Plant Stress 21 (2026) 101439

Contents lists available at ScienceDirect

Plant Stress

journal homepage: www.sciencedirect.com/journal/plant-stress

Light-hormone crosstalk coordinates multiple stress adaptation pathways in salt-stressed tomato plants

Petra Bublavá [a,b], Kateřina Cermanová [a,b], Michal Karady [a,b], Martin Fellner [a,b,*]

[a] Laboratory of Growth Regulators, Palacký University, Faculty of Science, Olomouc, Czech Republic
[b] Laboratory of Growth Regulators, The Czech Academy of Sciences, Institute of Experimental Botany, Olomouc, Czech Republic

ARTICLE INFO

Keywords:
Abscisic acid
Blue light
hp1
Salt stress

ABSTRACT

Salt stress represents one of the major agricultural problems, limiting plant growth worldwide. The plant hormone abscisic acid (ABA) plays a crucial role in salt stress adaptation, and its level is regulated by light conditions. Our research was focused on studying the effect of light and ABA as well as their crosstalk, in plant responses to salt stress using the tomato (*Solanum lycopersicum*) photomorphogenic mutant *high pigment 1* (*hp1*), which carries a defect in the UV-DAMAGED DNA BINDING PROTEIN 1 (DDB1) locus. Early tomato seedlings of the wild type (WT) cv. Rutgers and *hp1* were stressed with 150 mmol/L NaCl under different light conditions: dark, white light (WL), and blue light (BL). Under BL and compared to the corresponding cv. Rutgers, *hp1* shoots exhibited enhanced salt tolerance, while root growth was compromised. Analyses of stable photosynthetic pigments and elevated phenolic content in the mutant also support BL-mediated enhancement of salt tolerance. Additionally, enhanced expression of *ELONGATED HYPOCOTYL 5* (*HY5*), particularly under BL, confirmed amplified light signalling in *hp1* plants. Hormonal analysis revealed light-dependent interactions between ABA and 1-aminocyclopropane-1-carboxylic acid (ACC). Under salt stress, BL significantly increased ABA levels in the mutant through upregulated *NCED1* and reduced *CYP707A3* gene expression, while decreasing ACC content. Moreover, salt-stressed *hp1* plants accumulated higher levels of stress-protective compounds (proline, polyamines) under all tested light conditions, correlating with increased expression of biosynthetic genes and precursor availability. Our findings demonstrate that amplified light signalling coordinates multiple stress adaptation pathways through shared metabolic precursors and hormonal interactions, with ABA signalling playing a central role. The pronounced responses under BL highlight its importance in these interactions. The tomato *hp1* mutant proves to be an effective model for studying complex plant stress mechanisms contributing to stress-resistant crop development.

1. Introduction

Research focused on plant stress has become more important in recent years due to deteriorating environmental conditions. Salt stress is one of the major agricultural problems, limiting plant growth and development (Vengosh, 2003). Declining crop yields pose a challenge to the agricultural sector in feeding a growing population (Kopittke et al., 2019). Development of stress-tolerant plant genotypes will be one of the key strategies for adapting to future environmental shifts.

Abscisic acid (ABA) is a plant hormone that plays a crucial role in the plant adaptation to abiotic stress (Ohkuma et al., 1963; Tardieu et al., 2010). It is a key hormone involved in the regulation of dormancy and seed germination (Finkelstein et al., 2002, 2008). Light conditions alter the level of ABA (reviewed recently by Mahapatra et al., 2025). This fact indicates that light can be a critical regulator in plant stress adaptation mechanisms.

Light represents one of the most important environmental factors regulating plant behaviour, influencing growth and development. Plants sense light through photoreceptors, which are present in the whole plant organism (Wu et al., 2025). All four photoreceptor families were discovered in *Arabidopsis thaliana*. Phytochromes (phyA–phyE) sense red and far-red light (Quail et al., 1994), while cryptochromes (CRY1, CRY2) (Ahmad and Cashmore, 1993; Lin et al., 1996), phototropins (PHOT1, PHOT2) (Huala et al., 1997; Jarillo et al., 1998), and Zeitlupe proteins (ZTL, FKF1, LKP2) (Somers et al., 2000) respond to blue light and UV-A radiation. In the presence of light, photoreceptors translocate

* Corresponding author.
E-mail address: martin.fellner@upol.cz (M. Fellner).

https://doi.org/10.1016/j.stress.2026.101439
Received 12 January 2026; Received in revised form 21 May 2026; Accepted 2 June 2026
Available online 2 June 2026

from the cytoplasm to the nucleus or are already present in there to initiate light signal transduction. Activated photoreceptors transmit signals to downstream signalling components such as transcriptional activators and repressors, which control light-induced processes (Jing and Lin, 2020; Liu et al., 2023).

The light transcriptional activators known as PHYTOCHROME INTERACTING FACTORS (PIFs) carry signals to the downstream effectors, including ELONGATED HYPOCOTYL 5 (HY5), LONG AFTER FAR-RED LIGHT 1 (LAF1), and LONG HYPOCOTYL IN FAR-RED 1 (HFR1). These transcription factors are central regulators of light-mediated responses. The key repressor of photomorphogenesis, CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1), promotes the ubiquitination and subsequent degradation of positive regulators in light signalling during skotomorphogenesis (Bhatnagar et al., 2020; Jing and Lin, 2020). Significant interactions have been identified between transcription factors such as PIFs and HY5, and the ABA signalling pathway in response to abiotic stress. The ABSCISIC ACID INSENSITIVE 5 (ABI5) represents an important basic leucine zipper transcription factor in ABA signalling cascades (Finkelstein and Lynch, 2000) and may be a major convergence point in these interactions (Yadukrishnan and Datta, 2021). Crosstalk between light and ABA enables plants to coordinate growth and development under challenging environmental conditions. A well-known example of this interaction is stomatal opening activated by BL through PHOTs. These photoreceptors control ABA levels, affecting stomatal aperture regulation (Males and Griffith, 2017; Gupta and Nath, 2020).

Light can also modulate the biosynthesis of ethylene by regulating 1-aminocyclopropane-1-carboxylic acid (ACC), the immediate precursor of this gaseous phytohormone, which plays an important role in plant stress responses and development (Harkey et al., 2019). Furthermore, ABA and ethylene signalling pathways interact antagonistically or synergistically, depending on environmental factors, creating complex hormonal networks that regulate plant adaptation to stress (Benlloch-González et al., 2010; Li et al., 2019). In several species, there is evidence that light also influences stress-related substances such as phenolic compounds, proline, and polyamines. These compounds help plants cope with salt stress (Younis et al., 2010; Kovács et al., 2019; Gondor et al., 2021).

