



# Meta Analysis of Sugar Beet (*Beta vulgaris* L.) Transcriptome Profiles Under Different Biotic and Abiotic Stress Conditions

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## Abstract

Sugar beet (*Beta vulgaris* L.) meets the 21% of world sugar production. Soil pollution, biotic and abiotic factors in production areas greatly reduce product quantity and quality. Sugar beet responds to biotic and abiotic stresses such as drought, salt, heat, light, and infections of nematode, bacteria and fungi at the molecular level. Understanding molecular mechanisms require comprehensive genomics studies in order to control these mechanisms to increase the yield and quality. Transcriptome studies performed under stress conditions can shed light on the responses of plants at the molecular level. In addition, meta-analysis can help to find common responses under different stress conditions. In this study four different stress-related transcriptome data were used: two of them are related with biotic stress (nematode and fungi infection) and two of them are related with abiotic stress (ABA treatment and salt stress). In this study, we performed meta-analysis of studies conducted under biotic and abiotic stress conditions. Our results revealed 460 commonly regulated genes from biotic stress related data and 1031 commonly regulated genes from abiotic stress related data. Our data also showed that expression of ten genes is controlled regardless of the type of stress condition. The data can be useful for understanding the molecular aspect of adaptive stress response in sugar beet.

**Keywords** *Beta vulgaris* · Sugar beet · RNA-Seq · Transcriptome · Meta analysis

## Introduction

Environmental and anthropogenic stressors are one of the main causes of stress for organisms. Biotic and abiotic stress in plants can negatively affect the organisms (Ku et al. 2018). While biotic stress is related with the infection of plants by pathogens (viruses, nematodes, bacteria, and fungi) or infestation by herbivorous parasites, abiotic stress is usually related with the exposure of drought, heat, cold, nutrient imbalance, and excess salt or toxic metals. These stress conditions adversely affect plants and reduce crop yields by altering their physiology, phenotype, and biochemical and molecular structures. Through evolution, plants developed complex defense mechanisms to respond to environmental stresses.

*Beta vulgaris* L. is the most important sugar crop in the temperate zone and accounts for almost 21% of world sugar production (World Sugar Balance - November 2021 | International Sugar Organization, n.d.). It belongs to the order Caryophyllales. *Beta vulgaris* subspecies include leafy beets (chard), garden beet (red, white, yellow, or golden),

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fodder beet (fodder), and sugar beet. In addition to being a food source, sugar beet has been used as animal feed, and it has been a promising source for production of biofuels, alcohol, pharmaceuticals, and baker's yeast.

Majority of the studies regarding with impact of stress on *Beta vulgaris* has been focused on responses to salt and drought. Sugar beet considered as a moderately tolerant species among several other crop species. *Beta vulgaris* has the capacity to tolerate NaCl ions that has minor effects on the yield. Some of the key traits that contribute to salt tolerance include leaf relative water content, leaf area index, biomass accumulation, and photosynthesis (Shams and Khadivi 2023). Under salt stress, the genes involved in signal transduction, phosphorylation, and redox balance play an important role (Lv et al. 2019; Rasouli et al. 2020). In addition, expression of the genes associated with the ROS scavenging system are significantly differentiated along with photosynthesis-related genes (Lv et al. 2019). Response to biotic stress has been poorly studied in *Beta vulgaris*. In summary, there are studies covering the biotic and abiotic stress related genetic mechanisms on sugar beet. The data provided in previous studies can be a source for the search of insight on adaptive stress response in sugar beet through meta-analysis (Stracke et al. 2014; Zou et al. 2020a, b; Liu et al. 2020b; Xing et al. 2020; Ghaemi et al. 2020; Holmquist et al. 2021; Ibrahim et al. 2021). Meta-analysis is a set of quantitative methodological tools that combine the results of similar but independent studies to arrive at an overall conclusion and to evaluate the similarities between the studies. It is a promising approach to avoid controversial aspects of the study and for creating a qualified data summary (Nakagawa and Santos 2012).

