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Development of an atlas of stress responsive genes in *Arabidopsis thaliana*: *Arabidopsis thaliana* Stress Responsive Gene Atlas (AtSRGA)

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Summary

We have developed an easy-to-use application, AtSRGA (https://fusk-kpu.shinyapps.io/AtSRGA/), which enables users to retrieve stress responsive genes in *Arabidopsis thaliana*. This document introduces the usage of AtSRGA, as well as case studies useful for searching for stress response-related genes.

1. Introduction

Sessile higher plants must adapt to various environmental stressors to ensure their survival. With technological innovations in the post-genome era, a vast amount of gene expression data has been published and shared to understand the molecular mechanisms through which plants respond to stress (Sarkans et al., 2021; Clough et al., 2024). It is desirable to utilize information retrieval systems constructed by collecting, data processing, and reanalyzing this wealth of data. Recently, meta-analysis approaches that integrate and aggregate data from multiple studies, both plant and animal, have attracted attention, allowing accurate identification of candidate genes whose expression is altered by stress (De Toma et al., 2021; Tamura and Bono, 2022; Shintani et al., 2024). A database constructed by meta-analysis can yield more comprehensive and reliable information on stress-responsive genes in plants. We have developed an easy-to-use application, AtSRGA (https://fusk-kpu.shinyapps.io/AtSRGA/), which allows users to retrieve stress responsive genes in *Arabidopsis thaliana*. Here, this document introduces the usage of AtSRGA, as well as case studies useful for searching for stress response-related genes.

2. Data collection and meta-analysis methods

2-1. Data used

In this study, we focused on 11 biotic and abiotic stresses, including abscisic acid (ABA), cold, drought, heat, high light, hypoxia, osmotic stress, oxidation, salt, wounding, and *Pseudomonas syringae* pv. Tomato DC3000. We collected a total of 1,131 microarray and 1,050 RNA sequencing (RNA-Seq) datasets in *Arabidopsis thaliana* (Arabidopsis) (Table 1). Data sources included the public databases NCBI GEO (Clough et al., 2024) (https://www.ncbi.nlm.nih.gov/geo/), ArrayExpress (Sarkans et al., 2021) (http://www.ebi.ac.uk/arrayexpress/), and Sequence Read

Archive (SRA, https://www.ncbi.nlm.nih.gov/sra) (Katz et al., 2022). Two transcriptome analysis platforms were utilized: Affymetrix ATH1 GeneChip and Illumina-based RNA-Seq. Additionally, research projects with data available for at least four samples (two control and two stress-treated samples) were included in this study.

Table 1. The number of samples of microarray and RNA-Seq data by 11 stress type

Stress	**Microarray**			
	Study	**Control**	**Treated**	**All**
ABA	6	19	19	38
Cold	13	66	65	131
DC3000	7	25	26	51
Drought	14	56	60	116
Heat	12	64	45	109
Highlight	7	23	25	48
Hypoxia	15	57	70	127
Osmotic	3	42	36	78
Oxidation	5	23	23	46
Salt	16	116	167	283
Wound	7	52	52	104

Stress	**RNA-Seq**			
	Study	**Control**	**Treated**	**All**
ABA	16	51	57	108
Cold	12	67	92	159
DC3000	8	52	52	104
Drought	11	36	58	94
Heat	19	67	70	137
Highlight	14	69	91	160
Hypoxia	4	12	16	28
Osmotic	5	16	16	32
Oxidation	5	15	27	42
Salt	13	41	63	104
Wound	7	19	63	82

The sampling tissues for each dataset varied. We included all samples that provided comprehensive information, both tissue-specific and non-specific. For example, in the case of the drought stress microarray and RNA-Seq datasets, the most common tissue-specific samples were from the leaf and shoot systems (Figure 1).

