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Identification and characterisation of blue light photoreceptor gene family and their expression in tomato (*Solanum lycopersicum*) under cold stress

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ABSTRACT

The *Arabidopsis thaliana* L. photoreceptor genes homologues in tomato (*Solanum lycopersicum* L.) genome were analysed using bioinformatic tools. The expression pattern of these genes under cold stress was also evaluated. Transcriptome analysis of the tomato sequence revealed that the photoreceptor gene family is involved in abiotic stress tolerance. They participate in various pathways and controlling multiple metabolic processes. They are structurally related to PAS, LIGHT-OXYGEN-VOLTAGE-SENSING (LOV), DNA photolyase, 5,10-methenyl tetrahydrofolate (MTHF), flavin-binding kelch F-box, GAF, PHY, Seven-bladed β-propeller and C27 domains. They also interact with flavin adenine dinucleotide (FAD), (5S)-5-methyl-2-(methylsulfanyl)-5-phenyl-3-(phenylamino)-3,5-dihydro-4H-imidazol-4-one (FNM) and Phytochromobilin (PϕB) ligands. These interactions help to create a cascade of protein phosphorylation involving in cell defence transcription or stress-regulated genes. They localisation of these gene families on tomato chromosomes appeared to be uneven. Phylogenetic tree of tomato and *Arabidopsis* photoreceptor gene family were classified into eight subgroups, indicating gene expression diversity. Morphological and physiological assessment revealed no dead plant after 4 h of cold treatment. All the plants were found to be alive, but there were some variations in the data across different parameters. Cold stress significantly reduced the rate of photosynthesis from 10.06 to 3.16 μmol m^{-2} s^{-1}, transpiration from 4.6 to 1.3 mmol m^{-2} s^{-1}, and stomatal conductance from 94.6 to 25.6 mmol m^{-2} s^{-1}. The cold stressed plants also had reduced height, root/shoot length, and fresh/dry biomass weight than the control plants. Relative expression analysis under cold stress revealed that after 4 h, light stimulates the transcript level of Cry2 from 1.9 to 5.7 and PhyB from 0.98 to 6.9 compared to other photoreceptor genes.

Keywords: abiotic stress tolerance, bioinformatics, blue light signaling, expression analysis, photoreceptor genes, photosynthesis, tomato, transcriptome data.

Introduction

Tomato (*Solanum lycopersicum* L.) is one of the most popular vegetable species grown world-wide because of its taste, colour, flavour, and nutrient contents. It may be eaten fresh or processed (Shah *et al.* 2021). It contributes to a healthy, well-balanced diet as it has a few calories and is a source of vitamin A, vitamin C, and minerals (Elbadrawy and Sello 2016). It provides small amounts of the vitamin B complex, such as thiamine, riboflavin, niacin, and iron. Recent studies suggest that lycopene reduces the risk of prostate cancer (Fraser *et al.* 2020). Consumption of tomatoes can reduce the risk of developing gastroenteric diseases, such as colon, rectal, and stomach cancer. Finally, it is easily digestible, and its bright colour stimulates appetite (Zhu *et al.* 2020).

Above all these derivable health and nutritive benefits from tomato, its cultivation has been constrained by biotic and abiotic stress. Climate change and poor irrigation quality have aggravated and exposed plants to these stresses, resulting in morphological,

physiological, and molecular changes (Ostmeyer *et al.* 2020). These stresses adversely affect the quantity and quality of its yields. Plant response to abiotic stressors necessitates an understanding of the expression of certain stress-related genes. This is a complicated molecular networking that has not received much attention. Therefore, there is a need for more understanding on the contribution of these genes in response to cold stress (Allwood *et al.* 2021).

Cold stress poses a serious threat to crop yield sustainability as it restricts the geographical distribution and growing season of many plant species. In general, plants respond to cold stress by displaying many phenotypic symptoms such as poor germination, death of tissues or necrosis, stunting of seedlings, leaf yellowing and wilting among others. During reproductive stage of plants, cold stress can cause pollen sterility and delays heading, which is thought to be one of the primary factors causing crop yield reductions, as seen in the case of rice (*Oryza sativa* L.) plants during anthesis (floral opening) (Solanke and Sharma 2008). It also has also been shown that this stress can cause significant damage to plasma membranes in plants and affects nearly every aspect of plant cellular functions. Membrane disintegration is a major contributor to cold stress-induced dehydration. Such changes caused by cold stress have a negative impact on plant growth and development. As any type of environmental stimulus is sensed by receptor/osmosensor molecules, the signal is perceived and transmitted to the appropriate signal transduction pathways such as photoreceptor genes (Yadav 2010).

Photoreceptors are photo-reversible proteins that sense changes in light intensity using an intrinsic amino acid (tryptophan) or a prosthetic group/cofactor as a chromophore (Puggioni 2020). They affect plant growth and developmental mechanisms such as in de-etiolation, blooming initiation, photomorphogenesis, hormone signalling, and stress responses (Sancar 2003; Ahmad 2016). Some of them are present in the nucleus and actively or indirectly control more than 20% of total cellular transcripts (Jiao *et al.* 2007; Phee *et al.* 2007). Many studies have reported that these genes influence plant signalling pathways in response to biotic (insects and herbivory) and abiotic (high temperatures, UV-B radiation, salt, and drought) stressors (Ballaré 2009; Carvalho *et al.* 2013; D'Amico-Damião *et al.* 2015; Gavassi *et al.* 2017). Blue light photoreceptors in plants are basically the cryptochromes and phototropins. Understanding the mechanisms of blue light photoreceptor genes in plant responses to abiotic challenges is critical to accelerating the development of novel strains with improved stress tolerance. For example, Crys are flavoproteins that have a conserved N-terminal light sensing domain (PHR domain) and a comparatively less conserved C-terminal domain (designated CCE) of varying length that is required for light signalling and nuclear localisation (Chaves *et al.* 2011). In the PHR domain, Crys have two chromophores: the 5,10-methenyl tetrahydrofolate (MTHF) and the flavin adenine dinucleotide (FAD) (photomorphogenesis-inducing blue light chromophore) (Vishwakarma *et al.* 2017). Under blue light, Crys genes have been found to interact with proteins such as the WD-repeat protein SPA1, phytochromes (PhyA and PhyB), the E3 ubiquitin ligase COP1, and the bHLH transcription factors CIB in mitigating abiotic stress in *Arabidopsis thaliana* L. (Ahmad 2016). They are reckoned to have a complicated mechanism of action. Recent studies have shown that they play a function in the production of reactive oxygen species (ROS) under blue light (Consentino *et al.* 2015; Jourdan *et al.* 2015; El-Esawi *et al.* 2017). This is a key signalling pathways for abiotic stress-related genes whose transcription is regulated by ROS (Suzuki and Katano 2018). However, the processes that control cryptochrome during drought stress remain unknown because they are dependent on several variables, including abscisic acid (ABA) (Miller *et al.* 2010; Saradadevi *et al.* 2017) and phototropin (Mao *et al.* 2005). Phototropins, a membrane-associated LIGHT-OXYGEN-VOLTAGE-SENSING (LOV) protein (Molas and Kiss 2009), are well known for their photomorphogenesis activities, but little is known about their role in oxidative stress responses and photosynthesis.