A better understanding of an organism's response to stress conditions requires using molecular techniques and bioinformatics approaches. Development of new molecular strategies to reduce the negative effects of biotic and abiotic stress would benefit from these approaches (Zhang et al. 2016; Yu et al. 2020). Transcriptome profiling is a powerful tool for discovering the stress response genes. In previous studies of *Beta vulgaris*, individual transcriptome profiles

were analyzed to discover stress-related genes. There are novel transcriptome studies to enhance our understanding on improving stress tolerance levels in sugar beet (Zou et al. 2020a; Liu et al. 2020b). In this study, we aimed to find the common stress response genes that are differentially expressed under different biotic and abiotic stress conditions using meta-analysis approach.

## Materials and Methods

### Study Data

Eleven stress-related data of *Beta vulgaris* were selected from the NCBI database on March 30th, 2021, with the following filters: Source: "RNA" and Platform: "Illumina". Related data downloaded by SRA archive and compressed data was converted to "fastqc" format by SRA Toolkit (v. 2.11.0) fasterq-dump tool (Leinonen et al. 2011) (Table 1). The.

The quality-control of data was by FastQC (v. 0.11.9) (Andrews 2010). Cleaned raw data was mapped to Ref-Beet-1.2.2 reference genome from Ensembl plants database using Hisat2 (v. 2.1.0). (Kim et al. 2019). The data with less than 60% of alignment rate was eliminated from the study. FeatureCounts (v. 2.0.0) (Liao et al. 2014) was used to obtain gene count numbers. The required GTF file was downloaded from Ensembl plants (Ref-Beet-1.2.2) (Dohm et al. 2012).

### Differential Gene Expression Analysis

For differentially expressed gene analysis DESeq2 (v. 1.30.1) package for R version 4.0.5 (Love et al. 2014) was used. Studies were compared to their control groups and the p-adjusted value was set to 0.05. Raw counts were normalized by the negative binomial model. To work with better efficiency, the Log2 transformation was applied using R. The same process was repeated for all data. Ensembl IDs for differentially expressed genes of *Beta vulgaris*

**Table 1** Summary of the data accessed from NCBI SRA archive

Condition	Stress	SRA Acc. #	BioProject #	GEO #	Ref.*
Biotic	Fungal Pathogen	SRP223381	PRJNA574280	GSM4097161	(Ibrahim et al. 2021)
Biotic	Fungal Pathogen	SRP095578	PRJNA358634	GSM2438805	(Holmquist et al. 2021)
Biotic	Nematod Pathogen	SRP217806	PRJNA559279	GSM4017124	(Ghaemi et al. 2020)
Abiotic	Alkaline Stress	SRP262530	PRJNA634158	N/A	N/A
Abiotic	Alkaline Stress	SRP140444	PRJNA450324	GSM3098240	N/A
Abiotic	Alkaline Stress	SRP126020	PRJNA420895	GSM2872808	(Zou et al. 2020b)
Abiotic	Salinity Stress	SRP149098	PRJNA473360	GSM3161753	(Liu et al. 2020b)
Abiotic	Salinity Stress	SRP145448	PRJNA453103	N/A	N/A
Abiotic	ABA Treatment	SRP235645	PRJNA594791	N/A	(Xing et al. 2020)
Abiotic	Heat Stress	SRP044105	PRJNA254489	N/A	(Stracke et al. 2014)
Abiotic	Stress Germination	SRP219737	PRJNA450098	N/A	N/A

\*Based on BioProject ID search in NCBI database as of August 25th, 2022

were converted to GO and KEGG ENZYME IDs through biomaRt (v. 2.46.3) R package (Durinck et al. 2005) based on the datasets parsed from the Ensemble plants database.

