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Arabidopsis thaliana Stress Responsive Gene Atlas (AtSRGA) Tutorial

Yusuke Fukuda[1], Kohei Kawaguchi[1], Atsushi Fukushima[1,2]*

*afukushima@kpu.ac.jp

[1]Kyoto Prefectural University, [2]RIKEN

Summary

We introduce a user-friendly application, AtSRGA (*Arabidopsis thaliana* Stress-Responsive Gene Atlas), enabling users to retrieve stress-responsive genes in *Arabidopsis thaliana* (Arabidopsis). presents stress-responsive genes in a heatmap format based on a stress responsiveness measure (*SRscore*, see section 2-3). It facilitates the comparative analysis of individual stress responses and groups of genes responsive to multiple stress conditions. Researchers can identify groups of genes with similar patterns by examining the *SRscore* pattern of a gene of interest across 11 stress conditions. This information enables the annotation of genes with unknown functions helps identify genome-editing targets, and provides a convenient pre-experiment screening tool. Here, this document introduces the usage of AtSRGA, as well as case studies useful for searching for stress response-related genes. AtSRGA can be accessed at https://huggingface.co/spaces/fusk-kpu/StressResponseGenesAtlas.

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://huggingface.co/spaces/fusk-kpu/StressResponseGenesAtlas), which allows users to retrieve stress responsive genes in *Arabidopsis thaliana*.

2. Data collection and meta-analysis methods

2-1. Data collection

This study focused on 11 biotic and abiotic stresses, including ABA, cold, drought, heat, high light,

hypoxia, osmotic stress, oxidation, salt, wounding, and *Pseudomonas syringae* pv. Tomato DC3000. We collected 1,131 microarray and 1,050 RNA-Seq datasets in Arabidopsis (Table 1). Data sources included the public databases NCBI GEO (https://www.ncbi.nlm.nih.gov/geo/) (Clough et al., 2024), ArrayExpress (http://www.ebi.ac.uk/arrayexpress/) (Sarkans et al., 2021), 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. Rresearch projects with data available for at least four samples (two control and two stress-treated samples) were also included.

Table 1. Number of samples of microarray and RNA-Seq data samples under 11 stress conditions

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).

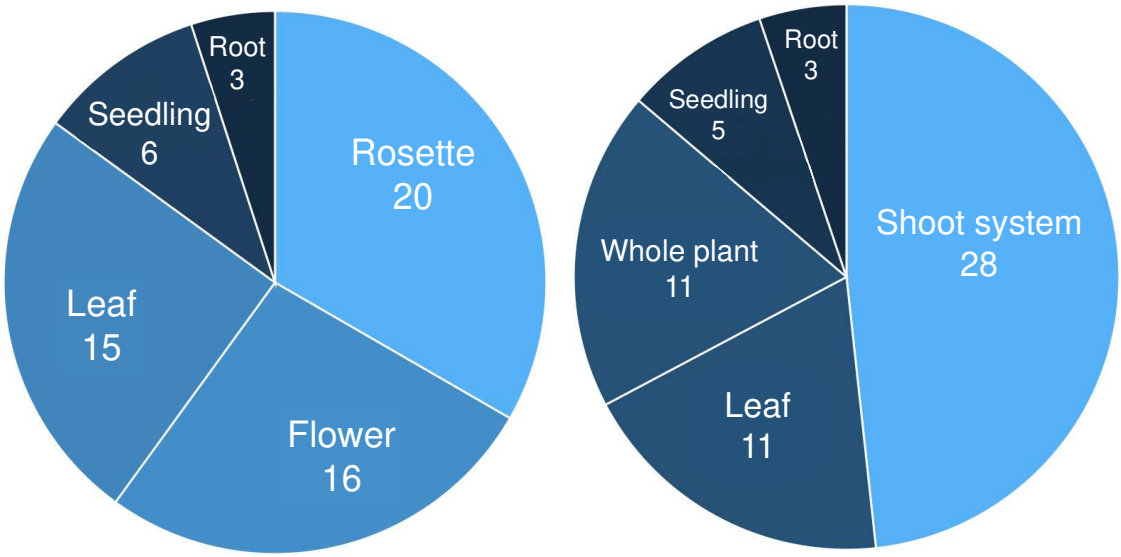


Figure 1. A pie chart illustrating the proportion of tissue-specific samples in microarray (Affymetrix ATH1 GeneChip) and Illumina-based RNA-Seq data for drought stress-treated samples.