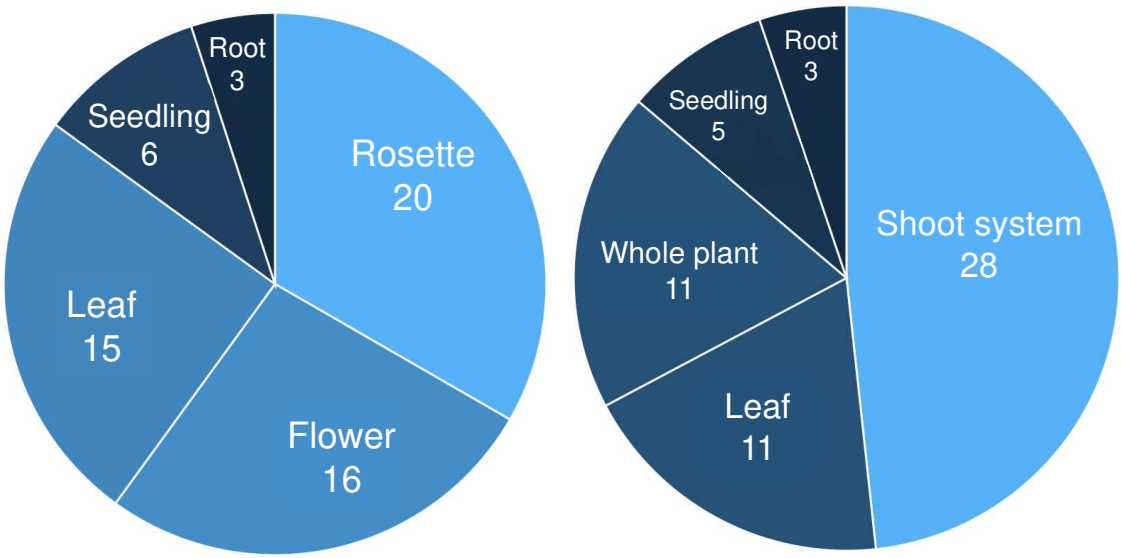


Figure 1. A pie chart illustrating the proportion of tissue-specific samples in microarray (Affymetrix ATH1 GeneChip) and Illumina-based RNA-Seq data for drought stress-treated samples.

2-2. Data pre-processing

2-2-1. Affymetrix ATH1 GeneChip microarray

Microarray datasets were manually retrieved and downloaded from NCBI GEO and BioStudies. Subsequently, these datasets were normalized and summarized by Robust Multiarrray Average (RMA) (Irizarry et al., 2003) using the Bioconductor affy package (v1.74.0) (Gautier et al., 2004) (Figure 2).

2-2-2. Illumina-based RNA-Seq data

RNA-Seq datasets were downloaded from the NCBI SRA using the prefetch and fastq-dump from SRA-Toolkit (version 3.0.0). Subsequent low quality sequences and adapters were removed using Trim Galore! (version 0.6.7) (https://www.bioinformatics.babraham.ac.uk/projects/trim_galore/). We used Salmon (v1.9.0) (Patro et al., 2017) to quantify transcript expression as Transcripts Per Million (TPM). Finally, tximport (v1.24.0) (Soneson et al., 2015) was used to convert the expression level of all transcripts to that of each gene (Figure 2).

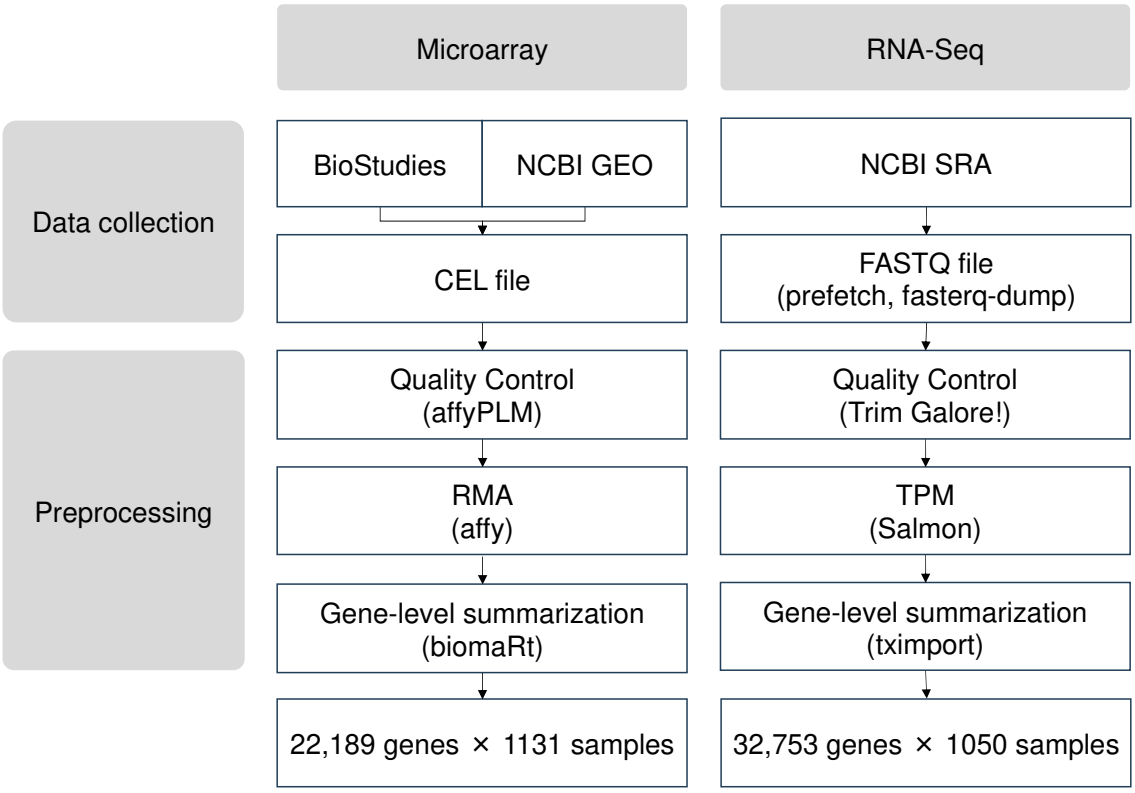


Figure 2. Schematic diagrams for microarray and RNA-Seq data acquisition and pre-processing workflows.