### Normalization Process

Eleven stress-related data of *Beta vulgaris* were used for this study (Table 1). The reference genome for mapping the raw RNA-Seq data was downloaded from the Ensemble plant database (RefBeet-1.2.2.). Sixty-percent alignment rate cut-off threshold was assigned to use the raw data for meta-analysis. According to the mapping results, four of the datasets were selected with an alignment rate above the threshold. These are studies based on effects of fungal pathogens (SRP095578) (Holmquist et al. 2021), nematodes (SRP217806) (Ghaemi et al. 2020), salinity stress (SRP149098) (Liu et al. 2020b), and ABA treatment (SRP235645) (Xing et al. 2020). Expression quantifications were carried out for each dataset for the analysis of differentially expressed genes (DEG) using R package DESeq2. Individual DEG analysis results obtained for each dataset were used for meta-analysis.

### Meta-Analysis of Transcriptome data

Differentially expressed genes (DEGs) data was collected for meta-analysis. For the meta-analysis, R package metaRNASeq version 1.0.7 (Marot et al. 2015) was used. The results of the meta-analysis converted to GO and KEGG ENZYME IDs. For Ensembl ID to ENTREZ ID conversion, the NCBI E-utilities (v. 2.0) was used (Sayers 2009).

### Multiple Sequence Alignment (MSA) and PFAM Analysis

For MSA, ClustalW version 2.0 (Larkin et al. 2007) was used in default settings. For the PFAM-analysis, peptide sequences were scanned through the Pfam database (Mistry et al. 2021).

## Results and Discussion

### Meta-analysis of Transcriptomes

In this study meta-analysis was carried out under three different groups: i-biotic stress, ii-abiotic stress, iii-cumulative (biotic and abiotic stresses). The meta-analysis was carried out for transcriptome data for each biotic stress and abiotic stress to evaluate the DEGs separately in addition to the

meta-analysis of the data from cumulative (biotic and abiotic) stress conditions.

### Meta-analysis of Transcriptomes for Biotic and Abiotic Stress Response

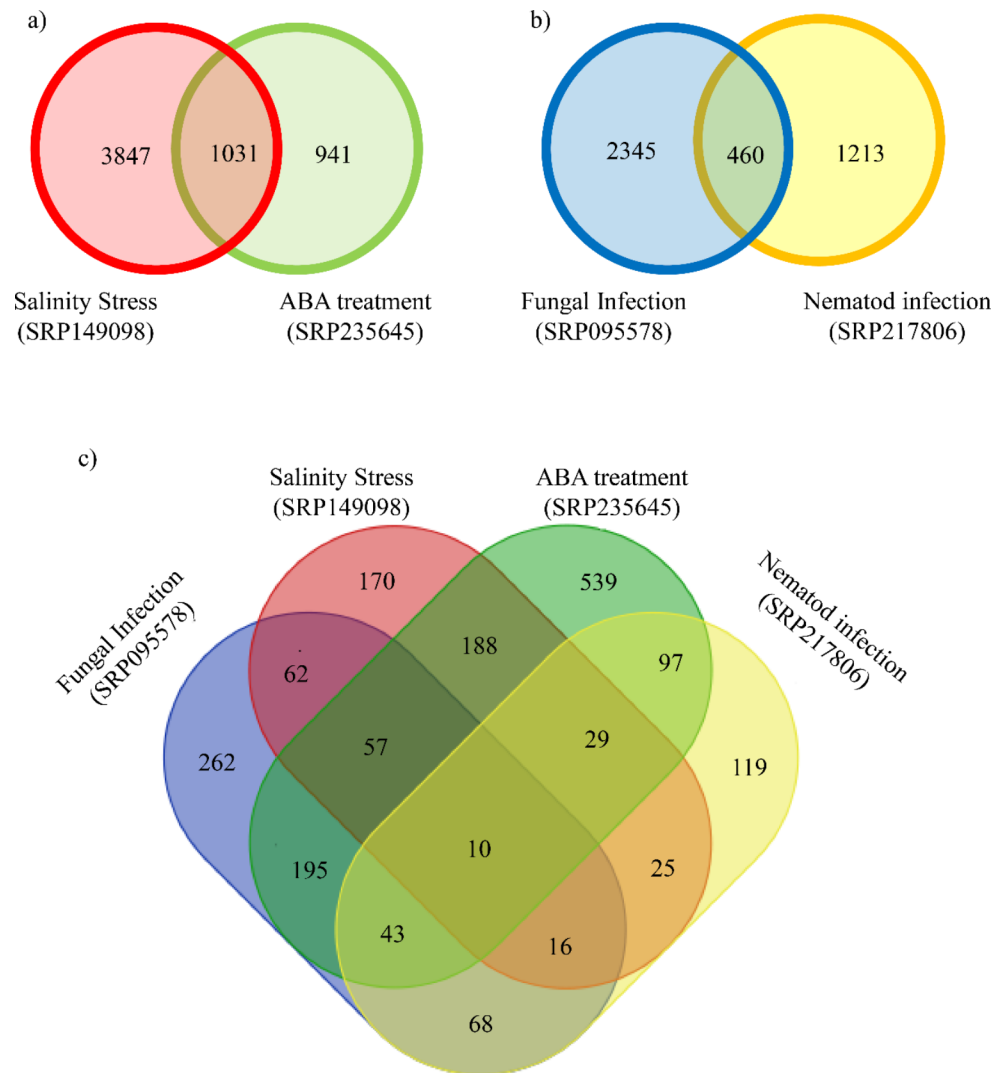
Meta-analysis of biotic-stress related data resulted with 460 common DEGs (Fig. 1a). Analysis of GO term distributions for biotic stress related DEGs showed 268 “biological process”, 146 “cell component”, and 350 “molecular function” terms (Fig. 2). 1031 common DEGs were retrieved during the meta-analysis of abiotic-stress related data (Fig. 1b). Analysis of abiotic stress related DEGs for GO term distributions showed 736 biological process terms, 415 cellular component terms, and 1020 molecular function terms. A summarized representation of GO term distributions is provided in Fig. 3.

