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Identification of conserved genes linked to responses to abiotic stresses in leaves among different plant species

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Abstract. As a consequence of global climate change, certain stress factors that have a negative impact on crop productivity such as heat, cold, drought and salinity are becoming increasingly prevalent. We conducted a meta-analysis to identify genes conserved across plant species involved in (1) general abiotic stress conditions, and (2) specific and unique abiotic stress factors (drought, salinity, extreme temperature) in leaf tissues. We collected raw data and re-analysed eight RNA-Seq studies using our previously published bioinformatic pipeline. A total of 68 samples were analysed. Gene set enrichment analysis was performed using MapMan and PageMan whereas DAVID (Database for Annotation, Visualisation and Integrated Discovery) was used for metabolic process enrichment analysis. We identified of a total of 5122 differentially expressed genes when considering all abiotic stresses (3895 were upregulated and 1227 were downregulated). Jasmonate-related genes were more commonly upregulated by drought, whereas gibberellin downregulation was a key signal for drought and heat. In contrast, cold stress clearly upregulated genes involved in ABA (abscisic acid), cytokinin and gibberellins. A gene (*non-phototrophic hypocotyl*) involved in IAA (indoleacetic acid) response was induced by heat. Regarding secondary metabolism, as expected, MVA pathway (mevalonate pathway), terpenoids and alkaloids were generally upregulated by all different stresses. However, flavonoids, lignin and lignans were more repressed by heat (*cinnamoyl coA reductase 1* and *isopentenyl pyrophosphatase*). Cold stress drastically modulated genes involved in terpenoid and alkaloids. Relating to transcription factors, *AP2-EREBP*, *MADS-box*, *WRKY22*, *MYB*, *homoebox* genes members were significantly modulated by drought stress whereas cold stress enhanced *AP2-EREBP*s, *bZIP* members, *MYB7*, *BELL 1* and one *bHLH* member. *C2C2-CO-LIKE*, *MADS-box* and a *homeobox* (*HOMEOBOX3*) were mostly repressed in response to heat. Gene set enrichment analysis showed that ubiquitin-mediated protein degradation was enhanced by heat, which unexpectedly repressed *glutaredoxin* genes. Cold stress mostly upregulated *MAP kinases* (mitogen-activated protein kinase). Findings of this work will allow the identification of new molecular markers conserved across crops linked to major genes involved in quantitative agronomic traits affected by different abiotic stress.

Additional keywords: abiotic-stresses, differentially expressed genes, leaves, meta-analysis, RNA-Seq, transcriptomic.

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Introduction

Development, productivity and quality of plants are frequently affected by various environmental stresses such as drought, salt, cold and heat (Najafi *et al*. 2018). Notably, the impact of the abiotic environmental stresses is becoming more significant due to the global climate change, with some stress factors (e.g. heat, drought and salinity) becoming more prevalent. The simultaneous occurrence of several abiotic stress factors is particularly lethal to crops, and as a response, plants have evolved particular complex molecular networks to cope with and survive such environmental stresses (Najafi *et al*. 2018). Due to the rapid progresses of the next-generation sequencing technologies, the number of transcriptomic studies has increased exponentially in ISI/Scopus databases in the last 10 years. Hence, numerous transcriptomic studies dealing with abiotic environmental stress responses have been conducted in a few plant species including *Arabidopsis thaliana* (L.) Heynh. (Ding *et al*. 2013; Imran *et al*. 2018), *Malus domestica* Borkh. (Wu *et al*. 2015; Yang *et al*. 2017) and *Vitis vinifera* L. (Rienth *et al*. 2014; Zenoni *et al*. 2016; Benny *et al*. 2019*a*). Although each of these studies allows insights into the genes, pathways and functional gene categories implicated in specific combinations of stress and plant species, obtained data are characterised by low reliability because of high external and uncontrolled environmental variability. Transcriptomic studies are usually conducted in a specific environment, using a single time of sampling, and usually with a low number of biological replicates, so results are often highly speculative. The power of these studies is reduced by the evidence that the potential key players in abiotic stress resistance/tolerance are regulated by a high number of physiological, developmental and environmental conditions. Thus, conclusions about the key transcriptomic mechanisms behind plant abiotic stress responses in plants are generally unreliable, and evidence to support hypotheses is weak. In an environmental context that becomes increasingly hostile and complex, a meta-analysis could provide a valuable tool since it aims to compare different transcriptomic studies concerning the same research purposes, identifying common molecular features and strengthen the power of next-generation sequencing (NGS) approaches reducing environmental variability and virtually increasing biological replicates. A meta-analysis could aid in a better understanding of the mechanisms underlying the problems of environmental stress that can compromise crop productivity and food security. Further, a meta-analysis could compare differentially regulated genes and affected pathways among different studies using the same bioinformatic methods (Rawat *et al*. 2015). In addition, a comparison of the molecular mechanisms related to different stress conditions would allow validation of potential candidate genes involved in specific and exclusive plant abiotic stress responses. Such information is crucial to shed light on the molecular regulatory networks related to abiotic stress responses in plants and to deliver stronger scientific evidence that could be used for next-generation crop breeding programs. This approach has been already used to identify key conserved genes involved in both biotic and abiotic stresses (Balan *et al*. 2017, 2018; Benny *et al*. 2019*b*). Finally, a meta-analysis could also provide information about an early alert for plant physiological status under stress, and aid the development of more sustainable management strategies.

The present study was conducted in order to identify key major genes involved in general plant abiotic stress conditions and those involved in specific and unique pattern of different abiotic stresses factors. We performed a bioinformatics analysis of previously published RNA-Seq studies on leaves through a careful selection of published studies related to four abiotic stress factors: drought, salinity, cold and heat.

Materials and methods

Search strategy to identify published studies for bioinformatic analysis

The published RNA-Seq studies related to abiotic stress responses in leaf tissues were searched using Scopus and PubMed with the combination of keywords 'transcriptomics' 'leaf' and 'abiotic stress' that were published in or before June 2018. We found 11 articles related to our purpose of meta-analysis of abiotic stress responses in plant leaves using next-generation sequencing approaches and with availability of raw data in public databases. Among these, we selected eight articles with publically available raw data (Xu *et al*. 2014; Corso *et al*. 2015; Forestan *et al*. 2016; Haider *et al*. 2017; Li *et al*. 2017*a*; Liu *et al*. 2017; Orcheski and Brown 2017; Shumayla *et al*. 2017).

From these considered studies, one manuscript was related with salinity (Forestan *et al*. 2016), four other works related to drought (Corso *et al*. 2015; Haider *et al*. 2017; Liu *et al*. 2017; Orcheski and Brown 2017), one paper related to cold (Xu *et al*. 2014), one related to heat (Shumayla *et al*. 2017) and the last one was related to salinity, heat and cold (Li *et al*. 2017*a*). So, in total, we gathered four articles related to drought, two works related to salinity, two studies dealing with cold and two related to heat. The raw files (SRA format) of the eight articles dealing with abiotic stress responses in leaves were downloaded from NCBI SRA (https://www.ncbi.nlm.nih.gov/sra, accessed 3 May 2019). In total, 68 samples were analysed. We downloaded the raw data of all the 'abiotic stress' selected studies and performed RNA-Seq analysis using a single analysis pipeline in Fig. 1 to obtain the differentially expressed genes (DEGs).