Light signals are well known for driving photomorphogenic development in plants as well as improving freezing tolerance caused by cold stress and other abiotic stresses (Pooam *et al.* 2021; Kim *et al.* 2002; Wei *et al.* 2022) in some plant variety of plants including *Arabidopsis*. According to Gilmour and Thomashow (1991), the expression analysis of stress-inducible genes in ABA-deficient and ABA-insensitive mutants, established the fact that, signal transduction from stress perception to stress inducible gene expression is mediated by ABA-dependent and ABA-independent pathways. ABA responsive elements (ABRE) and their *trans*-acting factor, which regulate gene expression via the ABA-dependent pathway, have been extensively studied, and several components involved in the signal transduction pathway have been identified through molecular genetic analysis. The c/DRE containing a core sequence of -CCGAC- has been shown to be essential for transcriptional activation in response to cold, drought, or high salinity stress in the ABA-independent pathway. Therefore, based on this assertion, we hypothesise that subjecting tomato plants to cold stress (4°C) increased/decreased the expression levels of phytochrome gene through C-repeat binding factor pathway (CBF) and or ABA pathway.

As a step forward in our understanding the cold stress tolerance mechanism in tomato, we first identified this gene family in tomato transcriptome using bioinformatic tools. Following successful identification and *in silico* characterisation, we examine whether the level of mRNA expression of these genes increased and or decreased under cold stress. This is baseline research towards understanding the role of light photoreceptor genes and abiotic stress tolerance. It will be used as a guide for future studies on environmental adaptation and genetic transformation of many important crops to improve abiotic stress tolerance in plants.

Materials and methods

Bioinformatic analysis for blue light photoreceptor genes detection in tomato genome

Basic Local Alignment Tools (BLAST) was used to identify homologs of the tomato (*Solanum lycopersicum* L.) blue light photoreceptor genes (Altschul *et al.* 1997) against *Arabidopsis thaliana* L. index databases at NCBI (http://www.ncbi.nlm.nih.gov/BLAST/), Sol Genomics Network (https://solgenomics.net/search/transcripts/est) and Tomato Functional Genomics Database (http://ted.bti.cornell.edu/). Data validation was performed using tBLASTx and tBLASTn tomato sequence searches against the *Arabidopsis* genome database (The Arabidopsis Information Resource; (https://www.arabidopsis.org/Blast/index.jsp) and the Integrating Genetics and Genomics to Advance Soybean Research: Soy-Base database (https://soybase.org/GlycineBlastPages/) were performed to validate results. For the hits, a threshold *e*-value of $1e-15$ filtered the resulting alignments and further analysed according to functional domain description.

The hierarchical clustering methods were used to explore and examine the role of blue light photoreceptor genes in the two model plant species at developmental stage under abiotic stresses. Results are based on the Euclidean distance and the ward linkage algorithm. GENEVESTIGATOR Software was used to investigate the biological processes enriched and expression pattern of photoreceptor genes from *Arabidopsis* and tomato. BIOVIA Discovery Studio ver. 16.1.0 was further used to generate 3D structures of blue light photoreceptor gene family in tomato. The chromosomal location image of photoreceptor gene family from *Arabidopsis* and tomato was generated by the Chromosome Map Tool (https://www.arabidopsis.org/jsp/ChromosomeMap/tool.jsp) and MapInspect tool (http://www.plantbreeding.wur.nl/uk/software_mapinspect.html) respectively, based on gene physical position data recorded.

KnetMiner tool (https://knetminer.com) was used to generate network maps for visualising gene-to-trait relationships among photoreceptor genes and their interactions in abiotic stress tolerance. A Phylogenetic tree was constructed to better understand the evolutionary relationships of photoreceptor genes in eight species including *A. thaliana*, *S. lycopersicum*, *Glycine max* L., *Populus trichocarpa* Torr. & Gray, *Zea mays* L., *Sorghum bicolor* L., *O. sativa* and *Triticum aestivum* L. using The CLC Sequence Viewer (ver. 8). Bootstrap analysis with 1000 replicates was used to test statistical support for each node using the Poisson correction neighbour–joining (NJ) method and the pair-wise deletion alternative.

Disinfection of plant material, growth conditions and stress treatment

S. lycopersicum (LA4024) seeds were surface sterilised with sodium hypochlorite solution (5% NaClO solution for 20 min followed by thorough seven times rinses with autoclave distilled water). The sterilised seeds were planted in pots containing soil mixture (clay, peat moss and sand in 1:1:1 ratio mix finely and moistened with distilled H_2O) and kept at temperature 30 ± 2°C in green house with light intensity of 250–300 μmol m^{-2} s^{-1}. Seedlings were reduced to one plant per pot after 2 weeks. The 21-day-old plants were exposed to cold stress by placing them in a 4°C growth chamber for 4 h. Morphological, physiological, and biochemical parameters were recorded.

To access the expression pattern of photoreceptor genes in tomato, plants were held in dark (D), blue light (BL), and red light (RL) for 0, 1 and 4 h. Leaf samples were randomly collected from stressed and control plants and were immediately homogenised in liquid N_2 to fine powder. Total RNA was extracted from control and stressed plants using ISOLATE II RNA Mini Kit (Bio-52077) as directed by the manufacturer and kept at −80°C for further analysis.