The cellular component GO terms of abiotic stress have been mainly related with terms under cell membrane and chloroplast. Membrane-related conditions are likely to be associated with balancing the cellular osmotic pressure. Since salt treatment affects the osmotic pressure of cells, transmembrane transport also appears to be abundant in abiotic stress data (Liang et al. 2018). Chloroplast-related terms are also abundant in abiotic stress data compared to biotic stress data. Chlorophyll levels are known to decrease under salt pressure (Hubbard and Cohen 1993). Among the DEGs obtained from meta-analysis of either biotic or abiotic stress related data, some of the DEGs associated with biotic stress was exclusive for the “Extracellular domain” GO term. It is well known that the concept of the “extracellular domain” is related to the space between cells, and the genes covered under this term are shown to be upregulated during the infection of a parasite (Bult et al. 2018).

The number of GO terms related with the defense response is the second most abundant term under “Biological process” term for biotic stress meta-analysis data, on the other hand there is no GO term about defense response in meta-analysis results for the abiotic stress conditions suggesting that these genes are specific for biotic stress. Also, “RNA binding” term that is under “molecular functions” is abundant. Molecular function terms of biotic data can be thought of as being primarily related to transcription and protein synthesis. As expected, data suggest a molecular activation of transcription during the biotic stress response (Cohen and Leach 2019).

Under the “biological process” abiotic data have 54 terms related to transmembrane transport, whereas biotic data have 6 related terms. The genes covered under “transmembrane transport processes” term are usually associated with plant physiology such as nutrition, solute storage, cell metabolism, signaling, osmoregulation, cell growth, and

**Fig. 1** Venn diagrams of meta-analysis results for transcriptome profiles related with biotic stress (a), abiotic stress (b), and cumulative (biotic and abiotic) stress (c)