Read alignment, gene differential expression and annotation

For all the articles selected, the latest available version of the corresponding crop genome and its annotation file were downloaded from Phytozome (https://phytozome.jgi.doe.gov, accessed 4 June 2020). The raw data files were downloaded from NCBI SRA(https://www.ncbi.nlm.nih.gov/sra) and EMBL ArrayExpress(https://www.ebi.ac.uk/arrayexpress/, accessed 10 July 2020) according to the accession number given in the article and converted to FASTQ format using SRA toolkit ver. 2.3.5. Raw data underwent pre-processing by trimming low quality bases followed by adaptor sequence removal to obtain high-quality clean reads using cutadapt ver. 1.8.1. The pre-processed high-quality reads (Phred-score > 30) were mapped to the corresponding genome with HISAT2 ver. 2.1.0 using '-novel-splicesite' option along with the default parameters. The resulted output of HISAT2 was then used for the identification of differentially expressed genes using Cuffdiff tool in Cufflinks version 2.2.1 pipeline with default parameters. Only up- and downregulated genes obtained with fold change cutoff ($\log2\ FC > 0.5$ or $\log2\ FC < -0.5$) and P-value < 0.05 were considered for the meta-analysis. The DEGs selected were annotated using corresponding crop genome mapping file downloaded from the Phytozome. Each of the *Arabidopsis* IDs were then selected and searched for identifying the corresponding orthologs using PANTHER and the functional similarities were identified using the UniProtKb and ensembl plants compara. DEGs were subjected to functional and enrichment analyses after identification of the corresponding orthologous genes in *Arabidopsis thaliana* (L.) Heynh. Since each study involving plants different from *Arabidopsis*, the entire list of gene IDs corresponding to DEGs was mapped to *A. thaliana*, and the best corresponding TAIR (The

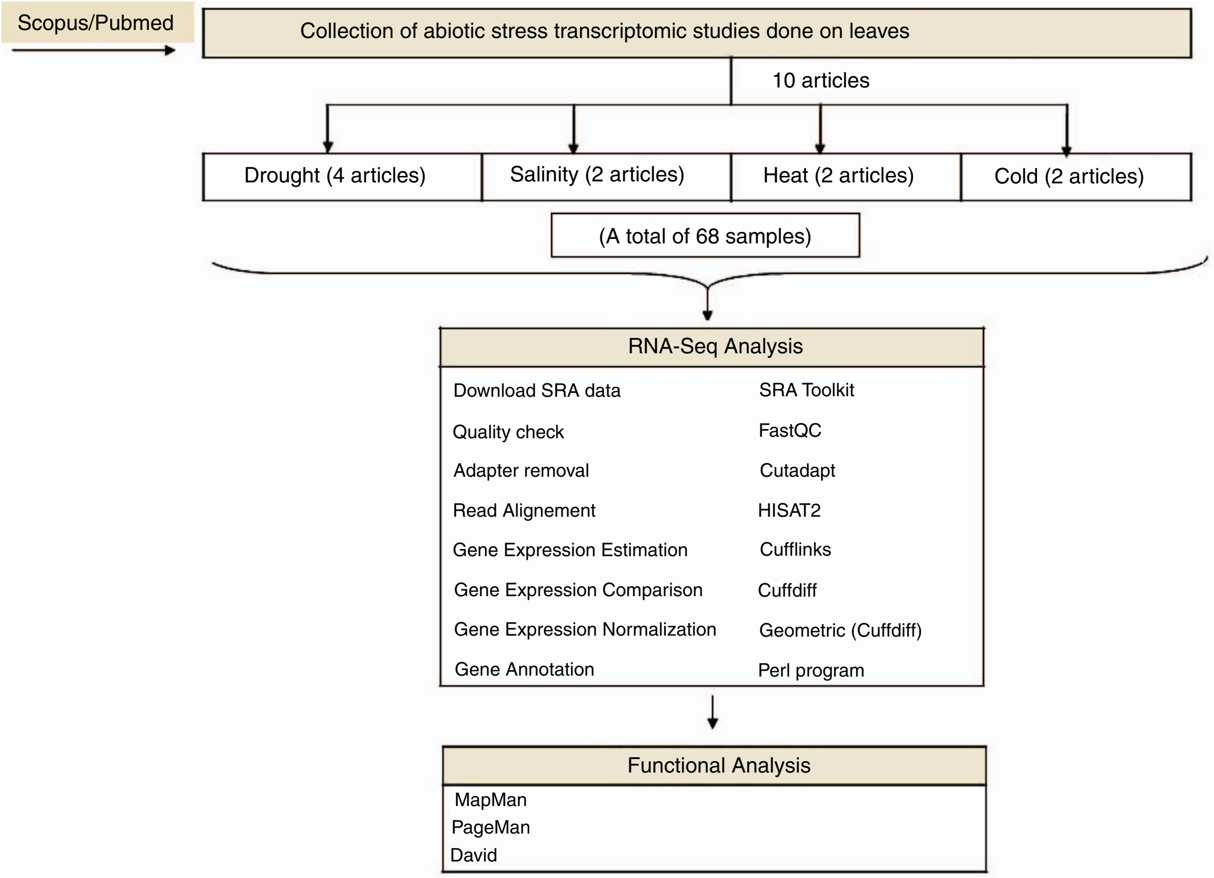


Fig. 1. Workflow of the meta-analysis of the 10 transcriptomic studies related with abiotic stress in leaf tissue. Functional data analyses are indicated.

Arabidopsis Information Resource) IDs were found by using the annotation file downloaded from Phytozome. During mapping to *Arabidopsis* orthologs, cases of 'many-to-one' mapping were solved by calculating an average expression value (log2 fold change).

Gene set enrichment analysis

We used MapMan (Thimm *et al*. 2004) with the *A. thaliana* mapping file to map and visualise the hormone regulation, secondary metabolism and transcription factors. We visualised the unique genes present in each of the stress separately. The PageMan (Usadel *et al*. 2006) analysis, plugin of MapMan, was used to visualise differences among metabolic pathways using Wilcoxon tests, no correction, and an over-representation analysis (ORA) cutoff value of 3. All the homologous TAIR IDs of the studies were searched against the Database for Annotation, Visualisation and Integrated Discovery (DAVID) ver. 6.8 (Huang *et al*. 2009). The gene ontology information related to biological process was extracted from the DAVID result.

Statistical analysis

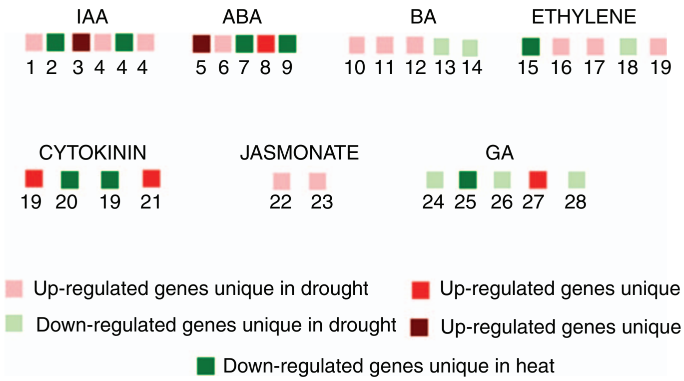
The DEGs corresponding to each studies were analysed separately when they had a P-value < 0.05 and log2 FC >0.5 or log2 FC < -0.5. All statistical tests were corrected for multiple comparisons using the Benjamini-Hochberg false discovery rate using p.adjust function of R. By adjusting the P-values, this approach can make the FDR at the desired level of α (in the present study = 0.05). Differences among the selected studies were adjusted using the sample normalisation. In order to remove systematic variation between different species, the normalisation procedure served as a crucial pre-processing step to adjust for the different sample sequencing depths and other confounding technical effects. We used the geometric normalisation method where FPKMs and fragment counts are scaled via the median of the geometric means of fragment counts across all libraries.

Protein–protein interaction network

NetworkAnalyst, a web-based tool for network-based visual analytics of protein–protein interaction networks, was used (https://www.networkanalyst.ca, accessed 12 March 2020). The list of unique homologous TAIR IDs for each genes uniquely modulated by each abiotic stress were uploaded and mapped against the STRING interactome database with default parameters (confident score cutoff = 900 and with experimental evidence) provided in NetworkAnalyst. The networks between drought-regulated genes in seedlings and in mature leaves

Table 1. Transcriptomic studies dealing with abiotic stress responses used for meta-analysis