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 (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).

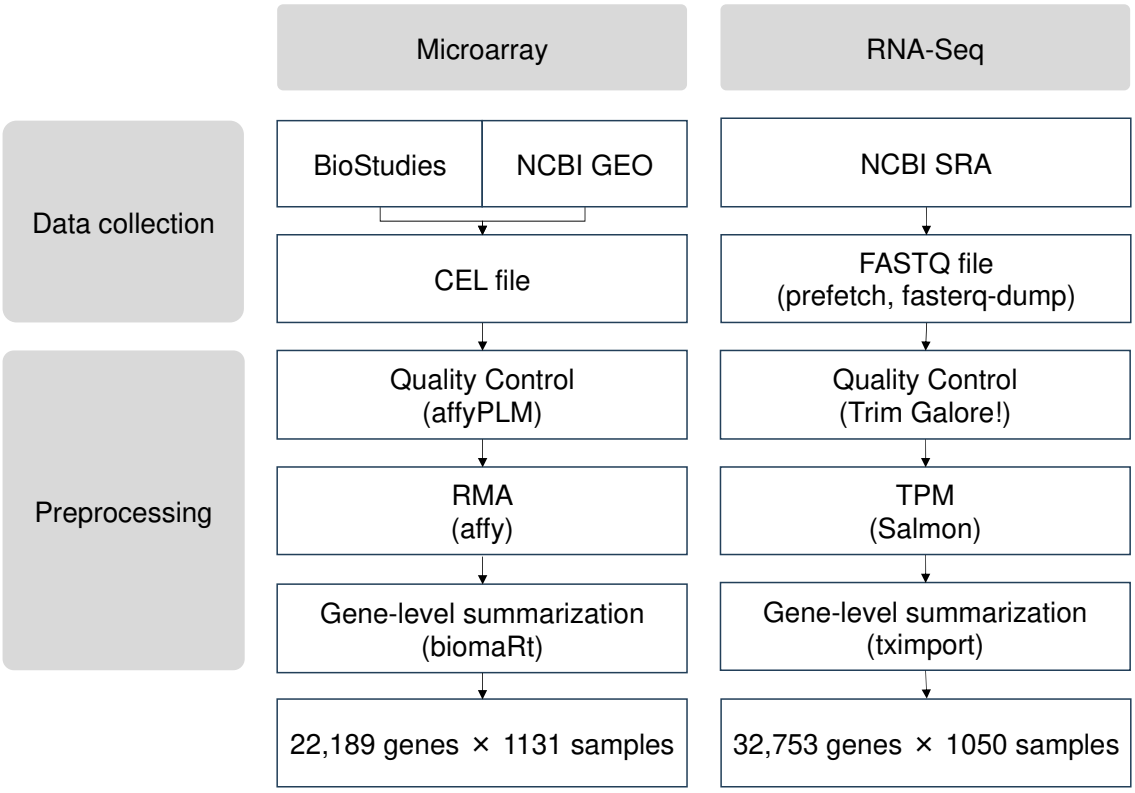


Figure 2. Analysis workflows of microarray (Affymetrix ATH1 GeneChip) and Illumina-based RNA-Seq.

2-3. *SRscore* calculation for transcriptome meta-analysis

Following the calculation of gene expression ratios between the control condition and each stress treatment 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). The *SRratio* is calculated as follows:

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

C and *m* represent the expression level and number of samples in the control condition, and *T* and *n* represent those under a stress condition. We focused on gene expression ratios where $|SRratio| \geq 2$ for each gene across the collected research projects. We then assigned the labels “U” (upregulation) and “D” (downregulation) for increased and decreased expression, respectively, while all other cases were labeled “N” (no change). The *SRscore* was defined to evaluate and score genes based on the

consistency of their regulation's direction (U, D, or N) under stress across the analyzed research projects. The *SRscore* is calculated as follows:

$$\boldsymbol{SRscore = U_g - D_g}$$

Ug is the total occurrence of "U" for a gene *g*, and *Dg* is the total occurrence of "D." 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 genes and their corresponding *SRscores* for each stress condition, was constructed. This matrix was then integrated into AtSRGA, developed using the Shiny package in R (https://huggingface.co/spaces/fusk-kpu/StressResponseGenesAtlas).