2-3. Calculation of *Stress Response score (SRscore)* for transcriptome meta-analysis

Following the calculation of gene expression ratios between the control condition and each stress treatment condition across all combinations within a research project (e.g., Series in NCBI GEO), the mean value was calculated and designated as the *SRratio* (Tamura and Bono, 2022). If the expression level and number of samples in the control condition are represented by *C* and *m*, respectively, and those in the stress treatment condition by *T* and *n*, respectively, the *SRratio* is calculated as follows.

$$\boldsymbol{SRratio_i = \frac{\sum_{j=1}^{m}(logT_i - logC_j)}{m}} \qquad (\boldsymbol{i = 1, 2, \ldots n})$$

For each gene, across the collected research projects, we focused on gene expression ratios where |*SRratio*|>=2. We then assigned the label 'U' (Up-regulation) for increased expression and 'D' (Down-regulation) for decreased expression, while all other cases were labeled 'N' (no change). The *SRscore* was defined to evaluate and score genes based on the consistency of expression change direction under stress treatment across the collected research project. If the total occurrences of label 'U' for a gene *g* is denoted as *Ug*, and the total occurrences of label 'D' is *Dg*, then the *SRscore* is calculated as

follows.

$$SRscore = U_g - D_g$$

Generally, the *SRscore* represents a modified form of the vote-counting method (Tseng et al., 2012)(Tamura and Bono, 2022). It was standardized using the Z-score to facilitate comparisons across different stress conditions. A data matrix, comprising all Arabidopsis genes and their corresponding *SRscores* for each stress condition, was constructed. This matrix was then integrated into an application named AtSRGA, developed using the Shiny package in R (https://fusk-kpu.shinyapps.io/AtSRGA/).

2-4. Template matching

Concerning a specified gene of interest, AtSRGA utilizes Template Matching (Pavlidis and Noble, 2001) to identify clusters of genes exhibiting *SRscore* patterns that are strikingly similar to one another. The distance or similarity between these patterns can be calculated using a variety of methods, including Euclidean, maximum, manhattan, canberra, correlation, and binary.

3. Reproducibility with some previous studies

Tamura and Bono conducted an exhaustive meta-analysis to identify candidate genes in *A. thaliana* responsive to hypoxic stress (Tamura and Bono, 2022). Figure 2 presents the list of genes associated with hypoxic stress and labeled 'UP' as detected by Tamura and Bono. For these hypoxia-induced genes, the *SRscores* calculated in our study exceeded 10 for both microarray and RNA-Seq data, indicating consistent up-regulation.

		SRscore	
HRGs	Meta-Analysis	Microarray	RNA-Seq
HRE1	UP	11	10
HRE2	UP	13	10
RAP2.12	—	0	0
RAP2.2	—	0	1
RAP2.3	—	0	3
LBD41	UP	15	16
PCO1	UP	13	15
PCO2	UP	13	14
ADH1	UP	13	15
PDC1	UP	13	13

Figure 3. Comparative analysis of hypoxia-responsive genes. This list shows known hypoxia-responsive genes (HRGs) identified in previous study (Tamura and Bono, 2022) (depicted with a black background) versus *SRscore* in our study (represented with an orange background).

We also focused on a gene encoding ADH1 (alcohol dehydrogenase 1) (App and Meiss, 1958; Chang and Meyerowitz, 1986), recognized as a critical stress response gene. Environmental stressors known to induce *ADH1* expression include low temperature, drought, hypoxia, salt, osmotic stress, and ABA treatment (Dolferus et al., 1994; de Bruxelles et al., 1996; Shi et al., 2017). The *SRscore* calculated for *ADH1* corroborates prior research, indicating enhanced expression in response to low temperature, desiccation, hypoxia, salt, osmotic stress, and ABA treatment (Table 4). The results of our analysis suggest that *SRscore* is useful to search for stress-responsive genes.

	SRscore	
Stress	Microarray	RNA-Seq
ABA	2	9
Cold	9	10
Drought	6	6
Heat	0	2
Highlight	1	3
Hypoxia	15	13
Osmotic	4	6
Salt	9	7
Wound	0	2

Figure 4. *SRscore* calculated in this study for the *ADH1* (*alcohol dehydrogenase 1*) gene.

4. Utilizing AtSRGA

AtSRGA is designed as an application that enables users to visually inspect a data matrix representing *SRscore* for various stress conditions, depicted as a pseudo-color heatmap. Each cell is shaded pink when the SRscore is positive and blue when the SRscore is negative, with the color intensity amplifying as the value diverges further from zero.

4-1. Search functionality

Users may input the Arabidopsis AGI code or gene SYMBOL (not case-sensitive) into the search box, allowing them to explore SRscores pertaining to specific genes or gene clusters of interest (Figure 5).