Gas exchange and chlorophyll fluorescence measurements

Photosynthetic parameters were performed concurrently at the second and third leaf counts. Two leaves from each plant were measured, with 3–9 plants per treatment. The gas exchange parameters were measured using a LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA), and the major fluorescence parameters (F_0, F_m and F_v) of chlorophyll were analysed simultaneously using a portable modulated fluorimeter (Plant Stress Meter, PSM Mark II, Biomonitor S.C.I AB, Umea, Sweden). The leaves were dark-adapted for 20 min before measuring the fluorescence transient over 2 s and with an actinic stimulation at 400 μmol m^{-2} s^{-1}. The maximum fluorescence (F'_m) and minimum fluorescence (F'_0) of light-adapted leaves were measured for 15 min. Variable fluorescence (F_v) was calculated from the difference between F_0 and F_m in dark-adapted conditions, and variable fluorescence (F'_v) was calculated from the difference between F'_0 and F'_m in light-adapted conditions. The non-photochemical quenching of variable ChlF (qN) was calculated using Roháček (2002) equation:

$$qN = (F_v - F'_v)/F_v.$$

Assessment of morphological and physiological traits

To assess phenotypic differences between control and stressed plants, plant root length, shoot length, plant height, dry and fresh weights were recorded. Initial height of 3-week-old seedling was measured from surface of soil to apex using ribbon metre. Plants were then subjected to the cold stress, and the initial and final heights of plants were measured. Percent increase in plant height was calculated as: (Final height − Initial height) × 100/Initial height. For fresh and

dry biomass (g), three seedlings were randomly harvested after cold treatment. Roots were washed with distilled water (H_2O) and plants were then placed on sterile filter paper to drain out the extra water. Fresh weight of each plant was taken using weighing balance and expressed in gram (g) per plant. After taking the fresh weight of the seedlings, the plants were covered in brown papers and dried out for 48 h at 80°C, and the dry weights were recorded. The dry biomass expresses as g per plant. Reduction percent in biomass was calculated as:

$$(\text{Fresh biomass} - \text{Dry biomass}) \times 100/\text{Fresh biomass}.$$

Expression analysis of photoreceptor genes in tomato leaf

cDNA was synthesised from the isolated RNA by using Super-Script III (Thermo Fisher Scientific). RT-qPCR was performed with gene specific primers pair (see Supplementary Table S1) on ABI 7500 real-time PCR machine (Applied Biosystems, USA). The PCR reaction mixture 20 µL was consisted of 10 µL SYBR Green Master Mix (Fermentas), 1 µL (100 ng) cDNA, primers forward and reverse (10 pM) 1 µL each, and 7 µL ddH2O (double distilled water). The RT-qPCR cycling conditions were initial denaturation at 95°C for 5 min; then 40 cycles of 95°C for 30 min for initial activation, annealing at 55°C for 30 s, extension at 72°C for 45 s and final extension at 72°C for 10 min. Delta CT method ($\Delta\Delta C_t$) was used to calculate the relative expression. GAPDH ID: MG930815.1 was used as internal control for data normalisation.

Statistical analysis

Data generated from multiple groups and physiological parameters were analysed using one-way ANOVA statistical analysis. Data on fold change was transformed and subjected to analysis of variance. The re-transformed means were separated using Tukey's honest significance test for differences at $P \leq 0.05$. To understand the relationship between light condition and time of exposure to stress, biplot graphs were generated with principal component axes 1 and 2 using MetaboAnalyst 5.0 (https://www.metaboanalyst.ca/).

Ethical approval

This article does not contain any studies with human participants or animals performed by any of the authors.

Results

Bioinformatic analysis for blue light photoreceptor genes detection in tomato genome

The search revealed 14 photoreceptor genes in both species. In tomato, four classes of cryptochrome were discovered (Cry1a, Cry1b, Cry2 and Cry-Dash), whereas in *A. thaliana*, only three classes were (Cry1, Cry2 and Cry3 homologue of Cry-Dash) were present. In both species, five classes of phytochrome genes were found: PhyA, PhyB1, PhyB2, PhyE, and PhyF for tomato; and PhyA, PhyB, PhyC, PhyD, and PhyE for *A. thaliana*. Two sets of genes in the zeitlupes class were discovered in tomato: LKP2 and KFF, while three sets of genes were present in *A. thaliana* (Table 1).

The functional domains of the identified genes in tomato were related to Per–Arnt–Sim (PAS), LOV, DNA photolyase, MTHF, flavin-binding kelch F-box, cGMP-specific phosphodiesterases, adenylyl cyclases and FhlA (GAF), phytochrome (PHY), seven-bladed-propeller, and C27, with phytochromobilin tetrapyrrol chromophore (PϕB) as cofactors (Table S2).

The bulk of these genes were implicated in multiple abiotic stress tolerance pathways (Fig. 1) and many developmental processes. The abiotic stress responses of these photoreceptor genes are detailed in Table S3. GENEVESTIGATOR analysis allowed us to compare the expression pattern of these genes to the public datasets. The hierarchical clustering results based on the Euclidean distance and the ward linkage algorithm were used in exploring and examining the role of blue light photoreceptor genes at developmental stage under stress condition in both species. Analysis of the dendrogram revealed two distinct clusters of the samples and are differentially expressed at different developmental stage (Fig. 2).

The distributions of blue light photoreceptors genes among tomato and *Arabidopsis* chromosomes appeared to be uneven.

Table 1. Number of light photoreceptors identified by tBLASTn searches in model species.