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. 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

A previous study conducted an exhaustive meta-analysis to identify candidate genes in Arabidopsis in response to hypoxic stress (Tamura and Bono, 2022). Figure 3 presents genes associated with hypoxic stress and labeled "UP" as detected by this previous study. For these hypoxia-induced genes, the *SRscores* calculated in our study exceeded 10 for microarray and RNA-Seq data, indicating consistent upregulation.

		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 alcohol dehydrogenase 1 (ADH1) (App and Meiss, 1958; Chang and Meyerowitz, 1986), recognized as a critical stress response gene. Environmental stressors that induce *ADH1* expression include low temperature, drought, hypoxia, salt, osmotic stress, and ABA (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 (Figure 4). The results of our analysis suggest that *SRscore* is helps 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* for *alcohol dehydrogenase 1* (*ADH1*).

4. AtSRGA content

AtSRGA is designed as an application enabling users to visually inspect a data matrix presenting an *SRscore* for each gene among 11 stress conditions, depicted as a pseudo-color heatmap. Each cell is colored pink if the *SRscore* is positive and blue if it is negative, with the color intensity increasing proportionally as the value deviates further from zero.

4-1. Search

Users may input the *Arabidopsis* AGI code or gene SYMBOL (not case-sensitive) into the search box and thus explore *SRscores* of 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 adjacent to each column header, users can organize the data matrix numerically or alphabetically for 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).

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).