Figure 5. Gene search on the AtSRGA. (A) The search box in the red frame allows sequential searches. Here, as an example, we show the results after typing "dreb1" in the search box for gene SYMBOL. (B) Bulk search is available from the sidebar, and clicking the “Submit” button displays the data matrix corresponding to the Arabidopsis AGI code or gene SYMBOL entered in the search box in the red frame. Here are the search results for seven genes as an example.

4-2. Sorting

By interacting with the up and down arrows situated adjacent to each column header, users can organize the data matrix either numerically or alphabetically, facilitating a streamlined analysis (Figure 6).

Figure 6. Sorting of gene information by *SRscore* on the AtSRGA. As an example, the results are shown here after sorting by *SRscore* in order of increasing drought stress.

4-3. Filtering of *SRscore* range

Users can specify the range of *SRscore* under each stress condition, allowing for targeted exploration of the dataset. This feature facilitates the extraction of genes that respond specifically to particular stressors (Figure 7).

ensembl_gene_id	ABA	cold	DC3000	drought	heat	highlight	hypoxia	osmotic	oxidation	salt	wound	SYMBOL
AT1G55530				0	7	0	0	0	0	0	0	BTL06
AT1G56440				0	7	0	0	0	0	0	0	SPAG/TPR5
AT2G07629	0	0	0	-1	7	0	0	0	0	0	0	AT2G07629
AT2G07678	0	0	0	0	7	0	0	0	0	0	0	AT2G07678
AT2G07701	0	0	0	0	7	0	0	0	0	0	0	AT2G07701
AT2G07702	0	0	0	0	7	0	0	0	0	0	0	AT2G07702
AT2G07719	0	0	0	0	7	0	0	0	0	0	0	AT2G07719
AT2G07727	0	0	0	0	7	0	0	0	0	0	0	AT2G07727
AT2G07749	0	0	0	0	7	0	0	0	0	0	0	AT2G07749
AT2G07768	0	0	0	0	7	0	0	0	0	0	0	AT2G07768

Figure 7. Filtering a range of *SRscore* obtained for each stress condition. Clicking on the search box in the red frame brings up the range slider. Here are the results after filtering the *SRscore* range below for all stresses except heat stress, and sorting by thermal stress in order of *SRscore*.

4-4. Viewing *SRratio* and associated metadata

AtSRGA enables users to access the *SRratio* and corresponding metadata for selected genes, facilitating the identification of experimental conditions where expression variations are most pronounced (Figure 8). This process involves two primary steps:

(1) Gene selection: Users select a gene by clicking on any row within the data matrix, which highlights the entire row in blue (Figure 8A).

(2) Tab switching: Initially, AtSRGA displays the 'Overview' tab at startup (Figure 8A). Users can navigate to different views by clicking on tabs named after each stress condition (Figure 8B). Upon switching, buttons labeled "Show SRratio" and "Show Metadata" become visible. Clicking these buttons sequentially will display the *SRratio* and metadata for the selected gene (Figures 8B and 8C). Values of *SRratio* that are 2 or lower are marked in pink and light blue, respectively, and the metadata can be filtered accordingly (Figure 8D).