Reference	Crop	Stress	Sample description		Number of differentially regulated genes		
			Control	Treated	Total	Up	Down
Li *et al.* (2017*a*)	Maize	Salinity	Control1 (SRR3984708) Control2 (SRR3984749)	Salinity1 (SRR3984762) Salinity2 (SRR3984771)	264	264	0
Forestan *et al.* (2016)	Maize	Salinity	Control1 (GSM1826055) Control2 (GSM1826071)	Treated1 (GSM1826057) Treated2 (GSM1826073)	424	424	0
Li *et al.* (2017*a*)	Maize	Heat	Control1 (SRR3984708) Control2 (SRR3984749)	Heat1(SRR3984794) Heat2 (SRR3984795)	228	228	0
Shumayla *et al.* (2017)	Wheat	Heat	Control 1 (SRR1542404) Control 2 (SRR1542405)	Treated1 (SRR1542412) Treated 2 (SRR1542413)	154	0	154
Li *et al.* (2017*a*)	Maize	Cold	Control1 (SRR3984708) Control2 (SRR3984749)	Cold1 (SRR3984802) Cold2 (SRR3984815)	219	219	0
Xu *et al.* (2014)	Vitis	Cold	Control (SRR922004)	Treated (SRR922126)	179	179	0
Haider *et al.* (2017)	Vitis	Drought	Control (SRR3466603)	Treated (SRR3466604)	174	174	0
Orcheski and Brown (2017)	Malus	Drought	Control 1 (SRR3160181) Control 2 (SRS1283365)	Treated1 (SRR3160081) Treated2 (SRR3160180)	432	178	254
Liu *et al.* (2017)	Tomato	Drought	SCK (SRR5282480) TCK (SRR5282476)	SD (SRR5282481) TD (SRR5282478)	159	88	71
Corso *et al.* (2015)	Vitis	Drought	Control1 SAMN02393571 Control2 SAMN02393572	Treated1 SAMN0239359 Treated2 SAMN02393595	2889	2141	748



1. IAA-Leucine Resistant 1
2. BIG
3. Non phototrophic hypocotyl
4. Auxin responsive protein
5. ABA deficient 1
6. ATHVA22A
7. ATHVA22E
8. GRAM-domain containing protein
9. ATHVA22D
10. 3-oxo-5-alpha-steroid 4-dehydrogenase
11. STEROL 1
12. DWARF 5
13. Cycloartenol synthase 1
14. Brassinosteroid insensitive 1
15. Oxidoreductase
16. Ethylene responsive element binding factor 1
17. AP2 domain containing transcription factor
18. MBF1B
19. UDP-glycosyltransferase
20. cytokinin oxidase 7
21. WOL (Wooden Leg)
22. ANAC028
23. LOX3
24. 2-oxoglutarate-dependent dioxygenase
25. GA2
26. Gibberellin 2-oxidase 1
27. RGA1
28. GASA1

Fig. 2. Abiotic stress-regulated genes involved in hormone-related categories that are uniquely regulated in the studies are shown. Genes were identified as *Arabidopsis* orthologs of each gene of the analysed plant species. Red indicates upregulation and green indicates downregulation in response to stress.

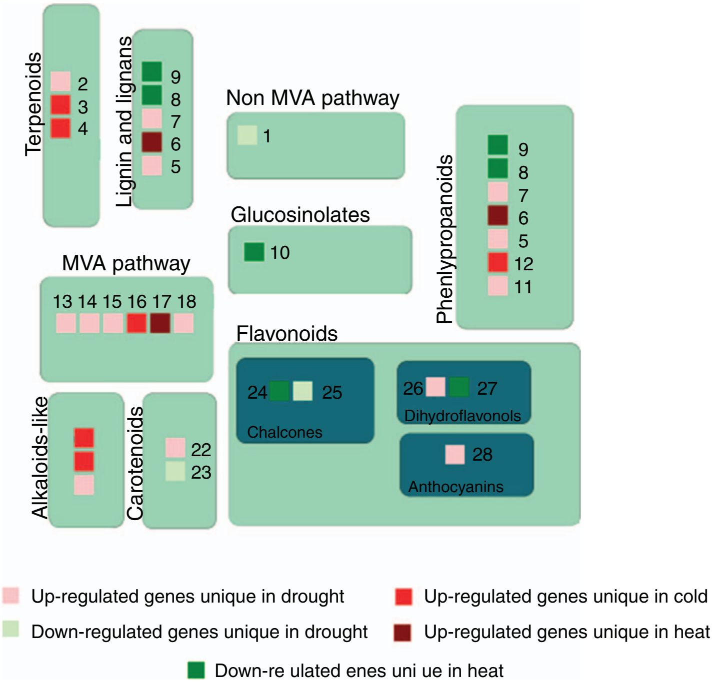
corresponding to the list of the visualised genes in MapMan were also obtained. To study the key connectives and to simplify the large network, we selected 'minimum network'.

Results

The articles and crops selected for the study, number of up- and downregulated genes are listed in Table 1.

Hormone-related pathways

Drought stress enhanced expression of some brassinosteroids like *3-oxo-5-α-steroid 4-dehydrogenase*, *STEROL 1* and *DWARF 5* and have opposite effects on the expression of *cycloartenol synthase 1* and *brassinosteroid insensitive 1* (Fig. 2). Two key jasmonate genes were upregulated by drought stress. All the gibberellin related genes (*GASA1*,



1. Geranylgeranyl transferase II beta subunit
2. Myrcene synthase
3. Terpene Synthase 21
4. Solanesyl diphosphate synthase 1
5 . Phenylalanine ammonia-lyase 4
6. CINNAMOYI COA REDUCTASE 1
7. ferulate 5-hydroxylase
8. mannitol dehydrogenase
9. CINNAMYL ALCOHOL DEHYDROGENASE 6
10 . Branched chain aminotransferase 3
11. 4-coumarate--CoA ligase
12. NICOTINAMIDASE 1
13. acetyl-CoA C-acyltransferase
14. ACETOACETYL-COA THIOLASE 2
15. acetyl-CoA C -acetyltransferase
16. hydroxymethylglutaryl-CoA reductase
17. ISOPENTENYL PYROPHOSPHATE
18. Solanesyl diphosphate synthase 2
19. STRICTOSIDINE SYNTHASE-LIKE 4
20. strictosidine synthase family protein
21. tyrosine decarboxylase
22. CAROTENOID CLEAVAGE DIOXYGENASE 1
23. NON-PHOTOCHEMICAL QUENCHING 1
24. aldo/keto reductase
25. TRANSPARENT TESTA 5
26 . DOWNY MILDEW RESISTANT 6
27. TRANSPARENT TEST A 7
28 20G-Fe(II) oxygenase

Fig. 3. Abiotic stress-regulated genes involved in secondary metabolism categories that are uniquely regulated in the studies were shown. Genes were identified as *Arabidopsis* orthologs of each gene of the analysed plant species. Red indicates upregulation and green indicates downregulation in response to stress.

gibberellins 2-oxidase 1 and *2-oxoglutarate-dependent dioxygenase*) were downregulated by the effect of drought. Several genes involved in ethylene biosynthesis and signalling were enhanced by drought stress such as *MBF1B*, *AP2* and *ERF1*. Heat stress downregulated one ethylene related gene – *oxidoreductase*. Cold stress upregulated ABA (*GRAM domain containing protein*), cytokinin (*UDP-glycosyltransferase* and *WOL*) and gibberellin (*RGA1*). Heat stress enhanced the expression of a gene involved in IAA (*non-phototrophic hypocotyl*) response.

Secondary metabolism

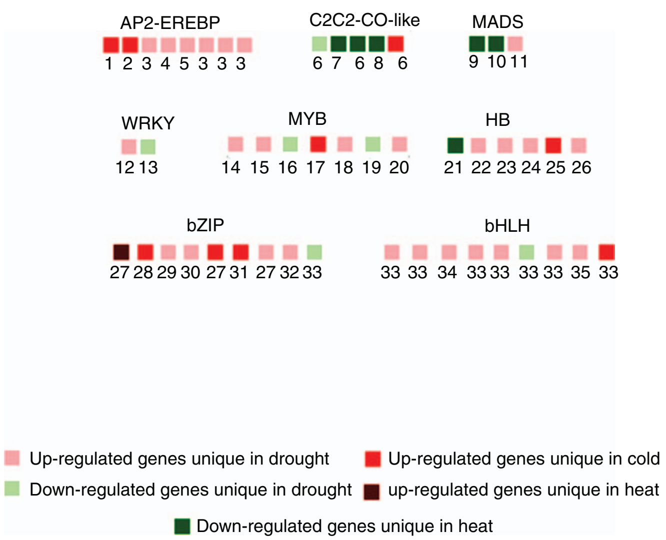
Secondary metabolism was significantly modulated by the expression of genes involved in the different analysed stress studies (Fig. 3). We noted that of the different stress related categories that come under mevalonic acid (MVA) pathway, terpenoids and alkaloids were upregulated. Heat stress repressed most of the flavonoids (*aldo-keto reductase*, *TRANSPARENT TESTA7*), lignin and lignans (*mannitol dehydrogenase* and *CINNAMYL ALCOHOL DEHYDROGENASE 6*), phenylpropanoids and glucosinolates (*branched chain aminotransferase 3*) but upregulated the *CINNAMYL COA REDUCTasE 1* and *ISOPENTENYL PYROPHOSPHATE*. The expression of cold stress-related genes involved in terpenoid (*terpene synthase 21* and *solanesyl diphosphate synthase 1*) and alkaloids (*STRICTOSIDINE SYNTHASE*).

