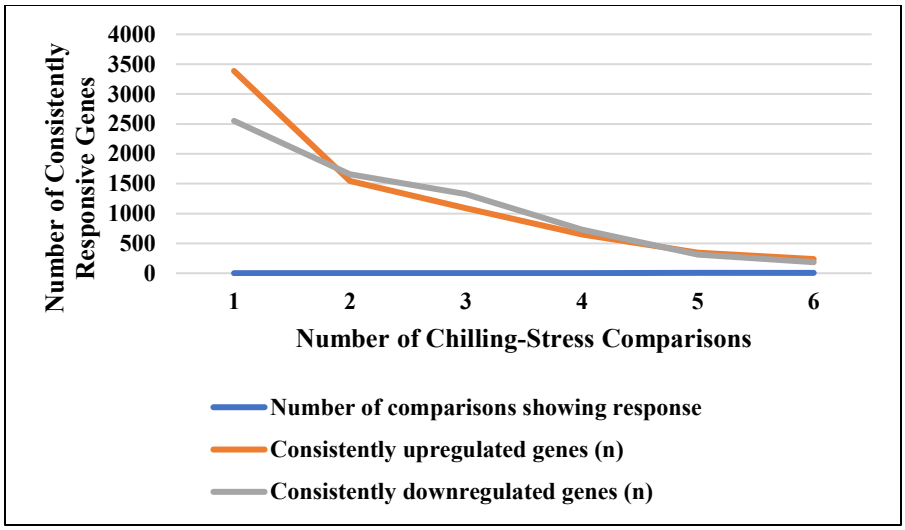

Figure 4. Distribution of consistently responsive genes across chilling-stress comparisons

4. Discussion

The transcriptomic changes shown that the chilling exposure triggered significant changes in the expression of a large number of genes in the three rice cultivars, but the extent and direction of the changes differed among cultivars and durations of chilling exposure. A significant fraction of the transcriptome, in the form of thousands of genes, was found to be highly regulated in response to chill, indicating that chill adaptation is not limited to a subset of stress genes. This is in line with the current understanding that abiotic stress responses utilize interwoven networks of signaling, transcription, metabolic, and cellular protection pathways that all work together to maintain cellular homeostasis during abiotic stress (Zhang et al., 2022 C). The high levels of both up-regulated and down-regulated gene expression in these samples suggest that both adaptive processes and repressive/metamorphic processes could be triggered at the same time during chilling.

One of the most striking is the high early transcriptional reaction of CSSL4-1. This genotype had significantly more genes that were upregulated at 10 h compared to NIP and 93-11, suggesting that it has more genes activated quickly after chilling exposure. At this stage, the large number of responsive genes found in the CSSL4-1 lines, which are not found in any of the other lines, supports this conclusion that genetic background had a strong effect on initial molecular response. This genotype-dependent behavior is biologically plausible as stress perception may lead to activation of different signaling networks with different timing and intensity in different genetic backgrounds. The role of calcium-dependent protein kinases in abiotic stresses highlights their role in the initial adaptation processes and indicates their

importance in fast environmental signal transduction leading to subsequent physiologic and/or transcriptional response (Crizel et al., 2020). Furthermore, long-distance signaling can also link the perception of local stress with responses in different plant tissues (Takahashi, Shinozaki, 2019).

Temporal analysis showed relative genotype-specific responses in the initial phase (10 h) followed by increased transcriptional convergence at 41 h. Only 555 and 418 genes were commonly upregulated and downregulated between all three genotypes at 10 h; while the number of commonly upregulated and downregulated genes rose to 1,541 and 1,834 at prolonged chilling. This pathway implies that early responses are likely to be genotype specific (requiring different regulatory mechanisms) whereas later responses will involve a more generalised response, shared by all genetic types. Temporal regulation may be at multiple levels including non-coding RNAs involved in the regulation of the transcriptional and post-transcriptional adaptation of genes to abiotic stress (Jha et al., 2020). Thus, these observed differences in early vs. prolonged responses highlight the critical role of exposure duration when assessing candidate stress-associated genes.