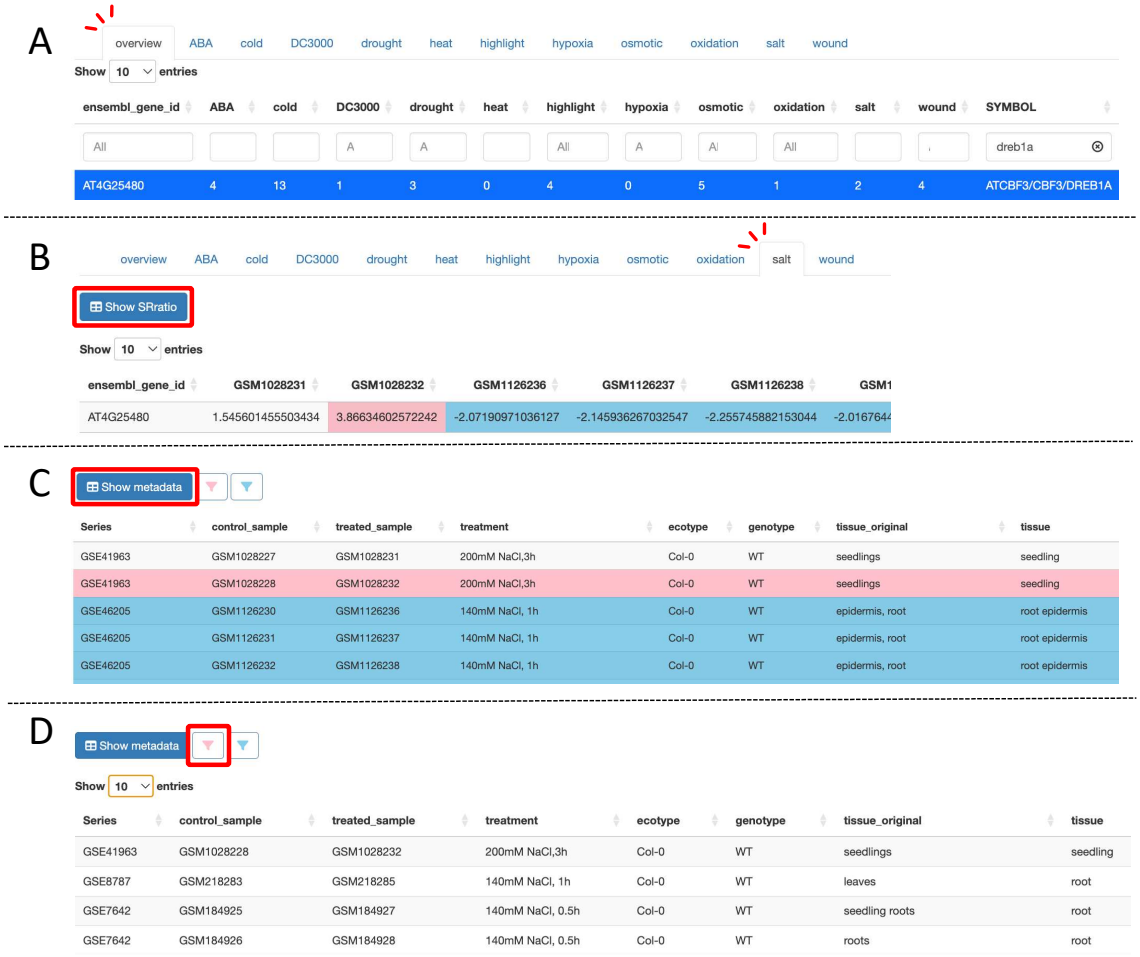


Figure 8. Example of viewing *SRratio* and their metadata

The process of displaying *SRratio* and their metadata for *DREB1A* (*AT4G25480*) gene in salt stress treated samples is shown. (A) Select the row corresponding to *DREB1A* from the overview tab. (B) Switch to the salt stress tab to display *SRratio*. (C) Display the metadata. (D) Filter by experimental samples with *SRratio* greater than or equal to 2 (pink).

4-5. Template matching

To identify a set of genes whose *SRscore* patterns closely resemble that of user-interested genes using Template Matching (Pavlidis and Noble, 2001), two steps are required:

(1) Gene selection: The user selects a gene by clicking on the corresponding row within the data matrix, as shown in Figure 8A.

(2) Menu switching: From the main menu located at the top of the screen, the user selects "Template Matching" from the submenu, which transitions the display to the template matching interface (Figure 9A). Within this interface, the user can choose the method for calculating distances or similarities between patterns from options available in the sidebar (Figure 9B). Upon activating the template matching screen with a gene selected, a data matrix appears, showcasing gene groups that

exhibit high similarity to the selected gene (Figure 9C). The calculated distances and similarities are then appended as "dists" columns to the matrix.