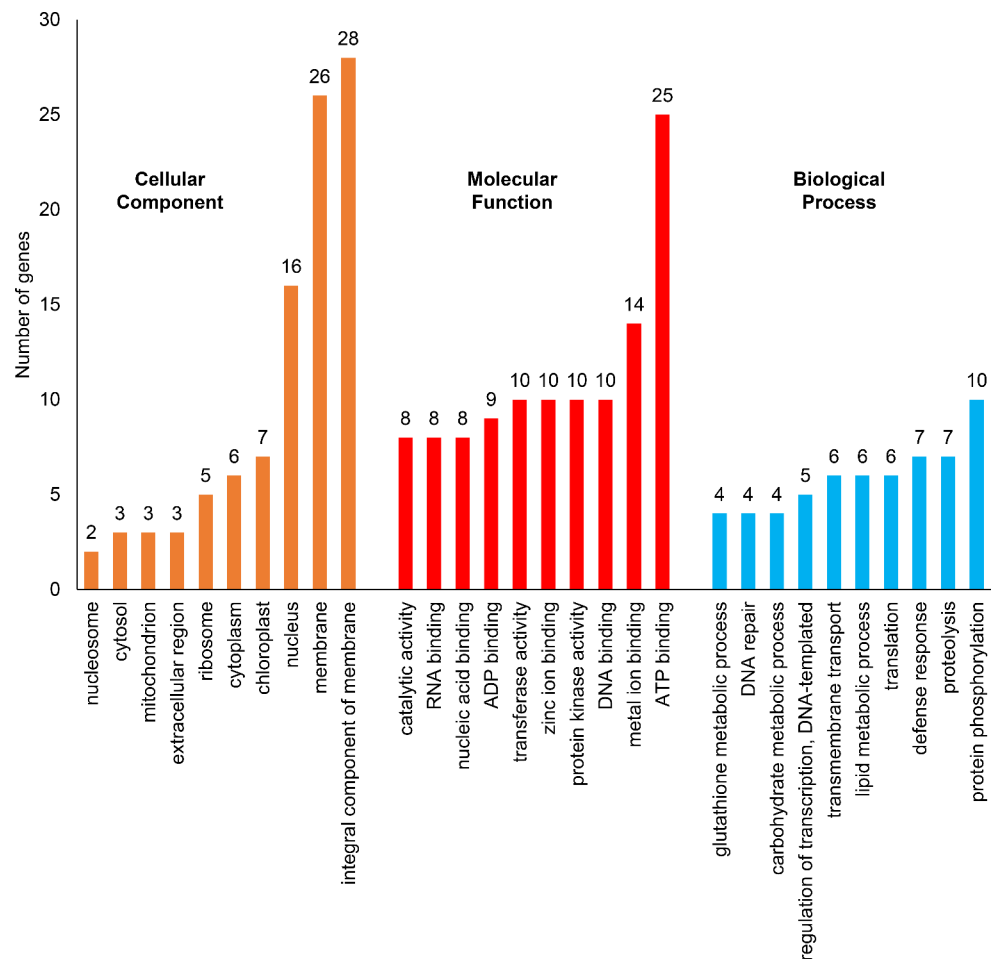
stress responses, in general. Data suggest that impact of abiotic stress is more severe in terms of changes in gene expression to change plant physiology. It is likely that plants have developed more stress-related responses against the abiotic stress due to the high density and diversity of abiotic stressors compared to biotic stressors. Under “molecular function”, the GO terms are covered as “iron ion binding”, “monooxygenase activity”, and “redox activity”. Iron is an essential element for plants and plays important roles such as chlorophyll synthesis, and photosynthesis (Kobayashi et al. 2019). Data suggest activation of photosynthetic reactions under salt stress. GO terms associated with monooxygenase are also higher in abiotic stress data. The flavin and choline monooxygenase genes are known to increase drought resistance in *Arabidopsis* and increase abiotic stress tolerance in rice and spinach (Shirasawa et al. 2006; Lee et al. 2012). Our results are consistent with these studies since they also showed higher abundance under abiotic stress.

### Meta-analysis of Cumulative Transcriptome Data

DEG results from 4 different studies were used for meta-analysis. Cumulative analysis of the data showed that 10 genes were differentially expressed for every stress condition analyzed (Fig. 1c). Among the DEGs, cytochrome P450 81E8-like, thioredoxin domain-containing protein 2, probable mannitol dehydrogenase, glutathione transferase GST 23-like, an uncharacterized protein, and a hypothetical protein encoding genes were upregulated. On the other hand, one probable leucine-rich repeat receptor-like protein kinase encoding gene and three hypothetical protein encoding genes were down-regulated according to meta-analysis of biotic and abiotic stress related data, cumulatively (Table 2).