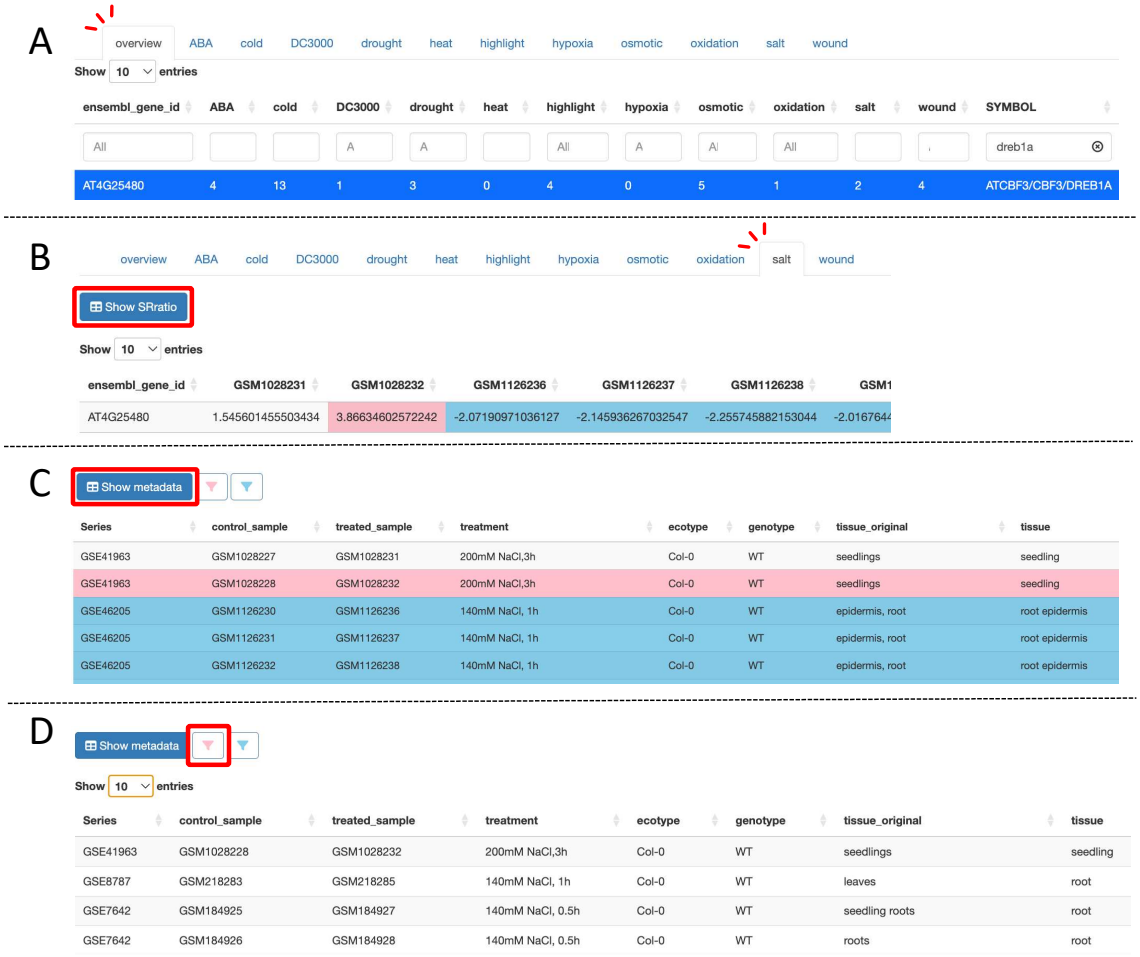


Figure 8. Example of viewing *SRratio* and their metadata. The process of displaying *SRratio* and their metadata for *DREB1A* (*AT4G25480*) in salt stress treated samples is shown. (A) Select the row corresponding to *DREB1A* from the overview tab. (B) Switch to the salt stress tab to display *SRratio*. (C) Display the metadata. (D) Filter by experimental samples with *SRratio* greater than or equal to 2 (pink).

4-5. Template matching

Identifying a set of genes whose *SRscore* patterns closely resemble that of a specified gene of interest using Template Matching (Pavlidis and Noble, 2001) requires two steps:

(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 at the top of the screen, the user selects “Template Matching” from the submenu, which transitions the display into the template-matching interface (Figure 9A). Within this interface, the user can choose the method for calculating distances or similarities between patterns from options in the sidebar (Figure 9B). Upon activating the template-matching screen with a selected gene, a data matrix displays gene groups highly similar to the

selected gene (Figure 9C). The calculated distances and similarities are then appended as “dists” columns to the matrix.