The aim of this research was to investigate the effects of light and ABA on plant responses to salt stress. As our model plant, we utilized tomato (*Solanum lycopersicum*), one of the world's most important crops. Specifically, the photomorphogenic tomato mutant *high pigment 1* (*hp1*), which exhibits enhanced sensitivity to light and changes in plant development. We hypothesize that BL is essential in enhancing salt stress tolerance, particularly through interaction with ABA signalling.

2. Materials and methods

2.1. Plant material and growth conditions

The tomato *Solanum lycopersicum* L. cv. Rutgers (LA1090; hereinafter referred to as WT) and the photomorphogenic tomato mutant *high pigment 1* (LA3004; *hp1;* Kendrick et al., 1997) were used in all experiments. Additionally, the tomato *crya1cry2* double mutant (Fantini et al., 2019) in the cv. Money Maker (LA2706) background was included for comparative analyses presented in the Supplementary material and was subjected to the same growth conditions and treatments as described for cv. Rutgers and *hp1*. Seeds of *hp1* mutant were kindly provided by C. M. Rick, Tomato Genetics Resource Center, University of California (https://tgrc.ucdavis.edu), and seeds of *cry1acry2* mutant line was kindly provided by E. Fantini and E Heuvelink. The *hp1* mutant has a defect in the gene that encodes UV-DAMAGED DNA BINDING PROTEIN 1 (DDB1) (Lieberman et al., 2004). Experiments in vitro on tomato seeds were performed as described previously in Bergougnoux et al. (2009). Seed germination was induced in the dark for 3–4 days at 23 °C. The germinating seeds were transferred to a new MS medium (Murashige and Skoog, 1962) supplemented or not with NaCl (150 mmol/), ABA (1 μmol/L), 1-aminocyclopropane-1-carboxylic acid (ACC; 1 μmol/L), or aminoethoxyvinylglycine (AVG; 1 μmol/L; the NaCl concentration was selected based on dose-response analysis (*hp1*: Supplementary Fig. S1; *cry1acry2*: Supplementary Fig. S11–S13); ACC and AVG concentrations were selected accordingly; Supplementary Fig. S2, S3). The dishes with germinated seeds were placed vertically in a controlled growth chamber under continuous BL or in white light (WL) with a long day (16 h light/8 h dark) at 23 °C for 7 days (Microclima 1000E Snijders Scientific, The Netherlands – BL; FytoScope FS 160, Photon Systems Instruments, Czech Republic – WL). BL was provided by fluorescent tubes TLD-36W/18-Blue (Philips) with a maximum irradiance at 460 nm and a total photon fluence rate of 10 μmol m^{-2} s^{-1}. WL was supplied by LED Duris E 2835 White (Osram) with a total photon fluence rate of 100 μmol m^{-2} s^{-1}. For dark conditions, the Petri dishes were wrapped in aluminium foil and placed in the growth chamber (FytoScope FS 160, Photon Systems Instruments, Czech Republic) under the same temperature regime. Seven days after germination (DAG), the seedlings were collected, weighed, and stored in −80 °C for further use.

2.2. Growth measurement

Hypocotyl and root length of 7 DAG old seedlings were measured from digital images in the program ImageJ (https://imagej.net/software/imagej/). At least twelve seedlings per treatment were used in the experiment.

2.3. Determination of photosynthetic pigments

Photosynthetic pigments were determined in an acetone extract according to Lichtenthaler (1987). For determination, at least six plants (hypocotyl + cotyledons) were homogenized in liquid nitrogen and mixed with 2 mL of 80 % acetone. The samples were then centrifuged at 17,500 × g for 10 min. The supernatant was collected, and absorbance was measured at 663 nm, 646 nm, and 470 nm (chlorophyll a, b, and carotenoids, respectively) using a spectrophotometer (Biowave II, Biochrom Ltd, UK). The calculations of chlorophyll content were as following: Chlorophyll a = 12.25*A663 - 2.79*A646; Chlorophyll b = 21.50*A646 - 5.1*A663; Chlorophyll a + b = 7.15*A663.2 + 18.71*A646.8; Carotenoids = (1000*A470 - 1.82*Chl a - 85.02*Chl b) / 198 (Porra, 2002).

2.4. Determination of phenolic compounds

Phenolic compounds were determined by the Folin-Ciocalteu method using the same acetone extract as for photosynthetic pigments. The method was optimized for 96-well plates (GAMA 96-well ELISA plate (9.7 mm / 0.3 mL). Into each well, 60 μL of shoot extract, 60 μL H_2O, 5 μL Folin–Ciocalteu reagent, and 130 μL 2 % Na_2CO_3 were added. The reaction mixture was then allowed to stand for 30 min at room temperature in the dark. Absorbance of the samples was measured at 750 nm using a multi-mode microplate reader (Synergy LX, Biotek, USA). Gallic acid was used as a standard for the calibration curve with 0 to 16 mg/L concentrations.

2.5. Analysis of gene expression by RT-qPCR

The collected samples (whole seedlings, i.e. hypocotyl + root) were homogenized in liquid nitrogen. The maximum weight per sample was 100 mg. Total RNA was extracted using a Monarch® Total RNA Miniprep Kit (New England Biolabs, USA) according to the manufacturer's protocol. The cDNA synthesis was performed using 1 μg total RNA with SensiFAST™ cDNA Synthesis Kit (Meridian Bioscience, USA). For qPCR reactions, SensiFAST SYBR Lo-ROX Kit (Meridian Bioscience, USA) was used, with 200 nmol/L of each primer. Gene expression was analysed using primers specific to all tested tomato genes (Supplementary

Table S1). Three technical replicates were prepared for each sample. All cycle threshold (Ct) values of target genes were normalized against two housekeeping genes (*PP2Acs* and *Tip41like;* Supplementary Table S1). The results are reported as a fold change calculated by comparing gene expression differences in cycle numbers during the linear amplification phase using the ΔΔCT method (Pfaffl, 2001). Expression was normalized to dark-grown or WL-grown WT controls.