We were able to retrieve the gene identifiers for 6 DEGs by searching their Ensembl IDs through the NCBI database. These identifiers then converted to KEGG gene identifiers

**Fig. 2** GO term distribution of meta-analysis of data related with biotic stress. 10 most abundant terms are represented in each major GO Terms



(Table 3). The rest of the genes remained unknown in the KEGG database.

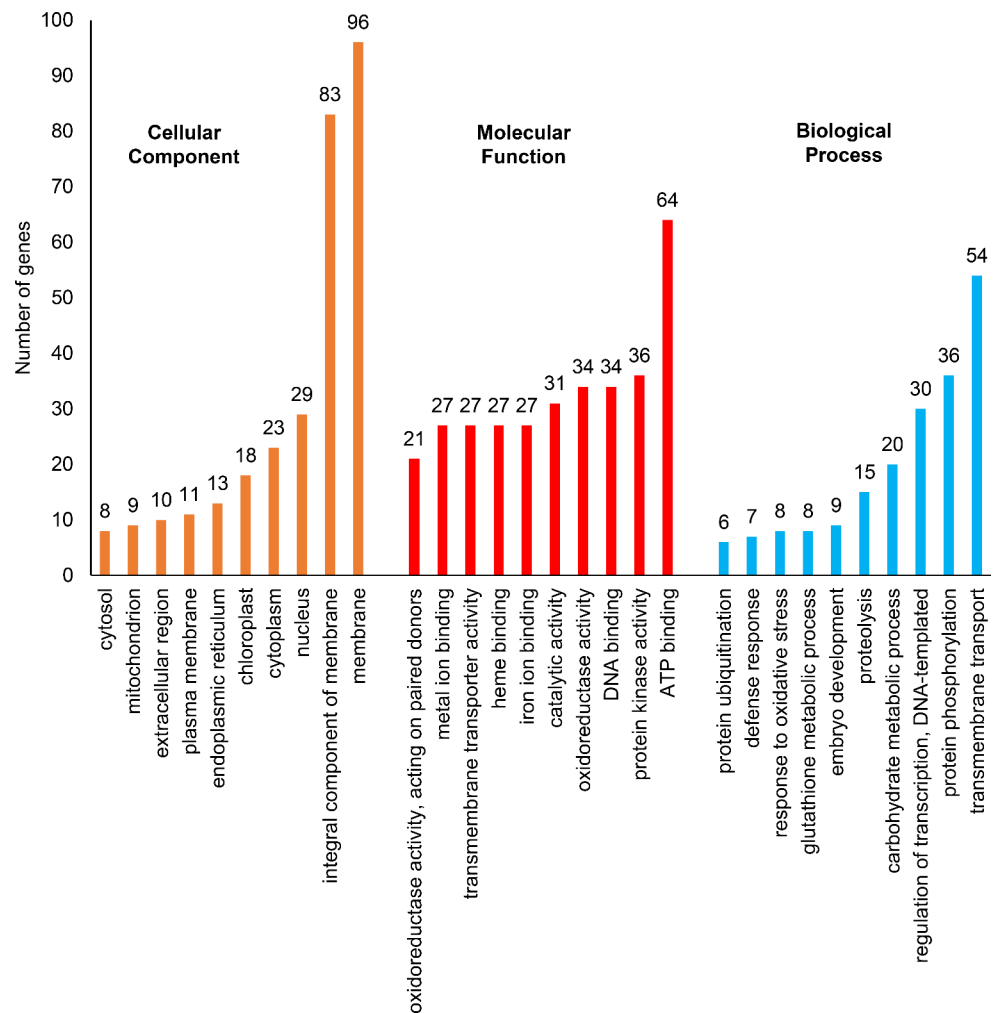
Meta-analysis of biotic and abiotic data shows that expression of genes especially related with photosynthesis and oxidative stress are affected in both stress types.