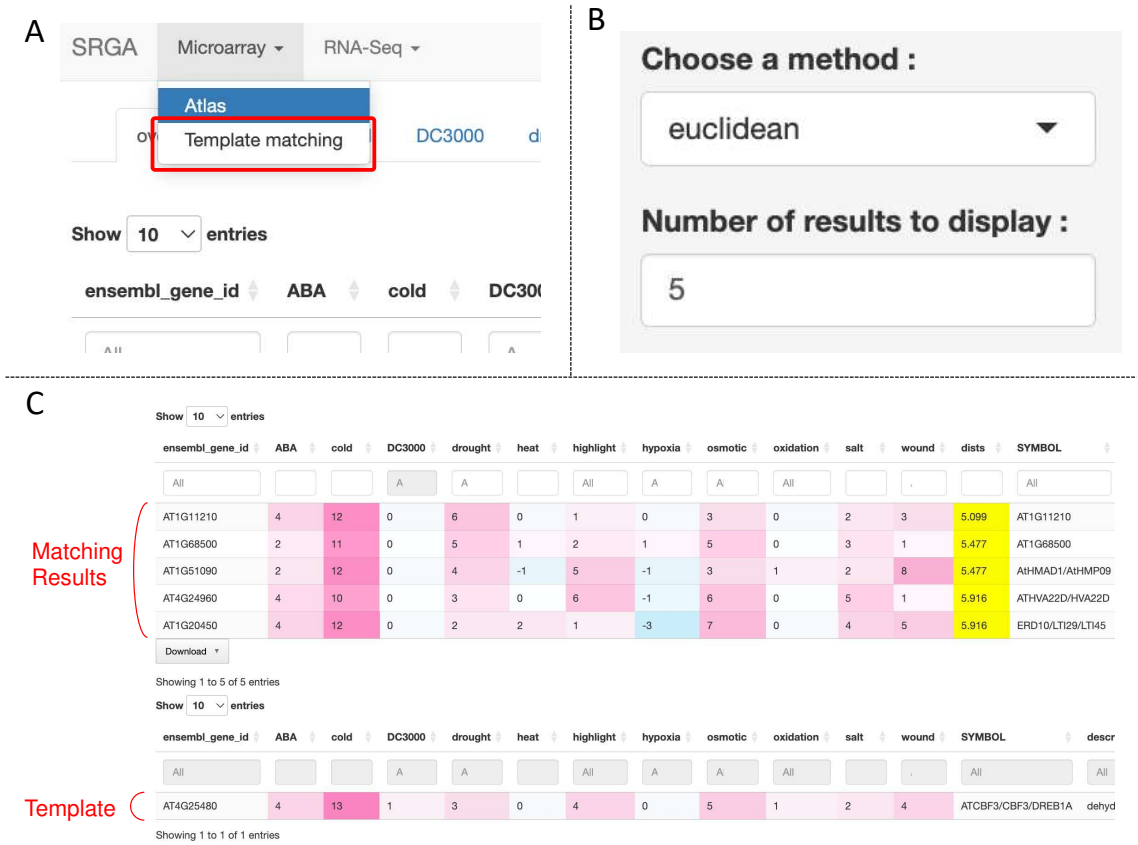


Figure 9. Example of Template Matching. The results of Template Matching are shown using *DREB1A* (*AT4G25480*) gene as an example. (A) Select "Template matching" from the submenu with the row corresponding to *DREB1A* selected from the overview tab. (B) Users can choose the distance calculation method (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 representation

AtSRGA can render 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 the AGI code or gene SYMBOL and the plot height can be adjusted using controls on the sidebar (Figure 10A). A modal dialog appears when clicking the “Plot” button, 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).

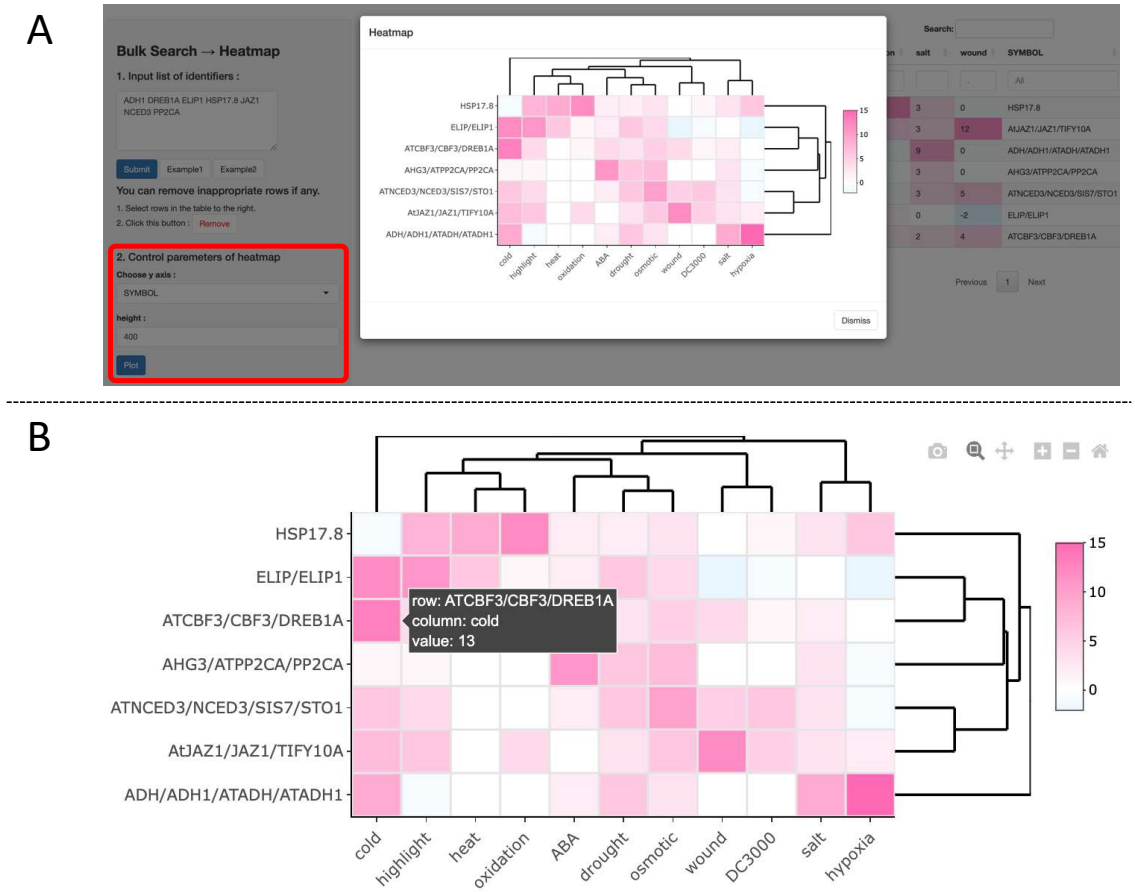


Figure 10. Heatmap display of the bulk search results.