Transcription factors

We used MapMan software to demonstrate the effect of abiotic stress in transcription factors and to identify the crucial and specific genes response in each type of abiotic stresses, Transcription factors were drastically affected by three of four analysed abiotic stresses (drought, cold, heat stresses; Fig. 4). Drought stress induced key genes encoding *AP2-EREBPs* such as *AP2 domain containing transcription factor*, *PLT1* and *TINY*, one *MADS box* transcription factors (*AGL42*), a *WRKY* factor (*WRKY22*), four MYB factors (*MYB6*, *MYB12*, *MYB78*, *MYB71*), four *homoebox* genes (*HB6*, *HB13*, *KNAT7*, *HAT3.1*), four *bZIP* members (*TGA1*, *HY5-Homologue, bZIP TFs*, *TGA6)*, three *bHLH TFs* (*Bhlh* protein, *ICE1*, *ILL3*). Among the downregulated genes in response to water deprivation there were two *MYB* factors (*MYB111* and *MYB66*), one *C2C2-CO-like* member (*B-box zinc finger*), one *WRKY* gene (*WRKY51*), one *bZIP* transcription factor and one *bHLH* member. Cold stress enhanced two *AP2-EREBPs* genes (*ACA4*, *ERFs*), three *bZIP* members. We also found that another three well-known drought-regulated transcription factors (*MYB7*, *BELL1* and 1 *bHLH* member) were enhanced. Heat stress specifically induced one *bZIP TF*. Other genes were repressed in response to heat, such as three *C2C2-CO-LIKE* (*B-box zinc finger*, *Salt Tolerance*, *STH*), two *MADS box* (*AGAMOUS-LIKE 12*, *AGAMOUS-LIKE 19*) and one *homeobox* (*HOMEOBOX3*).

Gene set enrichment analysis

Gene enrichment analysis was conducted using PageMan to identify any relation between the expression and function of differentially expressed genes in different abiotic stress conditions (Fig. 5). Analysis showed that drought stress



1. REGULATOR OF THE ATPASE OF THE VACUOLAR MEMBRANE
2. ethylene-responsive element-binding protein
3. AP2 domain-containing transcription factor
4 . PLETHORA 1
S. TINY
6. zinc finger (B-box type) family protein
7. SALT TOLERANCE
8. STH
9. AGAMOUS-LIKE 12
10. AGAMOUS-LIKE 19
11. AGAMOUS LIKE 42
12. WRKY22
13. WRKY51
14 . MYB6
15. MYB12
16. MYB111
17. MYB7
18. MYB78
19. MYB66
20. MYB71
21. HOMEOBOX 3
22. HOMEOBOX 6
23. HOMEOBOX 13
24. KNOTTED-LIKE HOMEOBOX 7
25. BELL 1
26. HAT3. 1
27. bZIP family transcription factor
28 . BASIC LEUCINE ZIPPER 9
29. TGA1
30. HY5-HOMOLOG
31. BZ02H1
32. TGACG MOTIF-BINDING FACTOR 6
33. basic helix-loop-helix protein
34. INDUCER OF CBF EXPRESSION 1
35. IAA-leucine resistant3

Fig. 4. Abiotic stress-regulated genes involved in transcription factors categories that are uniquely regulated in the studies were shown. Genes were identified as *Arabidopsis* orthologs of each gene of the analysed plant species. Red indicates upregulation and green indicates downregulation in response to stress.

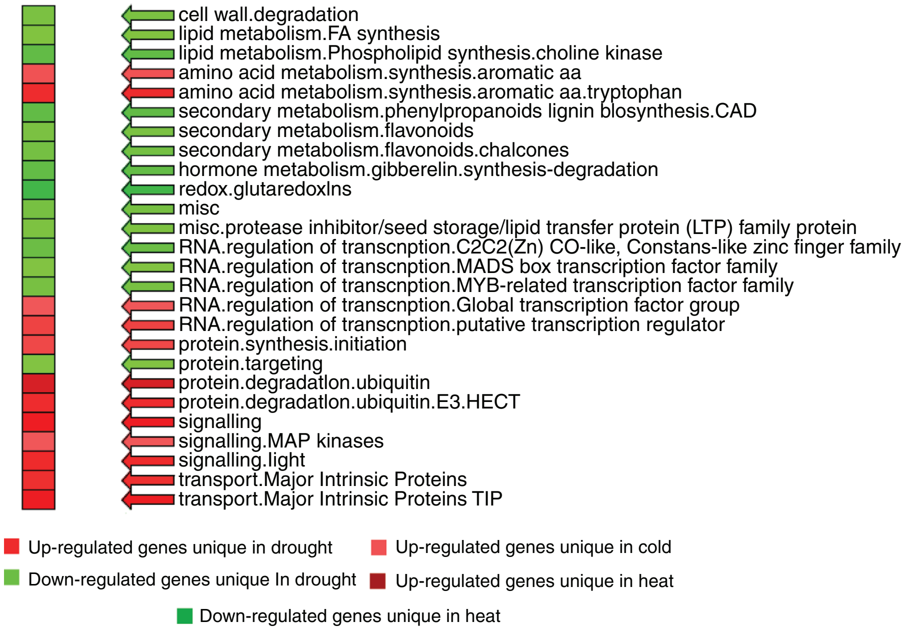


Fig. 5. The PageMan analysis was used to visualise differences among metabolic pathways using Wilcoxon tests, no correction, and an over-representation analysis (ORA) cutoff value of 3.

downregulated several genes categories such as those implicated in cell wall degradation, lipid metabolism (fatty acid synthesis, phospholipid choline kinase synthesis), secondary metabolism (phenylpropanoids, flavonoid, flavonoid chalcones), hormone metabolism gibberellin (synthesis and degradation), RNA processing (miscRNA), lipid transfer protein (LTP), RNA regulation of transcription *C2C2(zn) co-like constans-like zinc finger* family genes, and genes involved in RNA regulation of transcription *MADS-box* transcription factor family. Other genes involved in protein targeting process were also

Table 2. Significantly regulated biological processes (FDR < 0.05) that are uniquely regulated transcriptomic studies

GO_ID	Description	Count	*P*-value	Expression
	Unique genes in drought			
GO:0015992	Proton transport	3	0.032473	Down
GO:0045087	Innate immune response	9	0.00227	Up
GO:0015979	Photosynthesis	13	0.003343	Up
GO:0006096	Glycolytic process	8	0.011903	Up
GO:0007169	Transmembrane receptor protein tyrosine kinase signalling pathway	11	0.015973	Up
GO:0008652	Cellular amino acid biosynthetic process	7	0.033405	Up
GO:0009768	Photosynthesis, light harvesting in photosystem I	4	0.040003	Up
	Unique genes in cold			
GO:0006874	Cellular calcium ion homeostasis	3	0.03036	Up
GO:0006816	Calcium ion transport	3	0.0322	Up
	Unique genes in heat			
GO:0008152	Metabolic process	10	1.39E-05	Down
GO:0009813	Flavonoid biosynthetic process	5	5.08E-03	Down
GO:0052696	Flavonoid glucuronidation	4	0.016338	Down
GO:0009992	Cellular water homeostasis	3	0.010365	Up
GO:0006457	Protein folding	5	0.03212	Up

downregulated by drought stress. In contrast, aromatic amino acid metabolism genes, protein degradation *ubiquitin ligases HECT* genes, genes involved in signalling, in light signalling and key genes encoding major intrinsic proteins such as those encoding tonoplast (*TIPs*), where upregulated by drought. Heat stress enhanced specifically key genes implicated in ubiquitin-mediated protein degradation and repressed *glutaredoxin* genes. Cold stress upregulated key genes implicated in RNA regulation, and involved in initiation of protein synthesis, and encoding MAP kinases signalling pathways.