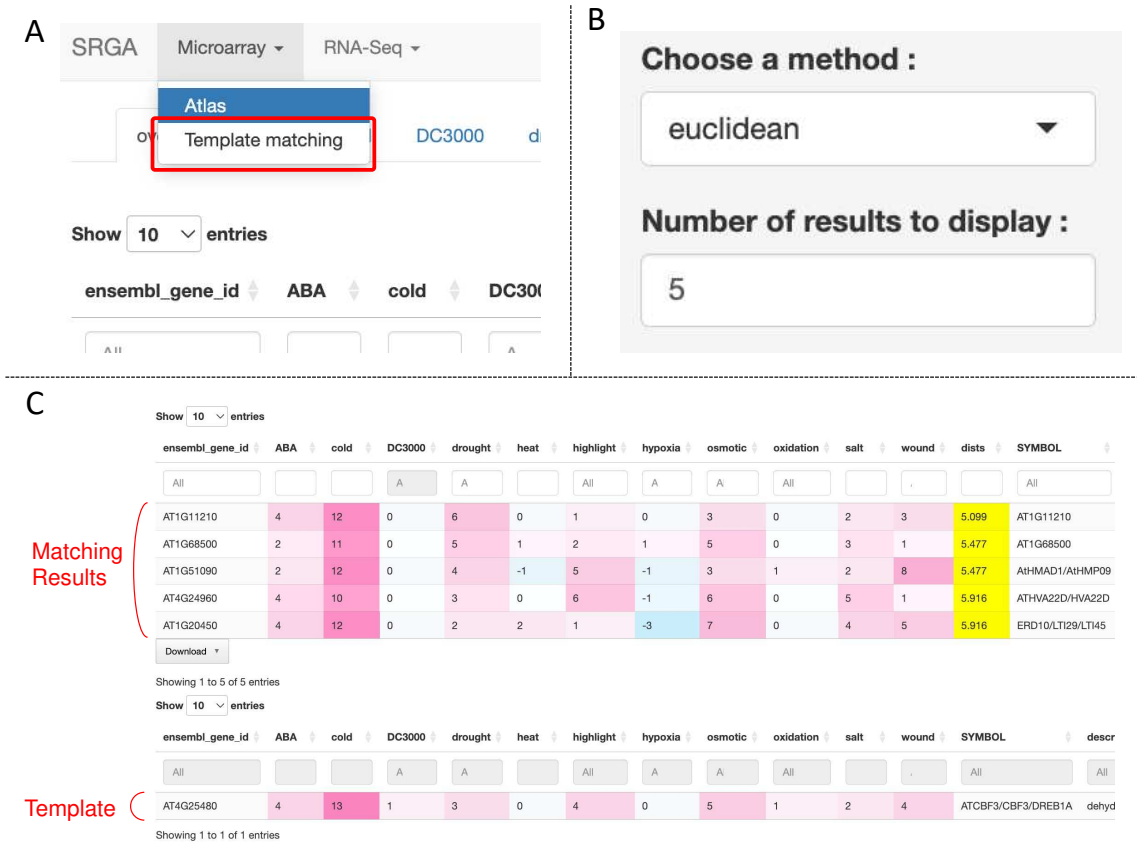


Figure 9. An example of Template Matching. The results of Template Matching are shown using *DREB1A* (*AT4G25480*) gene as an example. (A) Select "Template matching" from the submenu with the row corresponding to *DREB1A* selected from the overview tab. (B) Users can choose the distance calculation method (default is euclidean) and the number of genes to display (default is 5). (C) The selected genes are displayed at the bottom and the group of genes with high similarity in *SRscore* pattern are displayed at the top.

4-6. Heatmap display properties

AtSRGA is capable of rendering the data matrix, sourced from both bulk search and template matching, as a heatmap diagram (Figure 10). The y-axis of the heatmap, which displays either the AGI code or gene SYMBOL, along with the plot height, can be adjusted using controls on the sidebar (Figure 10A). By clicking the "Plot" button, a modal dialog appears, generating a dynamic heatmap based on the data matrix currently being viewed. Hovering over any specific cell within the heatmap activates hover text, providing the user with detailed information including the AGI code or gene symbol (row), stress type (column), and *SRscore* (value) (Figure 10B).

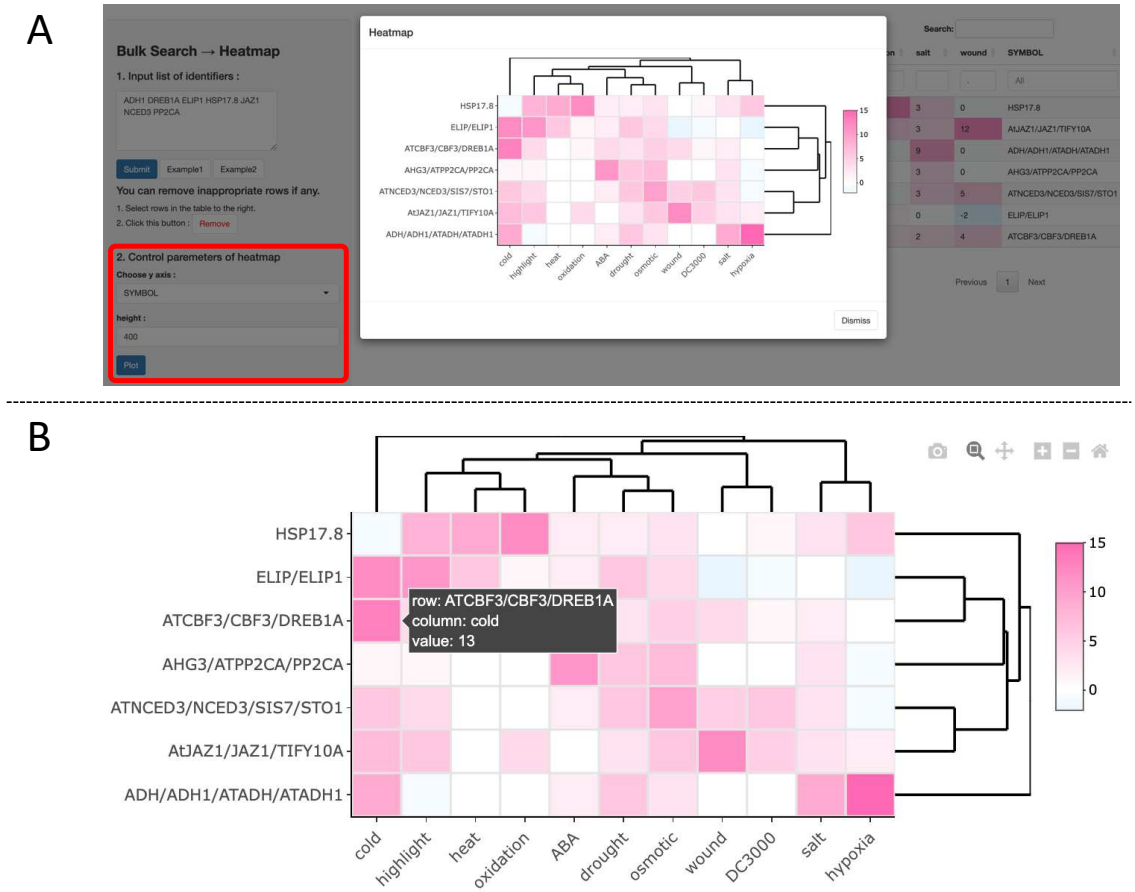
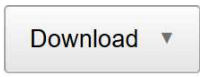


Figure 10. Heatmap display of the bulk search results.