Our results show the up regulation of mannitol dehydrogenase gene under biotic and abiotic stress. Mannitol is also well-known ROS scavenger. Mannitol is a by-product of photosynthesis, and they move from leaf to root. Mannitol dehydrogenase is a catalyst for the catabolism of mannitol (Upadhyay et al. 2015). It is mainly used to defend the plants against pathogens by mannitol to catabolize the pathogen's secreted mannitol under biotic stress and work as osmoprotectant and/or osmoregulator under abiotic stress conditions (Upadhyay et al. 2015). Thus, our data highlight the role of mannitol dehydrogenase in general stress response in sugar beet. Previous studies showed that induction of ROS scavengers would enhance the capacity of *Beta vulgaris* to tolerate stress like excessive salt. It is shown that enhancement of the photosynthesis, water status, antioxidant system and ion homeostasis by exogenous metabolites such as melatonin and allantoin have positive impact on improving the tolerance levels. It is possible that these

mechanisms may have overlapping components on mannitol dehydrogenase gene regulation and/or general stress response (Liu et al. 2020a; Zhang et al. 2021).

Under stress conditions, ROS increases dramatically. The increase in ROS is associated with the plant's defense mechanisms (Houghton 2005). While ROS are damaging the cells molecular structures, they are also used as signaling molecules. In this study we found the gene products that are mainly related to ROS as we expected. Firstly, our data show that mitochondrial thioredoxin, which is a redox protein essential for the proper function of metabolic pathways, expressing gene is upregulated under all stress conditions. And it also takes roles in signaling pathways include stomatal opening, antioxidant metabolism, drought, salt exposure, and detoxifying hydrogen peroxide to reduce the damage of ROS to cell physiology. In addition, our data shows an increase in Glutathione S-transferases (GST), Cytochrome P450, and thioredoxin domain-containing protein 2 expression. These genes are known detoxifying enzymes along with their role in regulation of oxidative stress (Xu et al. 2015). A novel study also showed differentiated expression of genes related with ROS metabolism, carbohydrate metabolism and hormone signaling under salt stress which

**Fig. 3** GO term distribution of meta-analysis of data related with abiotic stress. 10 most abundant terms are represented in each major GO Terms



**Table 2** Log fold changes of meta-analysis results of cumulative transcriptome data

Ensembl_IDs	Definition	Log Fold Changes				Regulation status
		SRP95578	SRP217806	SRP149098	SRP235645	
BVRB_1g021740	cytochrome P450 81E8-like	2.284	2.260	1.832	4.898	Up
BVRB_2g030930	uncharacterized	1.626	0.821	1.090	1.838	Up
BVRB_2g043720	thioredoxin domain-containing protein 2	0.337	0.253	0.501	0.252	Up
BVRB_6g133980	mannitol dehydrogenase	3.352	4.028	2.640	7.936	Up
BVRB_7g166460	glutathione transferase GST 23-like	4.651	0.967	1.054	0.919	Up
BVRB_4g086310	hypothetical protein	6.767	1.781	0.836	1.289	Up
BVRB_6g145450	leucine-rich repeat receptor-like protein kinase	-0.816	-1.498	-1.669	-0.449	Down
BVRB_5g126270	hypothetical protein	-0.596	-0.788	-0.999	-0.495	Down
BVRB_8g187810	hypothetical protein	-0.350	-0.805	-0.839	-0.439	Down
BVRB_2g030970	hypothetical protein	-1.219	-1.523	-1.160	-1.213	Down

increases the low temperature tolerance for *Beta vulgaris* (Liu et al. 2023). Those genes can be a source to increase tolerance against different stress conditions when combined with salt stress in *Beta vulgaris*.