Biological process enrichment analysis

DAVID software was used to identify the gene ontologies (biological process, cellular component, molecular function) that were significantly affected by the three types of abiotic stresses. Metabolic pathways were divided into those up- or downregulated by drought, and gene-onthology (GO) ID, GO terms, count and *P*-values are shown in Table 2. We identified GO terms that were upregulated by drought such as innate immune response, photosynthesis, photosynthesis, light harvesting in PSI, glycolytic process, transmembrane receptor protein tyrosine kinase signalling pathway and cellular amino acid biosynthetic process. In contrast, proton transport was downregulated in response to water stress. Heat stress downregulated GO terms related to metabolic process, flavonoid biosynthetic process and flavonoid glucuronidation, but upregulated those related to cellular water homeostasis and protein folding. Cold stress enhanced cellular calcium ion homeostasis and calcium ion transport.

Protein–protein network analysis

The protein–protein interaction (PPI) network analysis was comprised of unique genes from each of the abiotic stress selected for our study. Minimum default settings were used to reduce the number of interacting proteins and the complexity of the networks (Fig. 6). Some key genes with a high number of interactions were highlighted (see Table S1, available as Supplementary Material to this paper). Among the upregulated hub (highly interacting) proteins we noted some key proteins that may play a key role in drought response such as *HLL*, *RPS12C*, *RPS4D* and *RPP0A*. Further, drought downregulated highly interactive proteins such as *RPS30C*, *RPL24* and *RPS19*. PPI network analysis was performed for unique genes in cold stress, and showed a downregulation in *IAA34*, *IAA9* and *IAA20* and an upregulation in *ARF5* and *IAA3*. Among the genes uniquely modulated by heat, we could find only upregulation in *MRPL11*, *RPS3C*, *RPL10AC*, *RPS7B* and *RPS2D*.

Discussion

The number of plant transcriptomic works published in the last few years has been increasing, and more meta-analysis studies are required to investigate the mechanisms of highly threatening effects of climate changes on agriculture, especially those in under-developing regions. In addition, most of these transcriptomic studies have been performed in only one season and using different agronomic, developmental and physiological conditions, weakening, thus, the data reliability is questionable.

The present study was conducted in order to shed light onto the abiotic stress response mechanisms in plants, and to identify specific responses to each abiotic stress condition. It was hoped that the identification of commonalities between similar independent studies would help us discover the most associated genes to the subject of the study and allow us to focus on the functional analysis only on those common findings (Benny *et al*. 2019*a*). Available RNA-Seq datasets related to abiotic stress responses in leaf tissues were used in order to deliver functional genomic information linked with

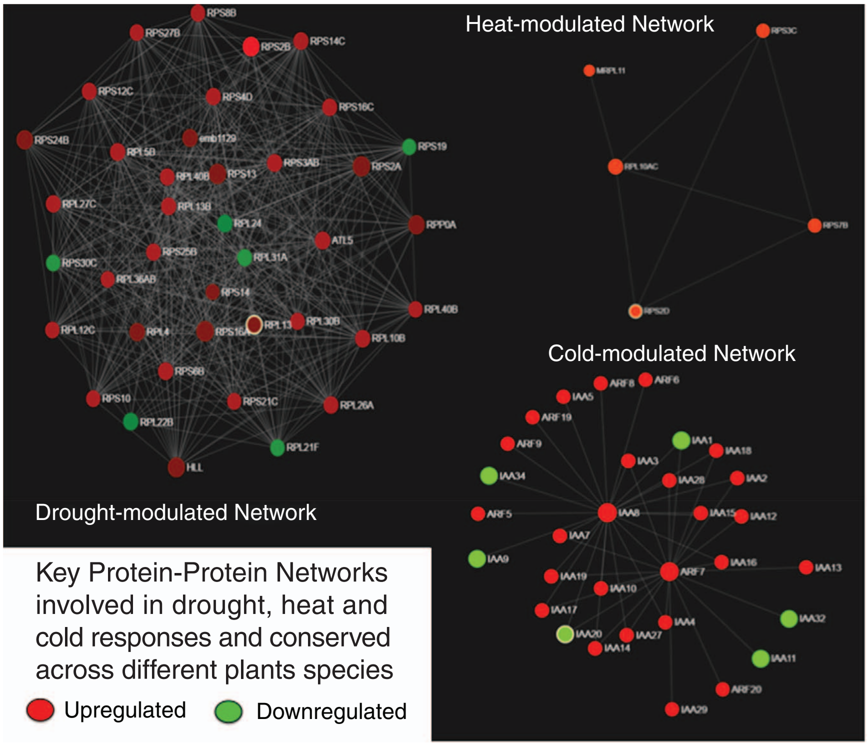


Fig. 6. Protein–protein network analysis is shown using STRING software among uniquely differentially regulated genes in response to drought, cold and heat. Key highly interactive proteins are indicated. Red indicates upregulation and green indicates downregulation by each stress.

exclusive molecular responses to specific types of abiotic stresses. The selection of papers included in the meta-analysis was based on four points. First, the type of tissue subjected to the transcriptomic analysis: we selected studies related to leaves but excluded studies concerned with other tissue types. Second, the availability of raw data (many of the published papers that we selected, the raw data were unavailable). Third, the type of stress: we focussed on the most significant abiotic stresses affecting crops today, these being drought, salt, heat and cold stress. Finally, the read alignment of the reference genome had to be of sufficient quality (i.e. have a high percentage of read annotation, mapping and homology with correspondent *Arabidopsis* orthologue).

These selection criteria resulted in 10 transcriptomic studies dealing with the chosen abiotic stress factors among a number of species. Similar meta-analyse of transcriptomic data have been conducted in single plant species including as *A.s thaliana* (Rest *et al*. 2016), rice (Muthuramalingam *et al*. 2017) and sunflower (Ramu *et al*. 2016*a*).

Transcription factors

Regarding transcription factors, our study revealed that drought stress significantly upregulated three *APETALA2/ethylene-responsive element binding protein* (*AP2/EREBP*) transcription factors (*AP2 domain containing transcription factor*, *PLT1* and *TINY*), whereas two of them (*ACA4*, *ERFs*) were induced by cold stress. *AP2/EREBP* family of transcription factors are well known to be involved in various environmental stresses responses including biotic and abiotic stresses such as pathogen infection, drought salinity and temperature (Dietz *et al*. 2010; Liu and Zhang 2017; Balan *et al*. 2018). Sun *et al*. (2008) reported that the expression of *TINY*, a *DREB-like factor* was induced by drought stress in *Arabidopsis*, and suggested that *TINY* plays a role in the cross-talk between biotic and abiotic stress-responsive gene expressions by connecting the DRE- and ERE-mediated signalling pathways (Sun *et al*. 2008). Previous studies have reported that overexpression of *ERF* family genes increases tolerance to a wide range of abiotic stresses in different plant species such as *Arabidopsis*, rice, tomato and tobacco (Park *et al*. 2001; Aharoni *et al*. 2004; Guo *et al*. 2004; Zhang and Huang 2010; Schmidt *et al*. 2013). These observations are in agreement with our data. We found that one *MADS box transcription factors* (*AGL42*) was induced by drought, whereas two of them (*AGAMOUS-LIKE 12*, *AGAMOUS-LIKE 19*) were repressed in response to heat. *MADS-box* genes are known to be key players in many developmental processes in plants such the flower development and floral induction (Causier *et al*. 2002), as well as crucial regulators in response to abiotic stresses (Gupta *et al*. 2012). However, *MADS-box* genes are also important molecular regulators of plant responses to low temperature, photoperiod and plant hormones such as cytokinin, ethylene and gibberellins (Lozano *et al*. 1998; Ando *et al*. 2001; Duan *et al*. 2006; Lee *et al*. 2008; Li *et al*. 2016). In addition, Jia *et al*. (2018) suggested a probable involvement of *LcMADS1*, *LcMADS2*, *LcMADS3*, *LcMADS7* and *LcMADS9* genes in abiotic stress responses in sheep grass (Jia *et al*. 2018). Indeed, *LcMADS1* and *LcMADS2* genes were significantly upregulated by cold stress, *LcMADS3* gene was upregulated in response to mannitol and ABA and *LcMADS9* was induced by salt stress (Jia *et al*. 2018). In *Oryza sativa*, *OsMADS26*, an *AGL12*-class gene, have been reported to be involved in drought tolerance (Khong *et al*. 2015). These data partially agree with our meta-analysis, which showed that *AGL42*, *AGAMOUS-LIKE 12*, *AGAMOUS-LIKE 19* may be crucial regulators involved in abiotic stress responses.