(A) Heatmap diagram of bulk search results. (B) An example of *DREB1A* gene hover text display.

4-7. File saving options

Search results generated by AtSRGA can be saved in either CSV or Excel format. This is accomplished by clicking the "Download" button located at the bottom left of each table, as illustrated in the corresponding figure.



4-8. Integration with external genome-wide resources for *A. thaliana*

Each gene listed in AtSRGA is annotated with links to external genome-wide resources, such as TAIR (Lamesch et al., 2012) and KEGG (Kanehisa et al., 2023), facilitating comprehensive genomic analysis (Table 2).

Table 2. External genome-wide resources at AtSRGA

DB name	URL	Publication

KEGG	https://www.genome.jp/kegg/	https://doi.org/10.1002/pro.4820
TAIR	https://www.arabidopsis.org/	https://doi.org/10.1002/dvg.22877
ATTED-II	https://atted.jp/	https://dx.doi.org/10.1093/pcp/pcac041
eFP Browser	https://bar.utoronto.ca/efp_arabidopsis/cgi-bin/efpWeb.cgi	https://doi.org/10.1371/journal.pone.0000718
Thale Mine	https://bar.utoronto.ca/thalemine/begin.do	https://doi.org/10.1105/tpc.20.00358
AlphaFold2	https://alphafold.ebi.ac.uk/	https://doi.org/10.1038/s41586-021-03828-1
STRING	https://string-db.org/	https://doi.org/10.1093/nar/gkac1000

5. Case studies

5-1. *DREB* and *GolS* genes

Here we show the usefulness of AtSRGA, focusing on the *DREB1*, *DREB2*, and *GolS* genes, which are recognized as important stress response genes. *DREB1* is rapidly induced by cold stress (Novillo et al., 2004), while *DREB2* responds to drought and salt stress (Sakuma et al., 2006). *GolS* gene encodes a galactinol synthase, a crucial enzyme in the sugar biosynthesis pathway, known for its roles in osmotic regulation and removal of reactive oxygen species during stress. Previous research indicates that *GolS3* is activated by low temperature stress, and *GolS1* and *GolS2* are triggered by desiccation and salt stress (Taji et al., 2002). We evaluated the alignment of these documented responses with results from AtSRGA. Initially, bulk searches for *DREB1A*, *DREB1B*, *DREB1C*, *DREB2A*, *DREB2B*, *GolS1*, *GolS2*, and *GolS3* were conducted across microarray and RNA-Seq datasets within AtSRGA (Figure 11A). Subsequently, the y-axis was configured to display gene SYMBOL, and a heatmap diagram was generated to visually represent these interactions (Figures 11B and 11C).