2.6. Metabolite extraction and HPLC-MS/MS analysis

Plant hormones, related compounds, and polyamines were quantified by high-performance liquid chromatography coupled with tandem mass spectrometry (HPLC-MS/MS) according to previously published methods. Approximately 15 mg of homogenized plant material (whole seedlings, i.e. hypocotyl + root) was extracted using 500 µL of cold extraction solution consisting of 10 % acetonitrile and 0.5 % formic acid. Isotopically labelled internal standards and zirconium oxide 2 mm beads were added to the samples, followed by further homogenization on a bead mill for 10 min at 27 Hz. Samples were centrifuged at 30,000 g for 20 min at 4 °C, and the supernatant was split into two 200 µL aliquots and evaporated to dryness. One aliquot was dissolved in 30 µL of 10 % acetonitrile and analysed for plant hormones according to Karady et al. (2024); the other was derivatized with AccQ-Tag Ultra Derivatization Kit from Waters, and polyamines and related compounds were quantified as described in Cermanová et al. (2025). The MRM transition 286.1 > 171.0 *m/z* at 8.9 min was used for proline quantification in derivatized aliquots of samples. Both analyses were conducted using Agilent 6495B Triple-Quad LC/MS coupled to 1260 Infinity II LC system (Agilent Technologies, Inc., Santa Clara, CA, USA).

2.7. Data processing and statistical analysis

Statistical analysis was performed using GraphPad Prism 9 software (GraphPad Software Inc., San Diego, CA, USA). For normally distributed data: ANOVA followed by the Turkey test, Welch ANOVA, or the unpaired t-test and the Welch t-test were used. When the distribution of results was not normal, a non-parametric test was conducted, using the Mann-Whitney test.

3. Results

3.1. Blue light improves hypocotyl salt tolerance in hp1 plants

The effects of salt stress on hypocotyl and root length were examined in 7 DAG old tomato seedlings of WT and the *hp1* mutant exposed to different light conditions (dark, WL, BL) (Fig. 1). Under control conditions (i.e., in the absence of salt stress), etiolated *hp1* plants exhibited the same length of hypocotyl as WT plants (Fig. 1A), whereas in both WL and BL, the *hp1* hypocotyl was significantly shorter than WT (Fig. 1B, C). In the dark, treatment with 150 mmol/L NaCl resulted in a similar reduction of hypocotyl length in WT and *hp1* (approx. 30 %). Differently, in WL and especially under BL, *hp1* hypocotyls demonstrated greater tolerance to salt stress compared to WT (WL: ~36 % growth inhibition in WT vs. 25 % in *hp1*; BL: 50 % in WT vs. 12 % in *hp1*). In the absence of stress, *hp1* roots were generally shorter in the dark than WT, while under WL and BL conditions, no significant difference in root length was detected between the genotypes. The roots of etiolated WT and *hp1* plants were unaffected by NaCl treatment (Fig. 1A). However, under light conditions (WL, BL) salt-stressed *hp1* roots showed slight growth inhibition, while WT roots continued to grow normally (Fig. 1B, C).

3.2. Blue light mediates enhanced photosynthetic pigment stability and antioxidant capacity in salt-stressed hp1 plants

In the absence of salt stress, the *hp1* and WT plants grown under WL conditions contained similar levels of chlorophyll, whereas in BL, *hp1* showed significantly higher chlorophyll accumulation than WT plants (Fig. 2A). During salt stress, chlorophyll levels did not change in either genotype grown in WL, while under BL, chlorophyll content significantly increased in salt-stressed WT plants (by approx. 45 %), but not in *hp1* mutant.

In non-stressed conditions, the *hp1* seedlings contained higher carotenoid levels compared to WT under WL as well as BL (Fig. 2B). Salt stress promoted carotenoid accumulation in BL-grown WT plants (approx. by 37 %), although carotenoid content in *hp1* remained stable. In WL, the carotenoid level in WT was unaffected by salt stress, while the *hp1* mutant showed a slight reduction in carotenoid content (by approx. 20 %). Despite this decline, tomato *hp1* plants consistently retained higher carotenoid levels relative to WT under WL (Fig. 2B).

Antioxidant capacity was estimated by measuring total phenolic compound (TPC) content in plants (Fig. 2C). Under control conditions, *hp1* plants displayed a higher TPC level than WT in WL as well as in BL conditions. Salt stress significantly increased TPC levels in both genotypes under the tested light conditions. In WL, the TPC level increased in stressed WT plants by approx. 135 %, whereas in *hp1* it was only 25 %, resulting in comparable TPC content between both genotypes. Under BL, salt stress induced similar increases in TPC accumulation in WT and *hp1* plants compared to their respective basal levels (Fig. 2C).

3.3. hp1 plants show elevated light sensitivity through altered HY5 and PIF4 expression patterns

HY5 and PIF4 are key transcription factors in the regulation of light signalling pathways (Toledo-Ortiz et al., 2014). Although HY5 plays a central role in light signalling, its gene expression was paradoxically higher in the dark than under light (WL, BL) in tomato plants (Supplementary Fig. S4). Under control conditions and in both genotypes, *HY5* is expressed more in BL than in WL (Fig. 3). During salt stress, transcript levels decreased in both genotypes under WL and BL, but more markedly in *hp1* plants. Despite stress-mediated downregulation, *HY5* expression was consistently elevated in the *hp1* mutant relative to WT except in the dark, where *HY5* transcript accumulation was comparable between *hp1* and WT plants (Supplementary Fig. S5).

Expression of the *PIF4* gene was generally higher under light conditions (WL, BL) compared to dark in WT plants, whereas the opposite pattern was observed in the *hp1* mutant (Fig. 4). In the dark, *PIF4* transcript levels were significantly higher in *hp1* plants than in WT, especially under control conditions. During salt stress, expression remained unchanged in dark-grown WT plants; in contrast, the *hp1* mutant displayed a dramatic reduction in transcript level relative to its elevated baseline expression. Under WL, *PIF4* transcript levels were similar in WT and *hp1* plants regardless of stress. In BL, salt stress had no significant effect on *PIF4* expression in either genotype. However, *hp1* plants grown in BL showed slightly elevated expression relative to WT under control conditions (Fig. 4).