	Light photoreceptors	*Arabidopsis*	Tomato
Blue light photoreceptors	UVR8 (280–315 nm)	1 (UVR8)	1 (UVR8)
	Cryptochrome (390–500 nm)	3 (Cry1, Cry2 and Cry-Dash)	4 (Cry1a, Cry1b, Cry2 and Cry-Dash)
	Phototropin (390–500 nm)	2 (Phot1 and Phot2)	2 (Phot1 and Phot2)
	Zeitlupe (390–500 nm)	3 (ZTL, KFF and LKP2)	2 LKP2, KFF
Red/far-red light receptors	Phytochrome (600–750 nm)	5 (PhyA, PhyB, PhyC, PhyD and PhyE)	5 (PhyA, PhyB1, PhyB2, PhyE and PhyF)
	Total	14	14

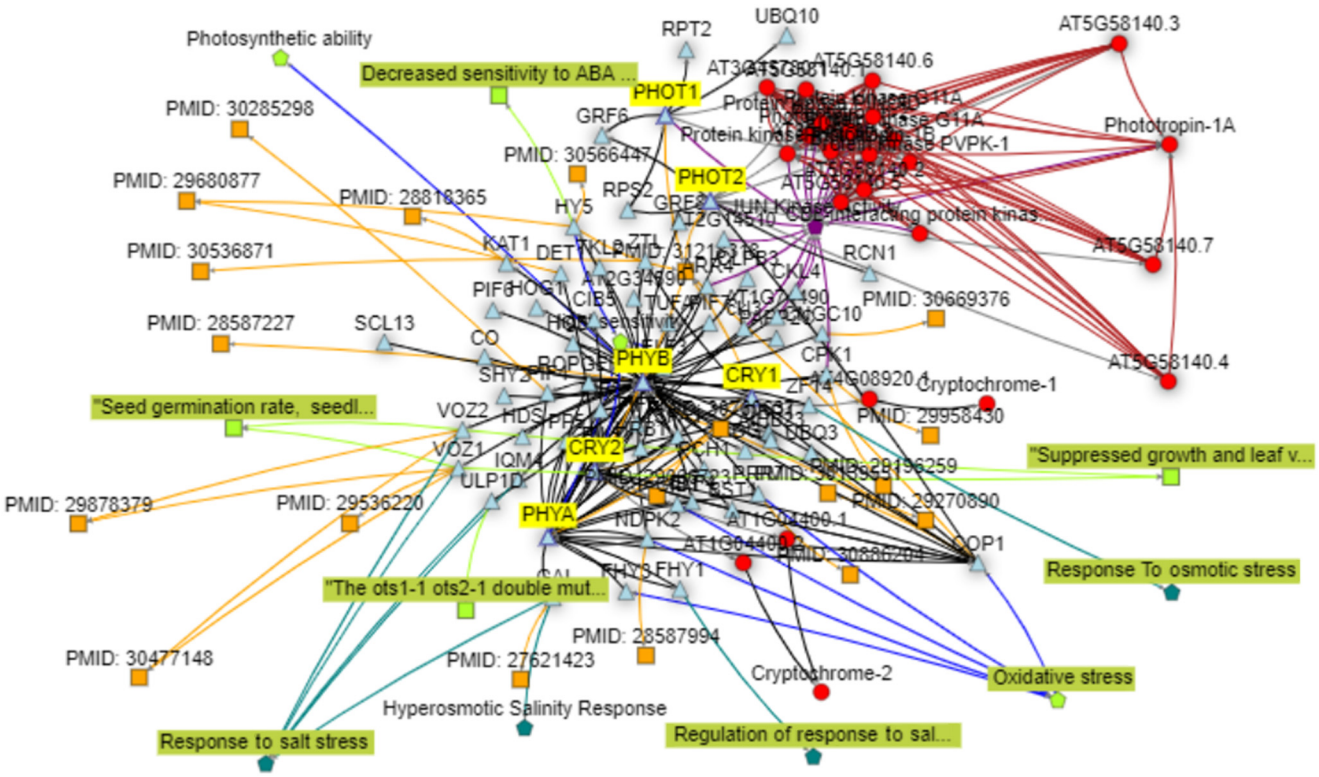

Fig. 1. The network maps of photoreceptor gene family in tomato associated with abiotic stress tolerance. Photoreceptor genes are highlighted in yellow and abiotic stress highlighted in pea green.

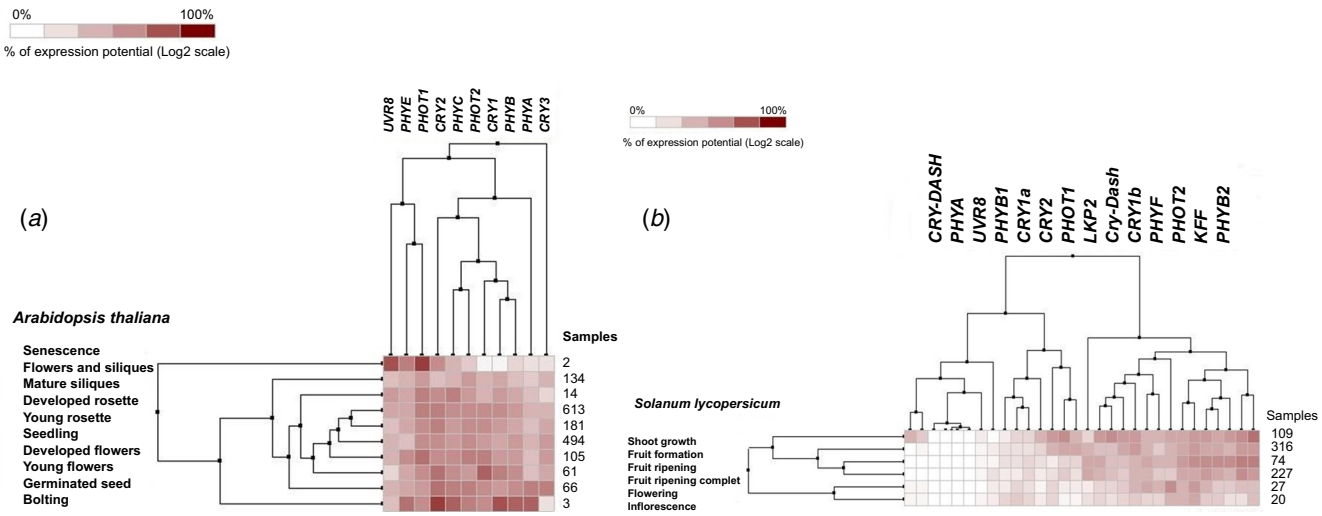

Fig. 2. The hierarchical clustering results showing the role of blue light photoreceptor gene family in *Arabidopsis thaliana* (*a*) and *Solanum lycopersicum* (*b*) at different developmental stage. The dendrogram revealed two distinct clusters of the sample and are differentially expressed. Scale: from brightest red equals most increased to white equals most decreased of the potential expression.