Our meta-analysis revealed that *WRKY22* and *WRKY51* are drought-regulated genes conserved across different plant species. *WRKY* family is well known to play important roles in abiotic stress responses, including, salinity (Niu *et al*. 2012; Liang *et al*. 2017), drought (Luo *et al*. 2013; Sun *et al*. 2015; Li *et al*. 2017*b*) oxidative stress (Yan *et al*. 2014), nutrient stress (Chen *et al*. 2009; Su *et al*. 2015; Dai *et al*. 2016), heat (Cai *et al*. 2015; He *et al*. 2016) and pathogen infection (Liu and Bai 2005; Mao *et al*. 2011; Chen *et al*. 2013; Dey *et al*. 2014). Sanchita *et al*. (2014) reported that *WRKY51* was found to have differential expression under abiotic stresses whereas *WRKY22* and *WRKY51* were enhanced by drought and cold stresses in Chiifu *Brassica rapa*. In addition, it was reported that *WRKY51* enhanced the lateral root formation in response to abiotic stresses or nutrition in wheat (Hu *et al*. 2018).

MYB family is a well-known TF category that plays a major role in organ development, regulation of primary and secondary metabolism, flavonoid biosynthesis and response to various biotic and abiotic stresses (Jin and Martin 1999; Li *et al*. 2015; Qi *et al*. 2015). However, the large number of members of this family makes identification of orthologs commonly regulated by each abiotic stress across plant species very difficult. Our results showed that four *MYB* factors (*MYB6*, *MYB12*, *MYB78* and *MYB71*) were enhanced in response to water deprivation whereas two (*MYB111* and *MYB66*) were repressed. In contrast, cold stress enhanced *MYB7*. Many studies reported the induction of *MYB* factors under drought conditions (Clauw *et al*. 2015; Li *et al*. 2017*a*; Benny *et al*. 2019*a*). Thus, the overexpression of *MYB1* enhanced drought resistance in transgenic *Arabidopsis* plants (Dai *et al*. 2007), and it was also reported that both *MYB96* (Lee *et al*. 2014, 2016) and *MYB94* (Lee *et al*. 2016) activated cuticular wax biosynthesis in *A. thaliana*. Additionally, Lee *et al*. (2014, 2016) suggested that these genes might play important role in drought stress responses in plants via activating this adaptive mechanism. We found that flavonoid pathways were modulated by each abiotic stress. In this regard, *MYB12* has shown to increase flavonol biosynthesis and accumulation, which contributes to reduced water loss and enhanced drought tolerance in *Arabidopsis* (Nakabayashi *et al*. 2014). Further, two *MYBS* in our meta-analysis (*MYB12* and *MYB111*) were found to be regulated by different light spectra in the turnip *B. rapa*, suggesting roles in light stress responses in addition to drought (Wang *et al*. 2012). Moreover, the *MYB7* played a key role in the ABA-mediated regulation of salt and osmotic stress via *ABA insensitive 5* (*ABI5*). In fact, *MYB7* repressed *ABI5* expression during seed germination, positively influenced the content of anthocyanins (which are crucial pigments in the abiotic stress responses), and positively regulated the lateral root growth under salinity (Kim *et al*. 2015; Skubacz *et al*. 2016). Ruan *et al*. (2018) reported that *MeMYB111* transcription factor was responsive to ABA, drought and cold stresses in cassava leaves, and suggested that this gene might has a role in ABA signalling during abiotic stress responses. Four *HOMEOBOX* genes (*HB6*, *HB13*, *KNAT7* and *HAT3.1*) were enhanced under drought, conditions, whereas *HOMEOBOX3* was repressed in response to heat. Our results suggest that *homeobox* genes *HB6*, *HB13*, *KNAT7* and *HAT3.1* may be involved in drought responses, whereas *HOMEOBOX3 TF* may be involved in heat responses. In rice, it was found that *OsHOX22*/*OsHOX24* homeobox proteins might be considered as negative regulators in abiotic stress responses (Bhattacharjee *et al*. 2016). *KNAT7* is a component of a transcription network regulating secondary cell wall biosynthesis, whose function remains unclear, although in *Arabidopsis*, *KNAT7* is considered as a negative regulator of secondary wall biosynthesis (Li *et al*. 2012). *HAT3.1* was one of the first transcription factors discovered with the typical PHD finger domain in plants (Schindler *et al*. 1993). Later, 45 others of this type of TFs were identified in *Arabidopsis*, 44 in rice (Feng *et al*. 2004) and 67 in maize (Wang *et al*. 2015). These large families play diverse roles during plant growth and development. *Arabidopsis PHD-domain ALFIN1-like protein*s were shown to promote seed germination (Molitor *et al*. 2014), and in *Arabidopsis*, they are involved in regulating flowering by modifying the *SOC1/FT* chromatin conformation (López-Gonzalez *et al*. 2014). It has been also suggested that *MS1* – another member of this family – plays a key role in pollen development (Fernández Gómez and Wilson 2014). However, the literature on these TFs is huge, so the role of this type of TF in environmental stress responses is yet to be fully elucidated. Wei *et al*. (2009) reported that the expression of six *GmPHDs* was induced by drought stress in soybean. Among them, *GmPHD4/5* expression was enhanced under cold stress conditions, whereas *GmPHD2/5* was identified to regulate salt stress responses (Wei *et al*. 2009; Wu *et al*. 2011). In maize, 15 of 67 *ZmPHDs* were revealed to respond to abiotic stresses, such as drought and salinity (Wang *et al*. 2015). Moreover, nine *PtPHDs* were differentially expressed under drought, salt and cold stresses (Wu *et al*. 2016). Sun *et al*. (2017) reported differential expression of *OsPHDs* gene under environmental stresses in rice, including ABA (abscisic acid), water deficit, cold and high cold (Sun *et al*. 2017). *OsPHD1/7/8/13/33* were differentially expressed under drought and cold stresses, *OsPHD5/17* were downregulated under water deficit and cold stresses whereas *OsPHD3/44/28* showed differential expression under Cd and ABA stresses (Sun *et al*. 2017).

We found that four bZIP members (*TGA1*, *HY5-Homologue*, *TGA6* and an uncharacterised *bZIP TF*) were induced by drought, three of them (*bZIP 9*, *bZIP TFs*, *BZO2H1*) were enhanced by cold stress and one was enhanced by heat. These results suggest a possible role of this TF family in abiotic stress responses. Xu *et al*. (2016) reported that the overexpression of *bZIP TF* (*ZIP110*) improved salt tolerance in soybean suggesting its role as a positive regulator involved in salt stress tolerance. In addition, functional analysis of *GmbZIP110* have found in regulating many downstream target genes by binding to the ACGT motif in *A. thaliana* (Cao *et al.* 2017). In potato (*Solanum tuberosum*), the overexpression of a hot pepper *bZIPlike transcription factor CaBZ1* in transgenic plants improved drought stress tolerance (Moon *et al.* 2015). Hence, in transgenic alfalfa (*Medicago sativa*), the overexpression of *ABF3* using sweet potato oxidative stress-inducible promoter *SWPA2* improved growth under water deprivation (Wang *et al.* 2016). We found that three genes encoding *bHLH TFs* (an uncharacterised *bHlH protein*, *ICE1* and *ILL3*) were enhanced under drought whereas one was downregulated. A previous study identified *TGA1* and *TGA4* transcription factors as putative regulatory factors that mediate nitrate responses in *Arabidopsis* roots (Alvarez *et al.* 2014). A recent study highlighted that *bHLH* genes are related to biotic and abiotic stress tolerance in wheat (Wang *et al.* 2019).