3.4. The hp1 mutant exhibits amplified hormonal responses under blue light: elevated ABA with decreased ACC during salt stress

The levels of ABA and ethylene precursor ACC were analysed in 7 DAG seedlings of WT and *hp1* treated or not with 150 mmol/L NaCl in the dark, or under WL, and BL conditions. Exposure to light generally promoted ABA accumulation. In the absence of salt stress, ABA content in WT was approximately 6-fold higher under WL and 3.5-fold higher under BL compared with dark-grown plants (Fig. 5 and Supplementary Table S2). The effect of salt stress on the accumulation of ABA was dependent on light conditions. In etiolated WT plants, the salt treatment did not significantly affect ABA levels, whereas in WL, ABA content declined by about 45 %, On the contrary, under BL, salt stress resulted in an increase of ABA accumulation by approx. 41 %. In the *hp1* mutant, salinity induced significant accumulation of ABA in dark- and BL-grown

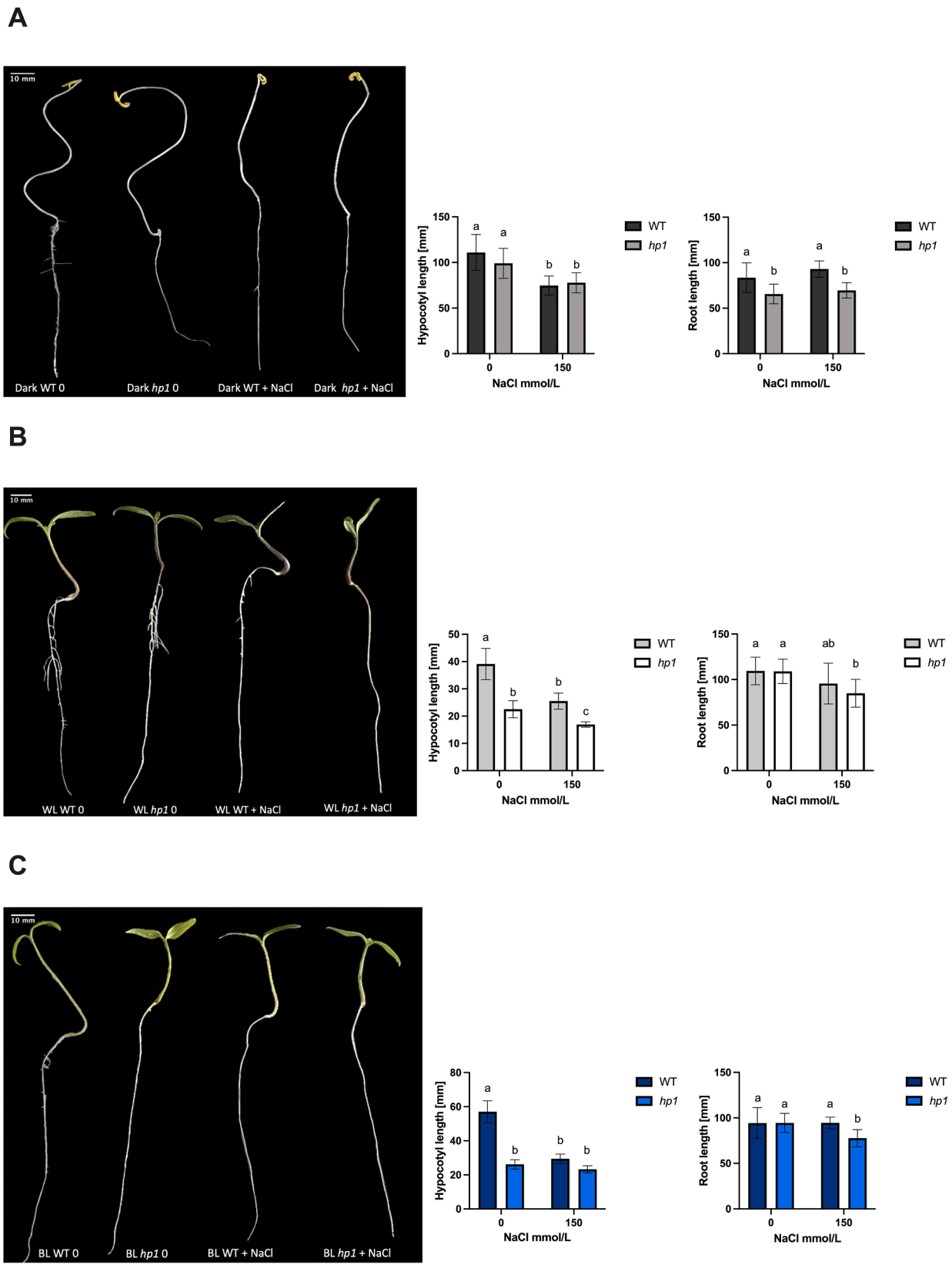

Fig. 1. Growth parameters of *Solanum lycopersicum* cv. Rutgers (WT) and *hp1* (*high pigment 1*) mutant plants under WL and BL conditions exposed to salt stress. Length of hypocotyl and root in WT and *hp1* 7 DAG old plants grown in the dark (A), under WL (B), and BL conditions (C) in the absence or presence of NaCl (150 mmol/L). Values are the mean ± SD of ±12 seedlings. Different letters indicate statistically significant differences (ANOVA + Turkey test or Mann-Whitney test, $p < 0.05$); SD, standard deviation.