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

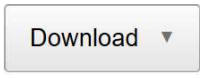
4-7. Functional enrichment analysis

Enrichment analysis is an effective tool for uncovering the biological pathways and functions associated with a gene list of interest. In AtSRGA, a gene list can be specified via bulk search as well as through sequential search and filtering functions (Figure 11). Clicking the “Analysis” button initiates the enrichment analysis. By default, Gene Ontology (GO) and KEGG pathways are set as the targets for analysis, but gene sets defined within AtSRGA can also be included. Upon completion, a dot plot of significantly enriched terms is displayed. The X-axis shows the GeneRatio (the proportion of input genes annotated with a specific term) by default, but it can be switched to “Count,” “pvalue,” “p.adjust,” or “qvalue” from the UI. Additionally, the UI allows adjustment of the number of terms displayed, the text wrap length, and the plot's vertical size.

Figure 11. Functional enrichment analysis. Shown here are the enrichment analysis results for a gene group with an *SRscore* of 1 or higher under ABA stress. (A) Specify the *SRscore* range for ABA stress in the atlas. (B) Click the "Entries shown above" button, followed by the "Submit" button. (C) Include the gene set with an *SRscore* of 1 or higher for a specific stress ("positive SRscore (SRscore ≥ 1)") as the analysis target, and click the "Analysis" button. (D) Display the enrichment analysis results as a dot plot (in this example, the number of displayed terms is adjusted to 20). For the implementation of functional enrichment analysis in AtSRGA, we used clusterProfiler (Wu et al., 2021) and PlantGSEA (Yi et al., 2013).

4-8. 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.



4-9. 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. *in silico* case studies

5-1. *DREB* and *GolS*

Here we demonstrate the usefulness of AtSRGA, focusing on *DREB1*, *DREB2*, and *GolS*, which are recognized as critical stress-responsive genes. *DREB1* is rapidly induced by cold stress (Novillo et al., 2004), while *DREB2* responds to drought and salt (Sakuma et al., 2006). *GolS* 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 temperatures, while *GolS1* and *GolS2* are triggered by desiccation and salt stress (Taji et al., 2002). We evaluated these documented responses using 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 12A). Subsequently, the y-axis was configured to display the gene SYMBOL, and a heatmap diagram was generated to present these interactions visually (Figures 12B and 12C).