In *Arabidopsis*, chromosome 5 contains five blue light photoreceptor genes, chromosomes 1 and 4 and 2 contain three and two blue light photoreceptor genes, respectively, and chromosome 3 contains only one gene. Based on our results, the photoreceptor genes are relatively uniformly distributed on tomato chromosomes. Cryptochrome genes (Cry1a and Cry1b) were discovered on chromosomes 4 and 12. Phototropin (Phot 1 and Phot2) on chromosomes 11 and 1, and phytochrome classes (PhyA, PhyB, and PhyB1) on chromosomes 10, 5, and 1, respectively (Fig. S1).

Analysis of the 3D structures of blue light photoreceptor revealed a complex interaction with cofactors (flavin mononucleotide (FMN, (5S)-5-methyl-2-(methylsulfanyl)-5-phenyl-3-(phenylamino)-3,5-dihydro-4H-imidazol-4-one) and FAD) (Fig. S2).

A phylogenetic tree analysis revealed that photoreceptor genes were distributed unevenly in all species. They were all divided into two classes (Class I and II), with 16 pairs of paralogous and seven pair of orthologous genes (Fig. 3).

Physiological and morphological evaluation of tomato responses to cold stress

When compared to the control plants, plant height, root and shoot length of cold-treated plants were all affected. Shoot length (SL) fell from 39.5 to 29.9 cm, root length (RL) from 10.5 to 9 cm, and plant height (PH) from 49.6 to 40 cm (Fig. 4*a*). The same pattern was observed for both fresh and dry biomass weight. Fresh biomass weight decreased from 12.9 to 9.8 g, while the dry biomass weight decreased from 2.7 to 1.6 g (Fig. 4*b*). Cold stress decreased photosynthesis from 10.06 to 3.16 mol m^{-2} s^{-1}, transpiration from 4.6 to 1.3 mmol m^{-2} s^{-1}, and stomatal conductance (g_{sw}) from 94.6 to 25.6 mmol m^{-2} s^{-1} (Fig. 4*c*).

Overall growth and development parameters of tomato plants were also evaluated via heatmap. Clustering analysis (top) showed four classes in three major groups: control plant in Group I, Group II, for plant kept for 1 h at 4°C and Group III for plant kept at 4°C for 4 h. The physiological and morphological parameters evaluated are depicted on the left as (i) and (ii) (Fig. 4*d*).

Expression analysis of photoreceptor genes in tomato leaf

The relative expression of photoreceptor genes in tomato leaves at 0, 1, and 4 h as a function of blue light revealed an increase in the target genes' transcript levels. None of the photoreceptor genes showed a particularly high level of expression at 1 h of exposure. It was gradually increased as

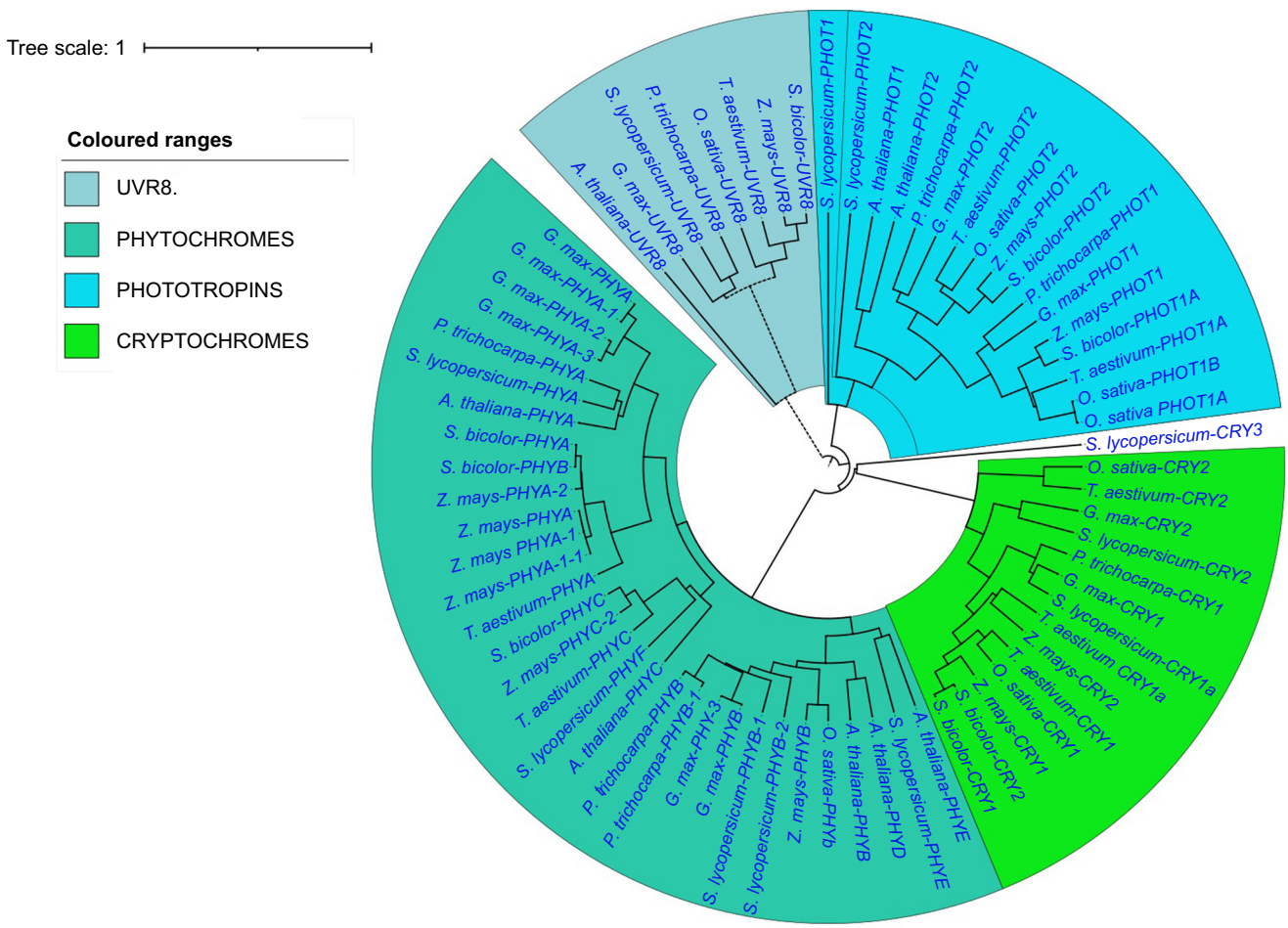

Fig. 3. Phylogenetic tree of 74 conserved domains amino acid sequences of photoreceptor gene family from *Arabidopsis thaliana* and *Solanum lycopersicum*, *Glycine max*, *Populus trichocarpa*, *Zea mays*, *Sorghum bicolor*, *Oryza sativa* and *Triticum aestivum*. CLC Software (ver. 8) was used to build the tree. The photoreceptor gene family is represented by various colours.