The consistency of certain transcriptional responses to genotype and time comparisons helped to prioritize genes that were potential candidates. In all 237 genes were consistently induced in all six comparisons while 185 genes remained repressed. Genes that are always activated or suppressed by cold exposure under either genetic background or time of exposure could be more stable parts of the chilling-response network. The fact that molecules like miR156 are conserved across species yet play roles in both development and environmental responses, suggests that there is a potential role for molecules that persist in coordinating plant performance under stress (Wang et al., 2023). Likewise, plant growth regulators such as polyamines participate in plant development and abiotic stress adaptation, which further links growth regulation and abiotic stress adaptation (Chen et al., 2019 B).

Functional characterization also revealed the chilling-responsive candidates were spread throughout stress regulation, signaling, metabolism, cellular activity, and growth associated processes. This functional diversity suggests the idea of coordinated adaptation of various biological systems as being necessary for successful stress adaptation. Related to this, while specialized metabolites may be produced or their production may change significantly when a stress occurs, metabolites can also generate compounds that contribute to protection, signaling or acclimation when exposed to stress (Zeng et al., 2019). Apocarotenoids are also involved in development regulation and environmental responses, showing how metabolic pathways can link developmental regulation with stress signaling (Felemban et al., 2019). The

molecular basis of the identified functional diversity is, therefore, a strong candidate for the wide range of transcriptional alterations present in the rice profiles.

Another pertinent factor of the observed response is oxidative regulation. Chilling may affect redox balance in cells, which consequently will require a higher demand for mechanisms to control ROS. In addition to their well-established functions in antioxidant regulation, cell-wall modification, development and tolerance to a range of environmental stresses, pathways involving the class III peroxidases represent good targets to exploit for crop improvement (Kidwai et al., 2020). However nutrient acquisition and metabolic activity must not be curtailed during environmental stress. The functional study of the rice nitrate transporter OsNPF4.5 showed the importance of specific transport systems for nutrient acquisition, which highlights the general role of transport and metabolism in plant function (Wang et al., 2020).

The results have implications for molecular targets in stress-tolerant breeding of crops. Genes that are consistently responding in different genotypes and exposure times are of particular interest, as the response to their transcription seems to be less dependent on single experimental conditions. However, before they are found to be functional, their possible role in chilling tolerance and growth needs to be confirmed. Some caveats are warranted, however. While conventional statistical differential-expression testing was not possible because biological replicates were not specified in the available FPKM matrix, direct phenotypic measurements of growth were not available. Gene expression changes should be combined with replicated RNA sequencing with physiological and growth characteristics to confirm genes of interest and prioritized genes using qRT-PCR, gene editing, gene overexpression, and/or gene knockout. Such validation would help determine if the persistent transcriptional signatures detected here are directly involved in chilling tolerance and/or maintenance of crop growth.

5. Conclusion

The gene expression profiling of rice transcriptome showed a significant reorganization of gene expression after being chilled, in terms of both the extent and the genotype-dependent differences in the extent of the reorganization, as well as its differences between exposure periods. Prolonged exposure led to more similarities in transcriptional responses, whereas early responses were clearly different among NIP, CSSL4-1 and 93-11. CSSL4-1 exhibited significant early transcriptional activation while the number of commonly activated genes at 41 h suggested a more coordinated response with continued chilling. The responsive genes were functional characterized and were related to stress regulation, cell signaling pathways, metabolic pathways, redox related pathways, and growth related pathways. Integrated

comparison also resulted in the identification of 237 consistently induced and 185 genes consistently repressed in all the genotype–time comparisons, which were then selected for further functional studies. These consistent expression patterns provide valuable clues as to how rice responds to chilling and the effect of both the genotype and the length of exposure to the chilling temperatures on transcription. The candidate genes and processes identified are important molecular targets that can be used for developing chilling-resilient rice varieties. To support their use in molecular breeding and crop improvement, further validation through replicated transcriptomic experiments, physiological measurements, and targeted functional approaches will be vital to confirm their primary functions in stress tolerance.

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