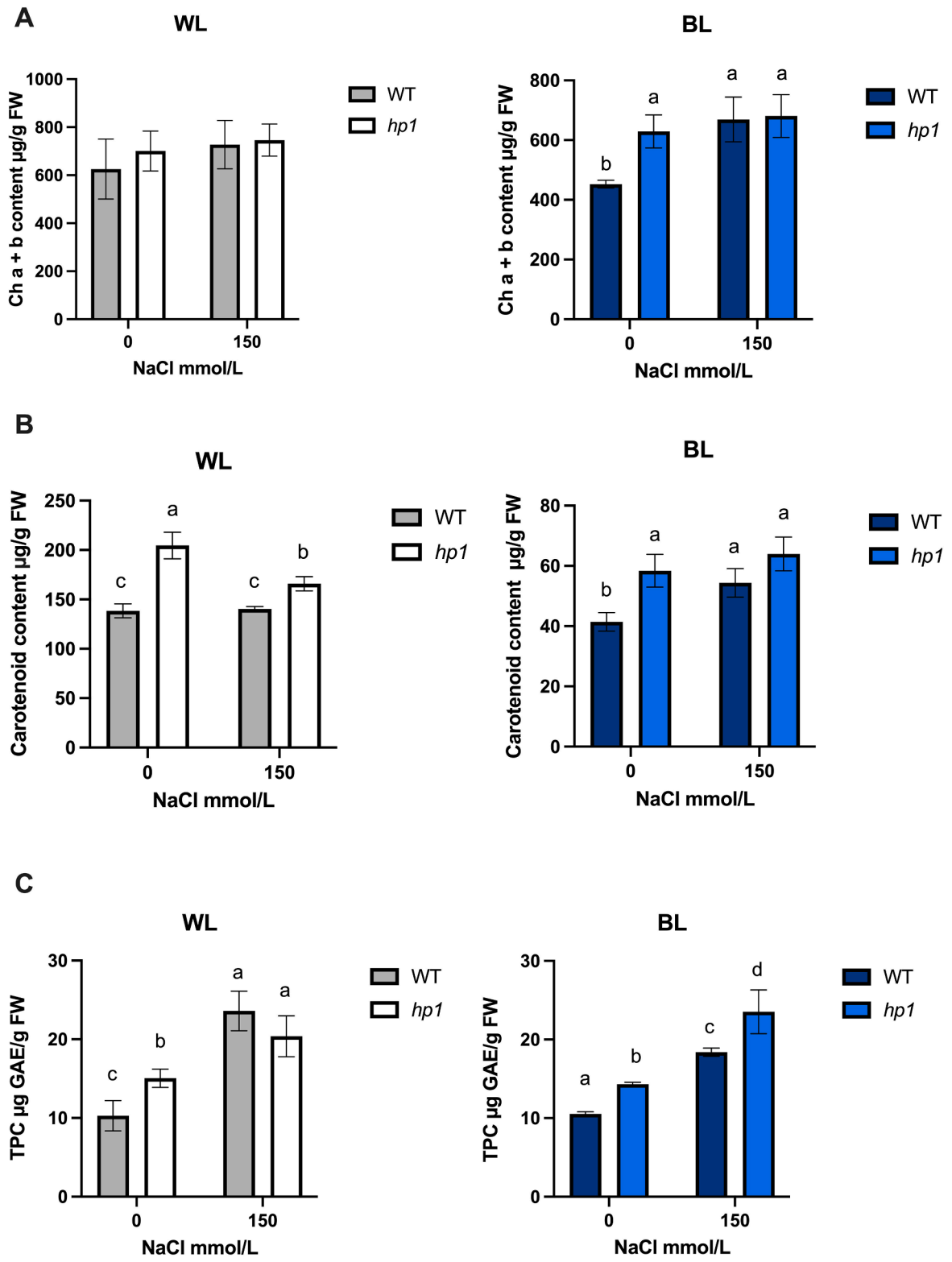

Fig. 2. Content of chlorophyll a+b, carotenoids, and total phenolic compounds (TPC) in *Solanum lycopersicum* cv. Rutgers (WT) and *hp1* (*high pigment 1*) mutant plants under WL and BL conditions exposed to salt stress.
(A) Level of chlorophyll a+b in WT and *hp1* 7 DAG old plants (hypocotyl + cotyledon) grown under WL and BL conditions in the absence or presence of NaCl (150 mmol/L). Values are the mean ± SD of 3–4 independent biological replicates. (B) Level of carotenoids in WT and *hp1* 7 DAG old plants (hypocotyl + cotelydon) grown under WL and BL conditions in the absence or presence of NaCl (150 mmol/L). Values are the mean ± SD of ± 4 independent biological replicates expressed in µg/g FW. (C) Level of TPC in WT and *hp1* 7 DAG old plants (hypocotyl + cotyledon) grown under WL and BL conditions in the absence or presence of NaCl (150 mmol/L). Values are the mean ± SD of ± 6 replicates expressed in µg GAE/g FW. Different letters indicate statistically significant differences (multiple t-test with Welch correction or Mann-Whitney test, $p < 0.05$); GAE, gallic acid equivalents; FW, fresh weight.

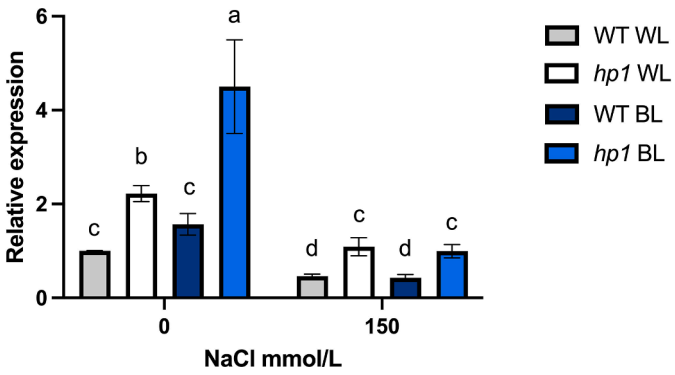

Fig. 3. Expression of *HY5* in *Solanum lycopersicum* cv. Rutgers (WT) and *hp1* (*high pigments 1*) mutant under WL and BL conditions exposed to salt stress.
Relative expression levels of *HY5* in WT and *hp1* 7 DAG old plants (whole seedlings) grown under WL and BL in the absence or presence of NaCl (150 mmol/L). Expression levels were normalized to control WT plants under WL. Values are the mean ± SE of three independent experiments. Different letters indicate statistically significant differences (unpaired t-test or Welch's t-test, $p < 0.05$); SE, standard error.

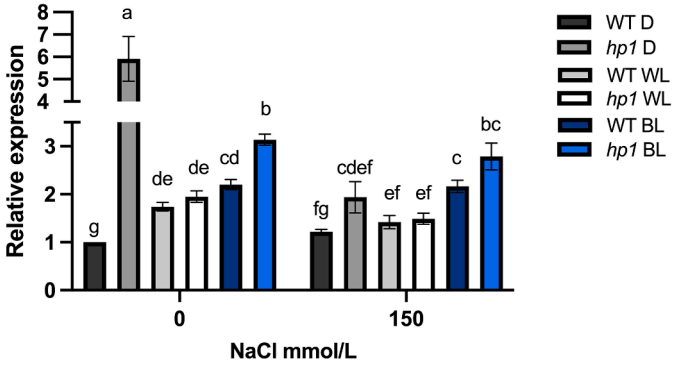

Fig. 4. Expression of *PIF4* in *Solanum lycopersicum* cv. Rutgers (WT) and *hp1* (*high pigment 1*) mutant in the dark and under WL or BL conditions exposed to salt stress.
Relative expression levels of *PIF4* in WT and *hp1* 7 DAG old plants (whole seedlings) grown in the dark, under WL and BL in the absence or presence of NaCl (150 mmol/L). Expression levels were normalized to control WT plants in the dark. Values are the mean ± SE of three independent experiments. Different letters indicate statistically significant differences (unpaired t-test or Welch's t-test, $p < 0.05$); SE, standard deviation.

plants (by approx. 88 % and 450 %, respectively), whereas under WL, salt stress reduced ABA level by approx. 30 % (Fig. 5A).