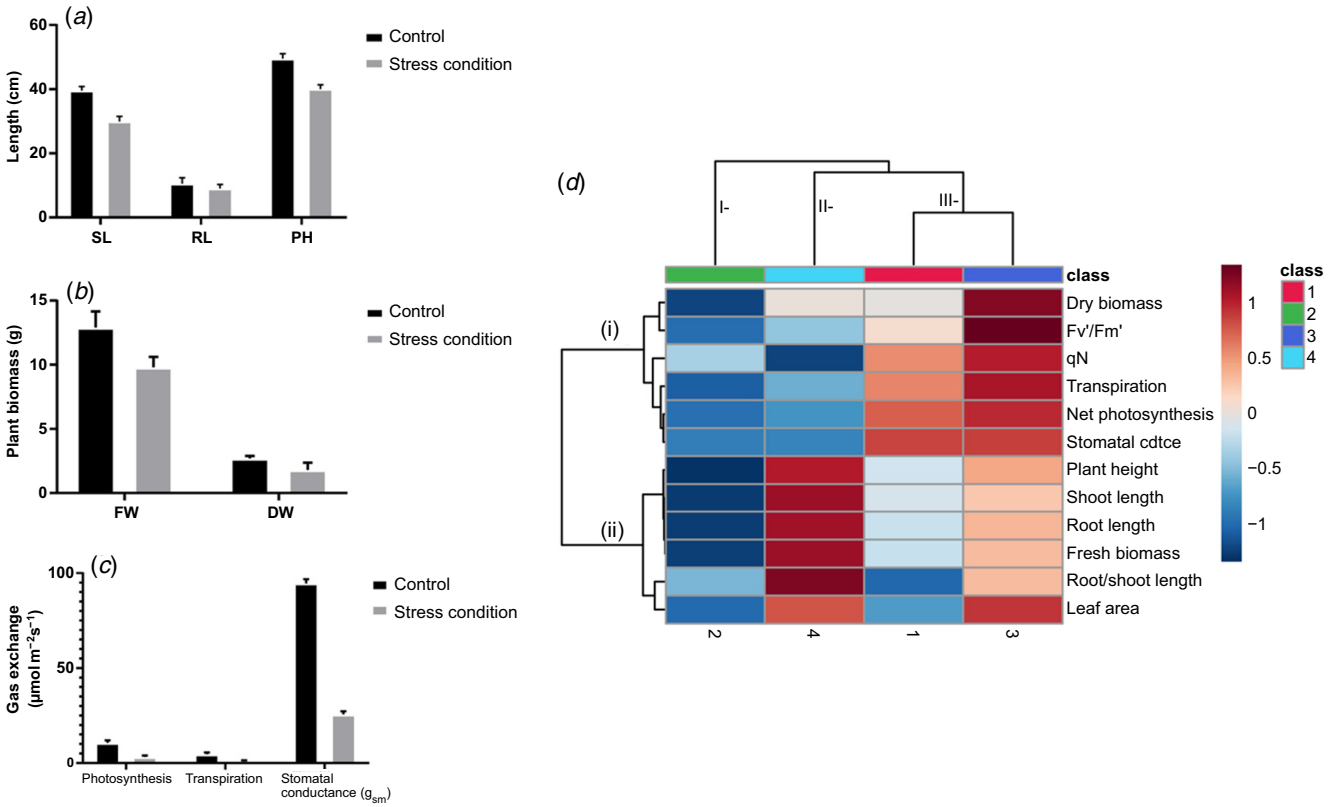

Fig. 4. Overall assessments of morphological and physiological responses of tomato plants under cold stress. (*a*) SL, shoot length; RL, root length; PH, plant heigh. (*b*) FW, fresh biomass weight; DW, dry biomass weight. (*c*) Gas exchange parameters. (*d*) Overall growth and development parameters of tomato plants evaluated via heatmap hierarchical clustering divided in three major groups: Group I for control plants Group II, for plant kept for 1 h at 4°C and Group III for plant kept at 4°C for 4 h. The overall physiological and morphological parameters evaluated are shown at the left two main groups were found (*a* and *b*). The overall physiological and morphological parameters evaluated are depicted on the left represented by (i) and (ii). Scale: from brightest blue equals most decreased to brightest red equals most increased.

the exposure time was increased. However, photoreceptor genes express differently in blue and red light. Under blue light, cryptochrome (Cry2) expression levels increased significantly from 1.9 to 5.7. Same pattern was also observed for phytochrome (PhyB) in red light: from 0.98 to 6.9 after 4 h of exposure. Tukey's honest at $P \leq 0.05$ revealed non-significant differences in the expression level of phototropin 2 (Phot2) after 1 and 4 h of cold stress exposure. For 1 and 4 h, the expression level ranged from 0.45 to 0.87. The biplot graph generated for each photoreceptor gene using the first two principal components (PC1 and PC2) of light condition reflects 76.6% of the total variation in expression level (Fig. 5).

Discussion

Identification and characterisation of the photoreceptor gene family using a comprehensive analysis of tomato transcriptome data revealed several groups of conserved domain sequences. Analysis of these conserved domain sequences showed that they are mainly involved in different biological processes, allowing them to withstand various abiotic stresses at different developmental stage.