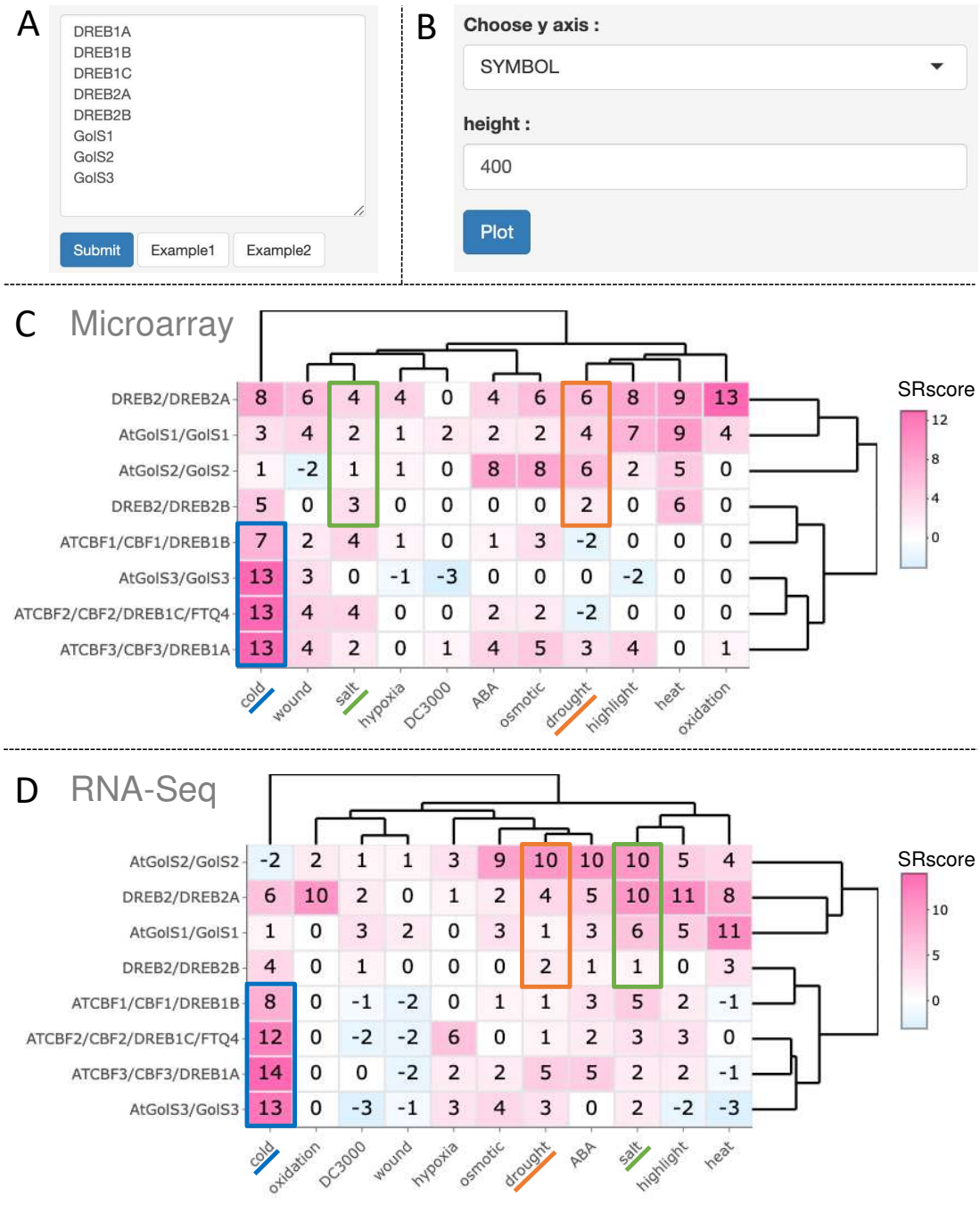


Figure 12. Examples of *DREB* and *GolS* in AtSRGA. (A) Bulk search results for *DREB* and *GolS* gene groups. (B) Y-axis selected as gene symbols. (C) Heatmap representation of AtSRGA microarray datasets. (D) Heatmap diagram from AtSRGA RNA-Seq datasets. Boxes point to cells corresponding to genes (y-axis) and stresses reported to be involved in inducing their expression (x-axis); they are color-coded according to the stress type.

DREB1A, *DREB1B* and *GolS3* 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; and *GolS2* displayed *SRscores* of 6 and 10 for drought stress and 1 and 10 for salt stress. These results confirm that each gene consistently displays an *SRscore* > 1 under stress conditions known to induce their expression.

5-2. cold stress-responsive gene *COR15A*

COR15A is a well-documented cold-inducible late embryogenesis abundant (LEA) protein; *COR15A* is notably upregulated in response to cold and is essential in chloroplast freezing tolerance (Artus et al., 1996). It is also induced by drought stress and ABA (Wilhelm and Thomashow, 1993). The *SRscore* pattern of *COR15A* was consistent with these findings (Figure 13A). Template matching was used to detect the top 10 gene clusters exhibiting *SRscore* patterns similar to *COR15A* (Figure 13B). The y-axis was configured to display gene SYMBOLS, and a heatmap diagram was subsequently generated (Figure 13C). 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 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 *early responsive to dehydration* (*ERD*) in Arabidopsis includes 16 members, with *ERD7* and *ERD10* contributing 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 13. Heatmap of the top 10 gene groups with *SRscore* patterns similar to *COR15A*.

6. Refereneces

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