Under control conditions, ACC content in WT plants was approximately 57 % higher in WL and approximately 30 % lower under BL than in the dark (Supplementary Table S2). The *hp1* plants displayed reduction in ACC levels (about 43 %) under WL, while showing significantly higher ACC content (by approx. 94 %) under BL relative to dark conditions (Supplementary Table S2). Salt stress induced varied ACC responses, depending on light quality. In WT plants, salt stress did not affect ACC level in the dark, however, it significantly increased (about 4 times) or decreased (about 2 times) the accumulation of ACC in seedlings grown under WL or BL, respectively (Fig. 5). Similarly, in the *hp1* mutant, the level of ACC increased due to salinity in etiolated (about 1.2 times) and WL-grown plants (about 5 times), but decreased (about 4 times) under BL exposure (Fig. 5).

For further characterization of the ACC metabolism in WT and *hp1* plants, they were treated with exogenous ACC and the ethylene biosynthesis inhibitor AVG. Based on dose-response analysis of growth parameters (Supplementary Fig. S2 and Fig. S3), a concentration of 1 μmol/L was selected for both ACC and AVG treatments. Plants treated with 1 μmol/L ACC showed significantly higher ACC content in *hp1* than in WT under all light conditions (dark, WL, BL), with the ACC treatment inducing a substantially higher increase in *hp1* relative to its control compared to WT, particularly in the dark and under WL (Supplementary Table S3). Under salt stress, the same trend was observed: the combined ACC and NaCl treatment resulted in significantly greater ACC accumulation in *hp1* over salt stress alone, and in WT across all light conditions (dark, WL, BL). However, AVG treatment induced a more pronounced reduction of ACC content in *hp1* compared to its control than in WT plants, particularly under BL. Combined AVG and NaCl treatment showed a greater decline in ACC content in *hp1* relative to salt stress alone than in WT under WL and BL, whereas in the dark, ACC levels increased in both genotypes (Supplementary Table S3).

To investigate the relationship between ABA and ACC, WT and *hp1* plants were exposed to exogenous ABA (1 μmol/L) in the dark, under WL, and BL conditions (Fig. 5C). In the dark and BL, the application of ABA reduced ACC accumulation in both WT and *hp1* plants, with ACC content under BL approaching the detection limit. Conversely, ABA treatment under WL resulted in elevated ACC accumulation in both genotypes. Additionally, this relationship was investigated through the effect of ACC or AVG on ABA levels under the same light conditions (Supplementary Table S3). In the dark, ABA levels in WT remained unchanged at 1 μmol/L ACC and 1 μmol/L AVG, but slightly increased in *hp1* plants. During salt stress, the addition of ACC or AVG had no effect on ABA levels in either WT or *hp1* dark-grown plants compared to salt stress alone. Under WL, ABA content was unaffected in WT by both treatments, while *hp1* showed a slight increase. In WT plants exposed to BL, ABA levels increased with both ACC and AVG treatments (more with ACC), whereas *hp1* showed a greater increase with AVG relative to its control. Salt stress combined with ACC or AVG generally increased ABA content compared to salt stress alone, except in *hp1* under BL, where no additional effect was observed (Supplementary Table S3).

ABA biosynthesis was further analysed through the expression of genes encoding key enzymes involved in its synthesis and degradation (Fig. 6). In control conditions, the expression of the *NCED1* gene, which plays a central role in ABA production (Thompson et al., 2000), was higher in etiolated WT plants than in the *hp1* mutant (Supplementary Fig. S4). However, under salt stress, *NCED1* transcripts remained at similar levels in WT dark-grown plants, while the expression increased in *hp1*, resulting in comparable values (Supplementary Fig. S6). Light (WL, BL) influenced *NCED1* expression differently in a genotype-dependent manner (Fig. 6A). In WL, transcript levels were similar between WT and *hp1* under both control and salt conditions (Fig. 6A). Under BL, *hp1* plants had lower *NCED1* expression than WT. Despite this, salt stress increased *NCED1* transcript abundance in both genotypes exposed to BL, with a more pronounced increase in the *hp1* mutant relative to its basal expression level.

CYP707A3 is one of four genes involved in ABA catabolism (Saito et al., 2004). In the dark, WT and *hp1* plants showed different expression patterns. Under non-stress conditions, expression of *CYP707A3* was much lower in WT than in the mutant. Salt stress did not affect the transcript level of *CYP707A3* in etiolated WT plants, whereas *hp1* plants displayed a significant decline (Supplementary Fig. S6). The *hp1* mutant exposed to WL and BL had significantly higher *CYP707A3* expression than WT under control conditions, although the transcript level declined sharply (by about 70 %) during salt stress (Fig. 6B). Interestingly, in WL or BL, WT plants exhibited a slight reduction or no change in *CYP707A3* expression in response to salinity compared to the control (Fig. 6B).

3.5. *The hp1 mutant shows enhanced ABA signalling with light-dependent transcriptional regulation*

Changes in the ABA signalling pathway were analysed based on expression of the *ABI5* gene, which encodes a key transcription factor involved in ABA signalling (Finkelstein and Lynch, 2000).