The analysis of network maps also indicates that, these photoreceptor genes were associated with different abiotic stress responses and agronomic traits such as osmotic, oxidative, salinity stresses, decrease in ABA sensitivity, seed germination etc. This result is in line with Fantini *et al.* (2019) and Wang *et al.* (2016) who reported that these photoreceptors genes are photosensory receptors that regulate growth and development as well as the circadian clock in plants by mediating important agronomic traits in crop species (entrainment of the circadian clock, guard cell development, stomatal opening, root growth, plant height, high-light stress response). A strong induction of blue light on root greening was observed in *PhyA* and *PhyB* single mutants but almost defective in *cry1* mutant and *PhyA/PhyB* double mutant as observed by Su *et al.* (2017), indicating that Cry and PhyA or PhyB facilitate blue light root greening. In response to abiotic stresses, the cryptochromes chromophores: MTHF and FAD bind to

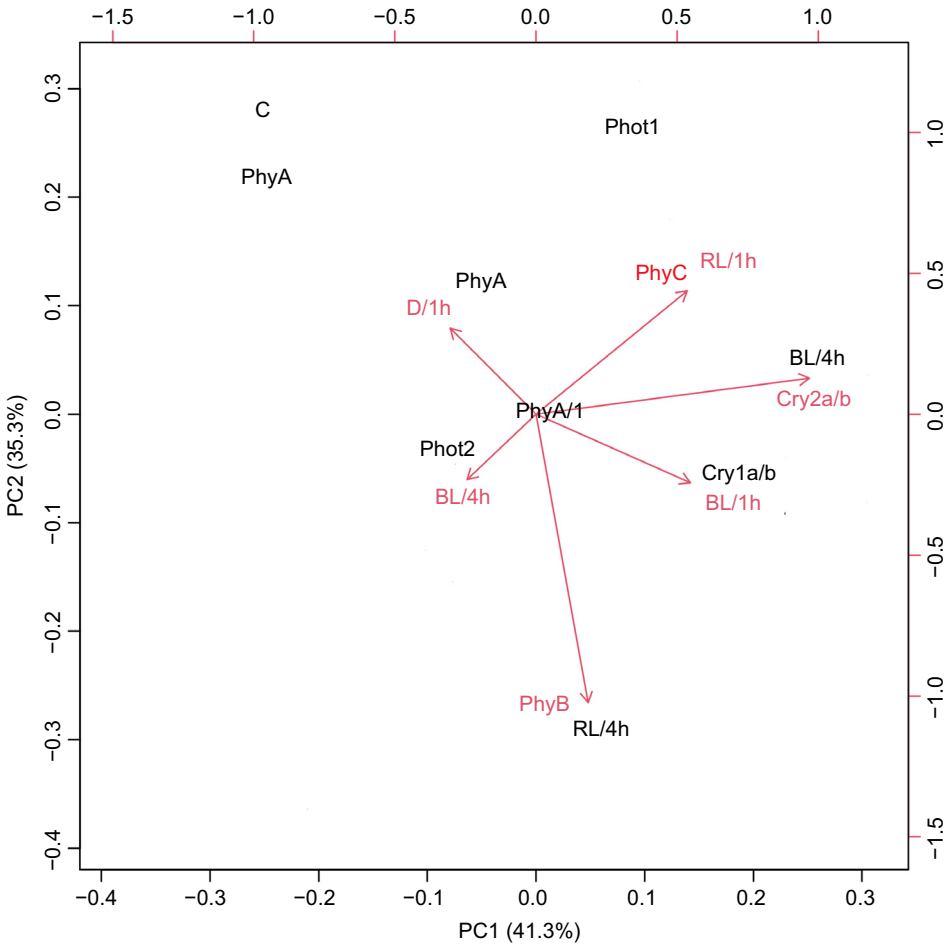

Fig. 5. The proportional distribution of photoreceptor gene mRNA expression levels in tomato under cold stress as a function of blue light. The expression level at 4°C for 0, 1, and 4 h was displayed using biplot graphs with principal component axes 1 and 2 showing 76 percent total variables. The fold difference was calculated using double delta C_t values.

Photolyase-Homologous Region (PHR) for the production of ROS (D'Amico-Damião and Carvalho 2018).

Phototropins are originally considered to be involved only in phototropic responses in plants, but they have since been discovered to control a variety of other plant functions, including chloroplast and stomata movement. Since then, several studies have revealed that these genes play a variety of other roles in plant growth and development (Christie *et al.* 2015). It was discovered that PHOT1 and PHOT2 are linked to a variety of agronomic traits, including biomass, stress tolerance, disease resistance, and shoot branching (Mawkhiew *et al.* 2021). Henry and Crosson (2011), reported the primary mechanism for the detection of light in *Phot* is the creation of a flavin-cysteinyl adduct in the LOV domain. For example, FMN binding domains are more closely related in structure to FAD-binding domains.

A light-dependent increase of polyunsaturated fatty acids in response to cold stress in olive mesocarp was reported (Hernández *et al.* 2019). There was an increase in linoleic and α-linolenic acids in cotyledons of cucumber in response to light, however, light had elevated only the α-linolenic acid level in oat (*Avena sativa* L.) leaves and *Arabidopsis* callus as reported by Hernández *et al.* (2011) and Dar *et al.* (2017). Under cold stress, FAD was found light-dependent and was because of an indirect hormonal effect or a direct effect of light regulatory elements. It is known that light inhibits ethylene synthesis, which in turn affects auxin distribution. Thus, the influence of light on gene expression under cold stress could be regulated by the ethylene/auxin gradient, which in turn, is regulated by light (Vanstraelen and Benková 2012). The synergistic effects of heat and light signals on hypocotyl elongation have also been reported where, *Arabidopsis* mutants with defective clock genes exhibited disturbed hypocotyl elongation under heat stress (Gil and Park 2019). Protein-ligand binding sites are extremely critical for gaining insight into the proteome's functional diversity (Khazanov and Carlson 2013). A set of amino acids available for interaction with ligands is one of