Increase of free radicals in plant tissues is a natural phenomenon and plants have active defense mechanisms to fight against damaging effects of these radicals. Limiting the role of these mechanisms to reduction of ROS would be

underestimating their values. Studies showed that there is a direct correlation between the expression of the genes and/or activating antioxidant enzyme mechanisms related with mitigating oxidative damage and improving stress tolerance in sugar beet (Zou et al. 2020a; Xing et al. 2020; Liu et al. 2023). Scavenging of ROS has an impact on plant physiology by controlling diverse mechanisms related with photosynthesis, lipid and energy metabolism, cell wall structure,

**Table 3** KEGG Summary of meta-analysis results of cumulative transcriptome data

Ensembl ID	KEGG Entry ID	Entry Name	Motif
BVRB_1g021740	104,905,737	cytochrome P450 81E8-like	p450
BVRB_2g030930	104,882,957	uncharacterized	-
BVRB_2g043720	104,887,745	thioredoxin domain-containing protein 2	-
BVRB_6g133980	104,895,532	mannitol dehydrogenase	ADH_N
BVRB_6g145450	104,896,981	leucine-rich repeat receptor-like protein kinase	Pkinase
BVRB_7g166460	104,899,342	glutathione transferase GST 23-like	GST_N
BVRB_4g086310	-	-	-
BVRB_5g126270	-	-	-
BVRB_8g187810	-	-	-
BVRB_2g030970	-	-	-

and signaling to improve plants' capacity to tolerate diverse stress conditions (Foyer and Shigeoka 2011; Rasouli et al. 2020; Liu et al. 2023).

A Leucine-rich repeat receptor kinase and three hypothetical proteins were down-regulated in the meta-analysis of biotic and abiotic stress related data. Leucine-rich repeat receptor kinases are the largest subfamily of transmembrane receptor-like kinases in plants. They regulate a wide range of defense-related processes (Torii 2004). Previous studies show the importance of transmembrane receptor-like kinases under biotic and abiotic stresses (Wu et al. 2015). While expression of most of known Leucine-rich repeat receptor kinases are increased under stress, leucine-rich repeat (LRR)-RLK gene (Leaf Panicle 2 (LP2) was a negative-regulator drought stress and higher expression of LP2 inhibits stoma closure. It is possible that Leucine-rich repeat receptor kinase encoding gene found in this study can have similar function as LP2 protein.

The overall results may show increased photosynthesis under biotic and abiotic stress conditions. Plants tend to decrease in the rate of their photosynthesis under stress, especially salt stress (Ashraf and Harris 2013). They close their stoma under stressful conditions to stop evaporation, preventing them from absorbing CO<sub>2</sub>. *Beta vulgaris*, on the other hand, is known to be a salt-resistant plant, which maintains osmotic pressure and absorbs more water than other plants (Ferreira da Silva et al. 2018). Therefore, our data suggest that evaporation does not significantly affect sugar beets under stress. The reduction of the Leucine-rich repeat receptor kinase and increase of mannitol dehydrogenase genes supports the phenomenon. Chloroplast is known as an environmental sensor and creates the first response for stress conditions. The relationship between photosynthesis

and ROS is a complicated process. ROS can be thought as double-edged sword. They can damage cells at high concentrations or they can also act as signaling molecules to enhance photosynthesis. (Foyer and Shigeoka 2011). Therefore, plant cells maintain ROS levels in an adequately required level and adjust the photosynthesis rate depending on the impact of all surrounding conditions by controlling the expression of several genes (Xu et al. 2015; Yu et al. 2020; Zou et al. 2020a). Since we covered the genes that are regulated in all stress conditions tested, our data may suggest photosynthetic rate can fluctuate depending on the type and the duration of the stress factors.

**Author Contributions** Burak Bulut: Conception and design, sampling, data collection and analysis, evaluation of results, and writing/editing the manuscript. Songül Gürel: Data evaluation and editing the manuscript. Ömer Can Ünüvar: Evaluation of results, and writing/editing the manuscript. Ekrem Gürel: Data evaluation and editing the manuscript. Yunus Şahin: R Coding and evaluation of results. Uğur Çabuk: Datanormalization. Ercan Selçuk Ünlü: Conception and design, sampling, Perl coding, data collection and analysis, evaluation of results, and writing/editing/revising the manuscript.

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## Declarations

**Ethics approval** Not applicable

**Consent to participate** Not applicable

**Consent for publication** Not applicable

**Conflicts of interest/Competing Interests** Authors declare that they have no conflict of interest/competing interest.

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