In WT plants, *ABI5* expression increased under salt stress in etiolated

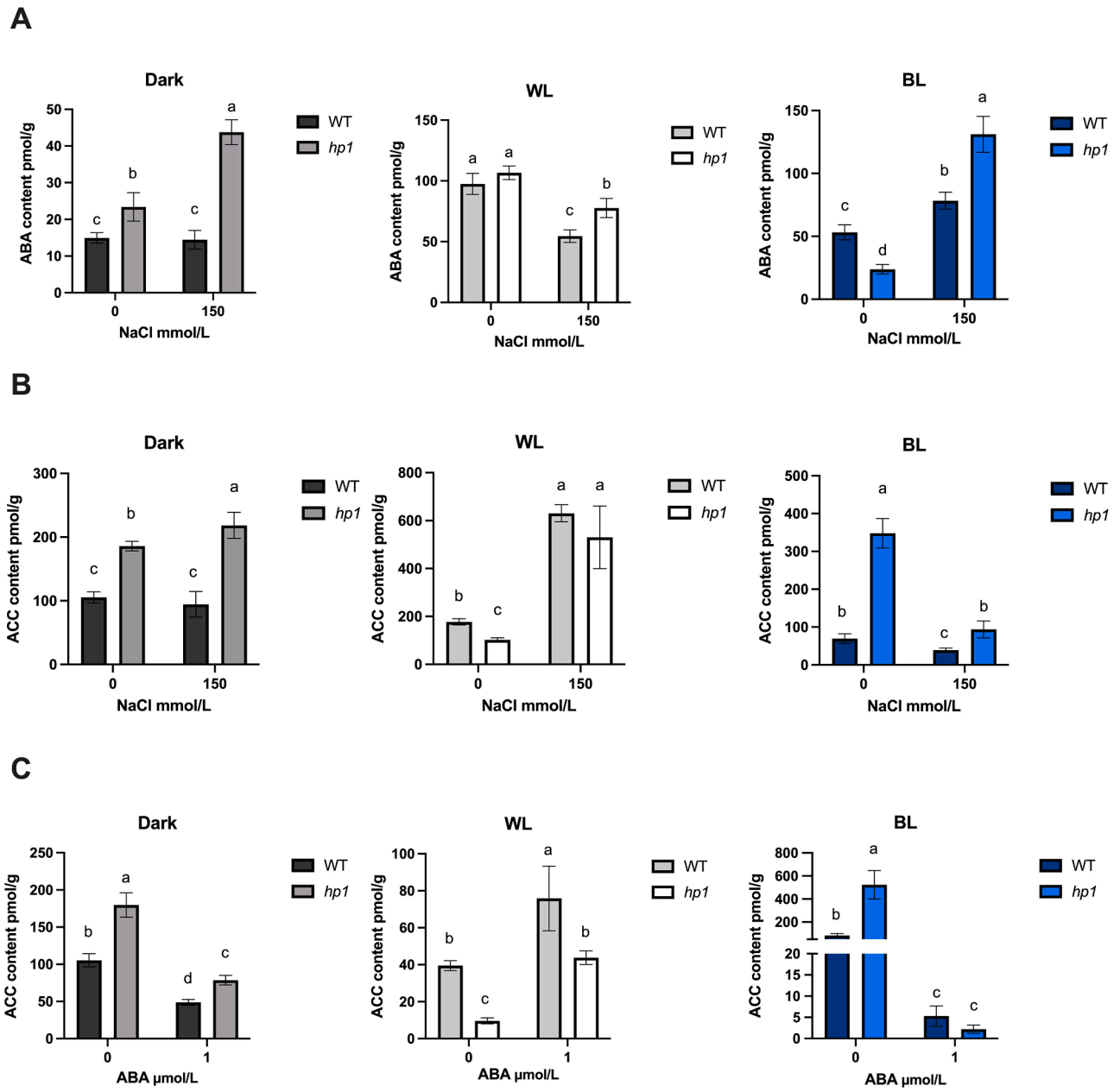

Fig. 5. ABA and ACC levels in *Solanum lycopersicum* cv. Rutgers (WT) and *hp1* (*high pigment 1*) mutant plants in the dark, under WL and BL conditions exposed to salt stress or exogenous ABA.
Level of ABA (A) and ACC (B) in WT and *hp1* 7 DAG old plants (whole seedlings) in the absence or presence of NaCl (150 mmol/L) grown in the dark, and in WL or BL conditions. (C) Level of ACC in WT and *hp1* 7 DAG old plants (whole seedlings) treated with exogenous ABA (1 µmol/L) and grown in the dark, and in WL or BL conditions. Values, expressed in pmol/g FW, are the mean ± SD of ± 6 technical replicates. Different letters indicate statistically significant differences (Welsh ANOVA with Dunnett correction or for non-parametric data, multiple Mann-Whitney test, $p < 0.05$); ABA, abscisic acid; ACC, 1-aminocyclopropane-1-carboxylic acid; FW, fresh weight; SD, standard deviation.

plants (Supplementary Fig. S4) as well as in light conditions (WL, BL) (Fig. 7). Under dark conditions, the *hp1* mutant showed slightly lower expression of *ABI5* compared to WT in controls, but during salt stress, the transcript levels increased similarly in both genotypes (Supplementary Fig. S7). However, *hp1* plants grown under WL or BL had higher *ABI5* transcript levels than WT, regardless of salt treatment, with the increase being more pronounced under BL (Fig. 7).

Expression of genes *SnRK2.2*, encoding a positive regulator of ABA signalling, and *PP2C2*, a negative regulator (Lin et al., 2021), was further analysed in WT and *hp1* plants (Supplementary Fig. S8). *SnRK2.2* transcript levels decreased or remained unchanged during salt stress across all light conditions tested (Supplementary Fig. S8A). In the dark, *SnRK2.2* expression was lower in *hp1* than in WT plants under control and salt conditions, whereas under WL and BL, *SnRK2.2* transcript levels were higher in *hp1* mutant compared to WT. Interestingly, *PP2C2* expression was significantly upregulated during salt stress under all light conditions (dark, WL, BL) in both genotypes (Supplementary Fig. S8B). In control conditions, dark-grown *hp1* plants exhibited lower *PP2C2* transcript levels than WT, with the difference most pronounced under salt stress. Conversely, under WL, *PP2C2* expression was higher in *hp1* than in WT plants during salt stress, while under BL, this difference was observed under both control and salt-stress conditions.