For hormone-related pathways, our results show that drought stress specifically enhanced genes involved in ethylene-related pathways (biosynthesis, signalling, response), which is known to play an important role in activating plant responses to water deprivation and flooding (Lee *et al.* 2009; Ramu *et al.* 2016*b*). Ethylene is responsible in activating signals affiliated with the synthesis of many transcription factors that controls the gene activation/ repression during stress such as the ethylene response factor *ERF1* (Bastola *et al.* 1998; Young *et al.* 2004; Seo *et al.* 2010). In *A. thaliana*, *ERF1* has been shown to be induced by both salinity and drought stresses (Cheng *et al.* 2013); however, the present study showed that the *ERF1* is induced in leaves only by drought stress. Similar results were found previously, confirming that *ERF1* is upregulated in mature leaves of different crops under drought conditions (Song *et al.* 2017; Benny *et al.* 2019*a*). Brassinosteroids represent another class of plant growth regulators (Adam and Marquardt 1986) for which related genes are differentially regulated in response to drought. Studies have reported that brassinosteroids (BRs) mediate abiotic stresses such as salinity, heat and drought (Clouse and Sasse 1998). Our results show that some brassinosteroids such as *3-oxo-5-α-steroid 4-dehydrogenase*, *STEROL 1* and *DWARF 5* were upregulated, whereas two (*cycloartenol synthase 1* and *brassinosteroid insensitive 1*) were repressed. There results agree with previous findings showing the induction of *3-oxo-5-α-steroid 4-dehydrogenase* in rice roots under drought conditions (Muthurajan *et al.* 2018).

Gibberellins are one of the most important groups of phytohormone in plants for the modulation of growth and development (Bari and Jones 2009). According to our study, a number of gibberellin-related genes show opposite trends of expression. For example, *GASA1*, *gibberellins 2-oxidase 1* and *2-oxoglutarate-dependent dioxygenase* were downregulated by the effect of drought, but gibberellin (*RGA1*) was upregulated by cold. Similar results have been found by Zhu (2016), which suggests a putative interaction between *RGA1* and a cold stress sensor required for chilling tolerance (Ma *et al.* 2015; Zhu 2016). Moreover, *GASA1* seems to play an important role under both abiotic (puffing) and biotic (Huanglongbing) stresses in citrus peel tissues (Martinelli *et al.* 2015). Our results indicate that the drought stress alters GA metabolism and signalling: GA signalling is reduced in response to cold, salt and osmotic stresses (Colebrook *et al.* 2014). Drought and high salinity increased the expression of three breadfruit *GA2-oxidase* genes (*AaGA2ox1*, *AaGA2ox2* and *AaGA2ox4*) and their possible involvement in abiotic stress response resistance was discussed by Zhou and Underhill (2016). The *2-oxoglutarate-dependent dioxygenase* (*2OGD*) superfamily represents the second largest enzyme family in the plant genome whose members are involved in various oxygenation/hydroxylation reactions. In addition, *2-oxoglutarate-dependent dioxygenase* gene may be involved in chilling stress responses in tomato by regulating JA accumulation and the expression of genes related with JA biosynthetic and signalling under chilling stress (Hu *et al.* 2019). The phytohormone ABA is known as important factor in plant growth and development in response to various environmental conditions including drought stress (Riemann *et al.* 2015). The main function is the control of stomata opening and closure to reduce water loss via transpiration (Wilkinson and Davies 2010; Mittler and Blumwald 2015). The induction of ABA synthesis presents one of the fastest phytohormonal responses to abiotic stresses, thereby triggering ABA-inducible gene expression (Yamaguchi-Shinozaki and Shinozaki 2006). Shinozaki and Yamaguchi-Shinozaki. (2007) also showed that in plants, high salinity or drought stress causes ABA accumulation and obvious changes in genes expression. Nevertheless, we showed that cold stress upregulated a GRAM domain containing protein involved in ABA-related pathways. The GRAM domain has ~70 amino acids, a length usually found in glucosyl transferases and other membrane-associated proteins (Doerks *et al.* 2000). Generally, this domain seems to be involved in membrane-associated processes such as intracellular protein- or lipid-binding signalling pathways (Doerks *et al.* 2000).

In relation to heat stress, our meta-analysis highlighted an enhanced expression of a genes involved in IAA (*non-phototrophic hypocotyl*) response. The phytohormone auxin, IAA, plays an important role in a plant's responses to abiotic stresses (Bari and Jones 2009). IAA also plays a crucial part in the adaptation of plants to salinity (Iqbal *et al.* 2014; Fahad *et al.* 2015), and participates in increasing the growth of root and shoot of plants under heavy metal or salinity stresses (Sheng and Xia 2006; Egamberdieva 2009). Salinity has been reported to reduce IAA levels in plants such as maize (Fahad and Bano 2012). In fact, auxin tends to enhance the transcription of several genes called primary auxin response genes, which have been characterised and identified in many plant species such as soybean, rice and *Arabidopsis* (Javid *et al.* 2011). Thus, auxins present a powerful constituent in the defence responses via many gene regulations and crosstalk mediation (Bari and Jones 2009; Ghanashyam and Jain 2009). PPI networks highlighted the role played by auxin-related genes in cold responses and particularly *ARF7* and *IAA8*, which were shown to be at a core position of network composed by several auxin-related genes.

The phytohormones jasmonates (JAs) represent signalling molecules that regulate plant growth and orchestrate systemically and locally the responses to many abiotic stress factors (Turner *et al*. 2002; Pauwels *et al*. 2009). Many studies have shown that JA levels are increased after drought and salt stresses exposure (Creelman and Mullet 1995; Wang *et al*. 2001). Further, experiments conducted on rice leaves and roots exposed to drought and salinity showed an increased content of JAs, and induced JA biosynthesis genes (Moons *et al*. 1997; Tani *et al*. 2008). Another study reported that the content of jasmonates is enhanced by sorbitol treatment to a degree enough to initiate JA-responsive gene expression (Kramell *et al*. 2000). The present study corroborates these previous results and showed the enhancement of two key genes involved in jasmonate genes that were also upregulated by drought stress. Moreover, under drought stress, endogenous JA content increased in maize root cells (Xin *et al*. 1997). Nevertheless, the main function of JA in drought stress remains unclear and controversial, since in some studies JA has been reported to improve the tolerance whereas it caused a reduction in growth in other works. This may be explained by the fact that the responses to drought conditions depend generally on the type and tissue of plant studied, the duration and intensity of the stress applied, and the dosage of JA applied (Lee *et al*. 1996; Kim *et al*. 2009).

Primary and secondary metabolism

It was reported that the overexpression of *solanesyl diphosphate synthase 1* (*SPS1*) enhanced tolerance to photo-oxidative stress in *Arabidopsis* plants, which was related to their increased capacities for plastoquinone-9 biosynthesis (Ksas *et al*. 2015). Our work also revealed that drought stress repressed fatty acid biosynthesis in leaves. Another primary metabolism pathway that was repressed by drought stress in leaves was phospholipid biosynthesis. Benny *et al*. (2019*a*) reported that two genes involved in phospholipid biosynthesis (*phosphatidylserine synthase* and *galactolipid galactosyltransferase*) were repressed under drought, and that water deficit inhibits fatty acid desaturation. Another previous study associated with drought resistance in cotton also produced a reduction of fatty acid metabolism that results in greater stability of the membrane system (Thi *et al*. 1985).