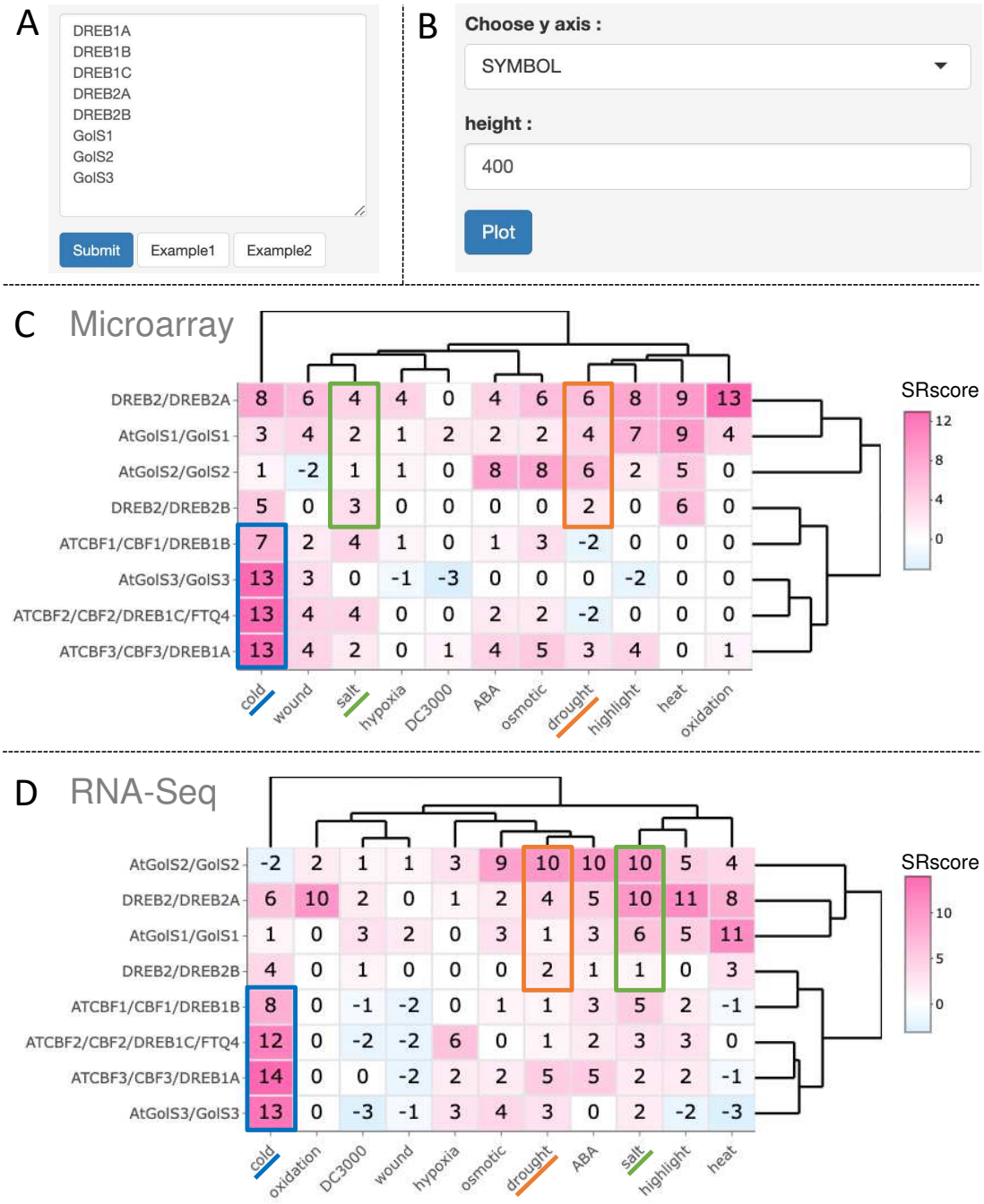


Figure 11. Examples of *DREB* and *GolS* genes in AtSRGA. (A) Bulk search results for *DREB* and *GolS* gene groups. (B) y-axis selected as gene symbols. (C) A heatmap representation in microarray datasets of AtSRGA. (D) A heatmap diagram from RNA-Seq datasets of AtSRGA. Boxes point to cells corresponding to genes (y-axis) and stresses reported to be involved in the induction of their expression (x-axis), and are color-coded according to the type of stress.

DREB1A, *DREB1B* and *GolS3* genes exhibited *SRscore* of 12 to 14 for cold stress. Specifically,

DREB1B registered an *SRscore* of 5 in microarray datasets and 8 in RNA-Seq datasets. DREB2A demonstrated an *SRscore* of 4 and 6 for drought stress, and 4 and 10 for salt stress; *DREB2B* recorded *SRscores* of 2 and 2 for drought stress and 3 and 1 for salt stress; *GolS1* revealed *SRscores* of 4 and 1 for drought stress and 2 and 6 for salt stress; *GolS2* displayed *SRscores* of 6 and 10 for drought stress and 1 and 10 for salt stress. These results confirm that each gene consistently shows an *SRscore* greater than 1 under stress conditions known to induce their expression.

5-2. *COR15A* gene

COR15A is a well-documented cold-inducible LEA (Late Embryogenesis abundant) protein; the *COR15A* gene is notably up-regulated in response to cold stress and plays a important role in chloroplast freezing tolerance (Artus et al., 1996). It has also been observed to be induced by drought stress and ABA (Wilhelm and Thomashow, 1993), and the *SRscore* pattern of *COR15A* was consistent with these findings (Figure 12A). Template matching, using the Euclidean distance method, was used to detect the top 10 gene clusters exhibiting *SRscore* patterns similar to that of *COR15A* (Figure 12B). The y-axis was configured to display gene SYMBOLS, and a heatmap diagram was subsequently generated (Figure 12C). The analysis revealed that the genes with the closest distance included *COR15B* (*AT2G42530*), *DREB1A* (*AT4G25480*), *AtHMAD1*/*AtHMP09* (*AT1G51090*), *HVA22D* (*AT4G24960*), *AIW2*, *ERD10*/*LTI29*/*LTI45*, *AT1G11210*, *FMO*, *ERD7*, and *PGX3* (Figure 12D). *COR15B* exhibits the highest sequence similarity to *COR15A*. Notably, *COR15A* is also recognized as one of the target genes of DREB1A (Seki et al., 2001). While our findings highlighted genes closely related to *COR15A*, we also identified genes that are less closely related but have functional significance or remain uncharacterized. For instance, the *ERD* (*Early Responsive to Dehydration*) gene cluster in *A. thaliana*. includes 16 members, with *ERD7* and *ERD10* thought to contribute to plant protection against cold and drought stress (Wu et al., 2023). Although *AT1G11210* has been infrequently reported, the current results suggest that it should be prioritized in future investigations into stress response mechanisms.

Figure 12. Heatmap of the top 10 gene groups with *SRscore* patterns similar to *COR15A*.

6. Refereneces

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