the most fundamental properties of the receptor surface (Lichtarge *et al.* 1996). Numerous studies have shown that a riboflavin FAD nucleic acid derivative is involved in a wide variety of biological processes and plays a key role in aerobic metabolism because of its ability to catalyse both one-and two-electron transfer reactions (Rodziewicz *et al.* 2014). The FAD ligand is probably one of the most important components of the blue light photoreceptor genes in mitigating abiotic stress tolerance. The photoreceptor gene family in tomato interacts with FAD ligand, as shown in the 3D structure, confirming the involvement of tomato photoreceptor genes in abiotic stress tolerance. Phylogenetic tree analysis revealed a set of orthologous and paralogous genes. Orthologs are genes produced by speciation events in different genomes, whereas paralogs are genes produced by gene duplication events in the same genome, as reported by Koonin (2005). We also observed from this study, six pairs of paralogous genes and one pair of orthologous genes, confirming the ancestral duplication process in these plant species. The results were consistent with those of Panchy *et al.* (2016), who found that gene duplication is a major mechanism for genomic rearrangement and expansion. Duplication of genes has also been shown to include stress response, indicating that these duplicates are critical for plant adaptation to rapidly changing environments (Batcho *et al.* 2020; Wang *et al.* 2021). The segmental duplication events in the expansion of photoreceptor genes in tomato transcript may thus be linked to the functions of these genes in abiotic stress tolerance.

Analysis of physiological parameters revealed that the rate of photosynthesis and transpiration dropped considerably under cold stress. The reason for this might be the fact that under cold stress, photosynthetic activity significantly reduces due to light and metabolic inhibition. The plant starts using accumulated starch as an energy resource instead of photosynthesising its metabolic demand as reported by Wang *et al.* (2018) and Dusenge *et al.* (2019). The cellular sucrose content becomes limited under stress and decreased the level of Rubisco carboxylase activity while ROS increased. The photosynthesis based-sucrose decreases when the inhibitors bind to the site of photosynthetic enzymes, resulting in a slower metabolism and the relocation of secondary metabolites that occur (Shahryar and Maali-Amiri 2016). Oliveira and Peñuelas (2005) reported that transpiration rate depends a lot on the growing stature of the plant and the field capacity. Plants appear to tolerate cold stress until they are permanently injured because of persistent cold stress conditions, after which they inhibit the photosynthetic system, causing photo damage, slowing the consumption of NADPH and ATP, and a reduction in plant growth, and limiting the transpiration rate.

Expression analysis of photoreceptors genes in tomato under cold stress and light condition revealed difference in the transcript levels (down/up regulated), especially phytochrome B (PhyB). The synergistic action between light/photoreceptor genes, co-regulates several physiological parameters at different developmental stage of the plant (root greening, de-etiolation, SAS, photoperiodic flowering). As previously stated, the mechanism of cold stress tolerance involved a CBF/DREB1 (C-Repeat/DREB Binding Factor/ Dehydration-Responsive Element Binding Protein 1)-dependent interaction. Even though CBF/DREB1 is the key master regulator for many known cold-regulated genes, it is unlikely to be the only one. According to Jung *et al.* (2016) and Legris *et al.* (2016), phytochrome functions as a temperature sensor in *Arabidopsis* and this function is carried out by the temperature-dependent dark reversion of the PhyB photoreceptor (relaxation of the active Pfr form to the inactive Pr form). Guy (2003) reported on the possible role of phytochrome C (PhyC) in cold stress tolerance, demonstrating that the ability of higher plants to acclimatise and/or resist cold stress is a complicated quantitative feature of many genes and phytohormones. Basically, phytohormones function as a signal molecule in regulation of expression of defensive gene and modification of enzyme activity. These phytohormones can act separately or coordinate with other signalling pathway in complex network. A crosstalk between hormones and photoreceptor genes in abiotic stress tolerance under light condition was also reported recently in wild-type plants under cold and light condition, in which the cold stress caused downregulation of cytokinin (CK and auxin) while ABA and jasmonates and salicylic acid (SA) were upregulated (Kurepin *et al.* 2013). Cold stress under dark strongly suppressed all phytohormones except ABA. It has been also proposed that cold stress tolerance evolved from the drought tolerance mechanism and the interaction of hormones. Li *et al.* (2021) found that Cry1 suppressed auxin biosynthesis to help *Arabidopsis* seedlings adapt to heat stress, resulting in morphological changes. Furthermore, at low temperature (chilling), Cry1 interacted with flavin-binding monooxygenase family protein (YUC8), indole-3-acetic acid inducible 19 (IAA19), and indole-3-acetic acid inducible 29 (IAA29) promoters in a PHYTOCHROME-INTERACTING FACTOR 4 (PIF4)-dependent, which is an important part of blue light-dependent signal transduction. Gangappa and Botto (2016) reported that plant acclimation to cold stress includes HY5, COP1, and Z-box (regulatory *cis*-element located in the promoter of responsive genes). These key regulators of light signalling are known to be mediated by Crys through various interactions with other photoreceptors such as phytochrome and signalling molecules (D'Amico-Damião and Carvalho 2018), raising the possibility that these blue light photoreceptors play a role in low temperature tolerance. However, as seen in this primary study, cold stress response modulated by photoreceptor gene in tomato is still uncommon, but more research on this topic is required to gain insight into the tolerance mechanism of cold and other abiotic stresses. Further research could determine whether the exact mechanism of

cold stress tolerance in tomato is based on a light-dependent pathway *via* HY5 (CBF pathway) or a light-independent pathway via ABA (ABA pathway).

Conclusion and remarks

A comprehensive analysis of photoreceptor genes in tomato transcriptome data and the expression profiling in cold stress contribute to a better understanding of their probable role in abiotic stress mitigation. One particularly interesting outcome of this study is that these genes can be stimulated by blue light and activated different stress-responses pathway. However, genetic studies on the possible interactions between different photoreceptors genes are required to elucidate their interdependence in response to abiotic stresses. To understand the mechanisms that plants use to tolerate abiotic stress, detailed profiling of the interaction pathway between light and photoreceptor genes under abiotic stress will be also required to figure out how ABA responsive elements and their transcription factor regulate gene expression in response to abiotic stress.

Supplementary material

Supplementary material is available online.

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Data availability. The authors confirm that the data supporting the findings of this study are available within the article and/or its supplementary materials. The original data files of the transcriptome are available on NCBI BioProject (PRJNA657974).

Conflicts of interest. The authors declare that he/she has no conflicts of interest.

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