Our results showed an upregulation of different categories of genes involved in secondary metabolism and selectively regulated by drought, salinity, heat and cold. Indeed, these stress-related genes come under the MVA pathway, which is known to be responsible for terpenoid biosynthesis and comprises a series of metabolites with peculiar protection roles to biotic attacks (Tholl 2015). In addition, as chemical signals, several volatile sesquiterpenes are implied in activating plant defence mechanisms to respond to biotic stresses. Terpenoids are widespread in plants and are expected to have played an important role in plant evolution as response to different biotic and abiotic aspects (Balan *et al*. 2017). Flavonoids are also crucial in defence against environmental stress such abiotic and biotic stresses. Nakabayashi *et al*. (2014) showed that flavonoids played an important role as a mitigator of oxidative and drought stress in *Arabidopsis*. These molecules are the most abundant hydrophilic antioxidants in fruits, and display significant biological activities in humans including an important role in the prevention of human disease and maintaining of good health (Peluso *et al*. 2018). Flavonoids and anthocyanins are found in many fruits and vegetables, and most of them are coloured compounds found especially in red fruits including grape skins, pomegranate, loquat, blueberries and red cabbages (Rop *et al*. 2010; Gentile *et al*. 2016; Passafiume *et al*. 2019; Mannino *et al*. 2020). Our results confirmed that drought stress enhanced flavonoids whereas heat stress repressed most flavonoid-related genes (*i.e. aldo-keto reductase*, *TRANSPARENT TESTA70*). It has been reported in previous studies that *aldo-keto reductase* activity and gene expression increased with osmotic and salt stress and abscisic acid (ABA), which plays a key role in abiotic stress responses in rice, wild oats, barley and *Xerophyta viscosa* (Li and Foley 1995; Roncarati *et al*. 1995; Mundree *et al*. 2000). *AKR* gene expression increased in bromegrass under low temperature exposure and ABA treatment suggesting a role of *AKR* enzymes in cold stress tolerance (Lee and Chen 1993). *AKR* gene expression also increased with various other abiotic stress factors including heat, drought, heavy metals and UV-B in digitalis and alfalfa (Oberschall *et al*. 2000; Gavidia *et al*. 2002; Hideg *et al*. 2003; Hegedüs *et al*. 2004). An over-induction of *aldo-keto reductase* was previously linked to oxidative and heat stress tolerance in rice (Turóczy *et al*. 2011). In the same way, expression of phenylpropanoid genes was induced by drought and cold but repressed by heat. The protective roles that are played by phenylpropanoid in plants against both biotic and abiotic stresses are well known (Liu and Osbourn 2015). This beneficial activity is due to the inhibition of the formation of reactive oxygen species (ROS) as reported by Commisso *et al*. (2016).

In this context, carotenoids are antioxidant molecules that protect plants from photo-oxidative processes, performing an effective scavenging action against ROS. Carotenoids are natural pigments with polyisoprenoid structure known to play important roles in plants as antioxidants and constitute photosynthetic organelles present in all the superior plants, mosses, ferns and algae resulting attractants for pollinators and seed dispersers for plants (Cazzonelli 2011; Khoo *et al*. 2011). Generally, these molecules are involved in photosynthesis and photoprotection. Carotenoids are not synthesised by humans and animals, so a diet consisting of fruits and vegetables provide the only contribution of exogenous carotenoids (Massenti *et al*. 2015; Perrone *et al*. 2016). They can work in different ways to improve health or to slow down a detrimental pathological state, thus counteracting oxidative stress (Perrone *et al*. 2014, 2016). They have a fundamental role in counteracting oxidative stress in humans and animals. In clinical and research settings, carotenoids in the blood or tissues can be detected after dietary intake (Perrone *et al*. 2016; Peluso *et al*. 2018). Therefore, plasma carotenoids or skin carotenoids may be a suitable indicator of total antioxidant status (Massenti *et al*. 2015; Perrone *et al*. 2016). Regarding their specific role in plants, a recent function for carotenoids has recently emerged and relates to the response of plants to environmental stresses. ROS can oxidise carotenoids and produce reactive electrophilic species (RES), characterised by a carbonyl function adjacent to a double bond that is able to react with nucleophilic atoms (such as S and N) common to many biological molecules such as thiols (Farmer and Mueller 2013). Consequently, thiol modification by these electrophilic lipids (RES) could activate transcription factors, thus inducing gene responses (Levonen *et al*. 2004). RES or oxidation of β carotenoids derivatives are potential signal molecules, the concentration of which increases in plants exposed to environmental stress (such as heat stress). For example, oxidised carotenoid molecules exogenously have been shown to influence the transcription of genes involved in cell survival and stress responses (Loeffler *et al*. 2005). The dominant gene families encode *glutathione-S-transferases* (*GSTs*), *UDP-glucosyl transferases*, *cytochrome P450* and *transporters*. The genes downregulated by the RES affected cell wall, cell division and auxin signalling. Furthermore, carotenoid oxidation molecules are bioactive compounds, and products derived from the enzymatic oxidation of carotenoids possess important signalling functions in plants. The abscisic acid hormone is an example of a molecule derived from the enzymatic oxidation of neoxanthin (Nambara and Marion-Poll 2005) that is involved in the response of plants to the environment stress and to pathogens, and also plays a role in seed germination, in the early development of the embryo and in stomatal regulation. Our research group has identified that the *carotenoid cleavage dioxygenase 1* (*CCD1*) was upregulated under drought stress. The gene that encoding the enzyme was involved in apocarotenoid biogenesis molecule of 20 or 27 atoms of C that originated from the oxidation of β carotene. Photosynthesis can be inhibited by high concentrations of carotenoid RES (Shao *et al*. 2011). In this regard, our results confirm that the *NON-PHYTOCHEMICAL QUENCHING* gene was downregulated by drought stress.

We observed that genes involved in lignin and lignans (*mannitol dehydrogenase* and *CINNAMYL ALCOHOL DEHYDROGENASE 6*), phenylpropanoids and glucosinolates were mostly repressed by heat stress. This evidence is well documented in published literature (Moura *et al*. 2010). Commisso *et al*. (2016) reported that the levels of most metabolites declined sharply after heat stress as result of cell death and subsequent metabolite degradation due to protein denaturation and aggregation, affect the RNA stability, membrane fluidity and integrity (Wahid *et al*. 2007). In contrast, two metabolites, *CINNAMYL COA REDUCTasE 1* (*CCR1*) and *ISOPENTENYL PYROPHOSPHATE*, were increased after heat stress (Wahid *et al*. 2007), but cold stress enhanced genes involved in terpenoid (*terpene synthase 21* and *solanesyl diphosphate synthase 1*) and in alkaloids (*STRICTOSIDINE SYNTHASE*). Previous work has highlighted the increase of *CCR* under different stress conditions such as wound or pathogen infection (Lauvergeat *et al*. 2001; Kawasaki *et al*. 2006). Nevertheless, the precise molecular role of lignin biosynthesis genes in abiotic stress remains unclear. Hence, several hypotheses have been proposed, the most accepted of which is that lignin-related enzymes such as CCR are associated with the drought and salt stress tolerance mechanisms (Chazen and Neumann 1994; Kawasaki *et al*. 2001; Kim *et al*. 2007; Lee *et al*. 2007). Taken together, these findings suggest that *CCR1* is closely associated to heat stress responses. Concerning the *terpene synthase*, Lee *et al*. (2015) showed that rice *terpene synthase 20* (*OsTPS20*) plays a major role in producing terpene volatiles during the abiotic stress (Lee *et al*. 2015). Another recent study identified three new *terpene synthase* genes in *Santalum* spp., demonstrating that *TPS1* play important roles in chemical defence and in protection against light and temperature stress (Zhang *et al*. 2019).

Conclusion

The meta-analysis presented here provides insights into molecular regulatory networks controlling resistance/tolerance/susceptibility to four major abiotic stresses in plants. It does not provide definitive information that could be quickly transferred in molecular tools for crop breeding, but future work will involve mapping in each crop chromosomes through ongoing projects of re-sequencing using the exponential progresses of next-generation sequencing technologies. This essential work will speed up the delivery of molecular markers for sustainable agronomic approaches for a future agriculture that will be needed to address the detrimental effects of a rapid climate change. Essential insights into the hormonal crosstalk modulating simultaneous abiotic stress responses were provided: upregulation of jasmonate-related genes was linked to drought, whereas gibberellin repression was downregulation by drought and heat. Cold stress induced genes involved in ABA, cytokinin and gibberellins. In relation to transcription factors, we found that different categories are involved in specific responses to abiotic stresses: *AP2-EREBP*, *MADS*, *WRKY22*, *MYB*, *homoebox* genes members were linked to drought stress whereas cold stress was associated to induction of *MYB7* and *BELL 1*. Heat repressed *C2C2-CO-LIKE*, *MADS* and *HOMEOBOX3*. Finally, the key findings of our meta-analysis were that (1) ubiquitin-mediated protein degradation is induced by heat, and (2) that cold stress upregulates *MAP kinases*.

Conflicts of interest

The authors declare no conflicts of interest.

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