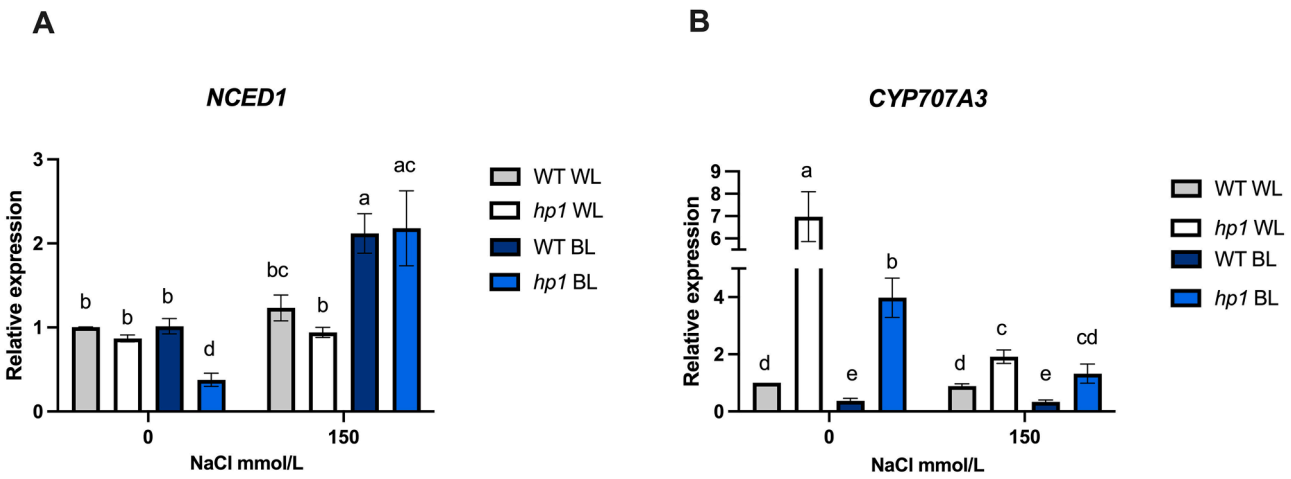

Fig. 6. Expression of *NCED1* and *CYP707A3* in *Solanum lycopersicum* cv. Rutgers (WT) and *hp1* (*high pigment 1*) mutant under WL and BL conditions exposed to salt stress.
Relative expression levels of *NCED1* (A) and *CYP707A3* (B) in WT and *hp1* 7 DAG old plants (whole seedlings), grown under WL or BL in the absence or presence of NaCl (150 mmol/L). Expression levels were normalized to control WT plants under WL. Values are the mean ± SE of three independent experiments. Different letters indicate statistically significant differences (unpaired t-test or Welch's t-test, $p < 0.05$); SE, standard error.

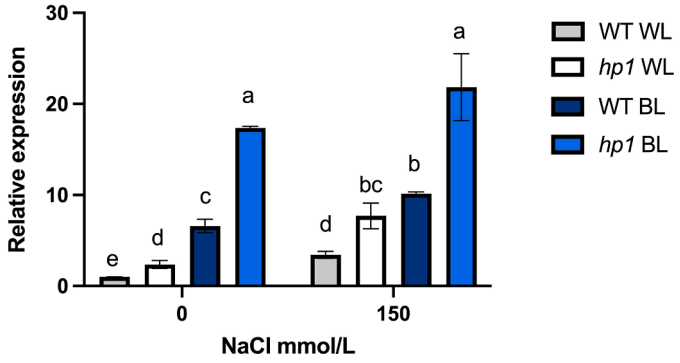

Fig. 7. Expression of *ABI5* in *Solanum lycopersicum* cv. Rutgers (WT) and *hp1* (*high pigment 1*) mutant under WL and BL conditions exposed to salt stress.
Relative expression levels of *ABI5* in WT and *hp1* 7 DAG old plants (whole seedlings) grown under WL and BL in the absence or presence of NaCl (150 mmol/L). Expression levels were normalized to control WT plants under WL. Values are the mean ± SE of three independent experiments. Different letters indicate statistically significant differences (unpaired t-test or Welch's t-test, $p < 0.05$).

3.6. Enhanced osmoprotectant accumulation in hp1 mutant provides better salt stress tolerance

Proline is an amino acid that plants accumulate as an osmolyte in response to abiotic stress (Liang et al., 2013). In the absence of salt stress, dark-grown WT and *hp1* plants exhibited comparable proline levels Conversely, under WL and BL, the proline level was significantly higher and lower in the *hp1* mutant relative to WT, respectively (Fig. 8A). Salt stress induced a significant increase in proline content under all tested light conditions, with the highest accumulation observed under WL across both genotypes (Supplementary Table S2). However, salt-stressed *hp1* plants accumulated higher proline levels than WT plants in all light conditions. It's in line with the expression of the *P5CS1* gene, which encodes Pyrroline-5-carboxylate synthase (P5CS), the key enzyme in proline biosynthesis (Pérez-Arellano et al., 2010) (Supplementary Fig. S9).

Ornithine (Orn) is a precursor in proline biosynthesis through the Orn pathway (Lou et al., 2020). Under control conditions, WT and *hp1* plants accumulated more Orn when grown in the dark and BL compared to WL (Fig. 8B). Additionally, Orn levels were significantly higher in the *hp1* mutant than in WT under all tested light conditions. In WT plants, salt stress reduced Orn levels in the dark and in BL, whereas content remained unaffected under WL. By contrast, *hp1* plants promoted Orn accumulation in response to salt stress under WL, but levels declined in the dark and BL conditions. Overall, *hp1* plants maintained higher Orn content than WT across all conditions, which correlated with proline accumulation (Fig. 8B).

3.7. hp1 plants displayed altered polyamine profiles with light-dependent accumulation patterns

Polyamines are organic compounds containing nitrogen that fulfil multiple functions in plants, such as enhancing productivity, regulating development, and coordinating responses to stress. The major polyamines in plants are putrescine (Put) and Put-derived spermidine (Spd) and spermine (Spm) (Blázquez, 2024). Precursors of these polyamines are arginine (Arg) and Orn.

Across all tested conditions, accumulation of Arg (Supplementary Fig. S11) and Orn (Fig. 8B) was significantly higher in the *hp1* mutant compared to WT. Under control conditions, light (WL, BL) did not essentially affect the Put content in WT plants. In contrast, the *hp1* mutant showed higher Put levels under WL and BL than in dark-grown plants (Supplementary Table S2). Spd and Spm contents were elevated under WL in both genotypes, whereas BL stimulated an increase only in *hp1* plants relative to the dark (Supplementary Table S2). During salt stress, Put and Spd levels under WL and BL were similar to their respective controls in both WT and *hp1* plants, while Spm content increased (Fig. 9). In the dark, salt stress reduced Put, Spd, and Spm levels in WT plants, but promoted the accumulation of all three polyamines in *the hp1* mutant. Under WL, the *hp1* mutant consistently showed higher Put and Spd levels than WT. In *hp1* plants exposed to BL, Spd remained elevated compared to WT regardless of stress, while Put was higher only under control conditions and decreased slightly during salt stress (Fig. 9A, B). In contrast, under control conditions, Spm content was elevated in *hp1* only under BL compared to WT plants (Fig. 9C).

4. Discussion

In this study, we investigated the interplay between light, ABA, and other endogenous compounds in plant responses to salt stress utilizing the photomorphogenetic tomato mutant *hp1*, which has a defect in the DDB1 locus (Lieberman et al., 2004). The DDB1 protein is part of

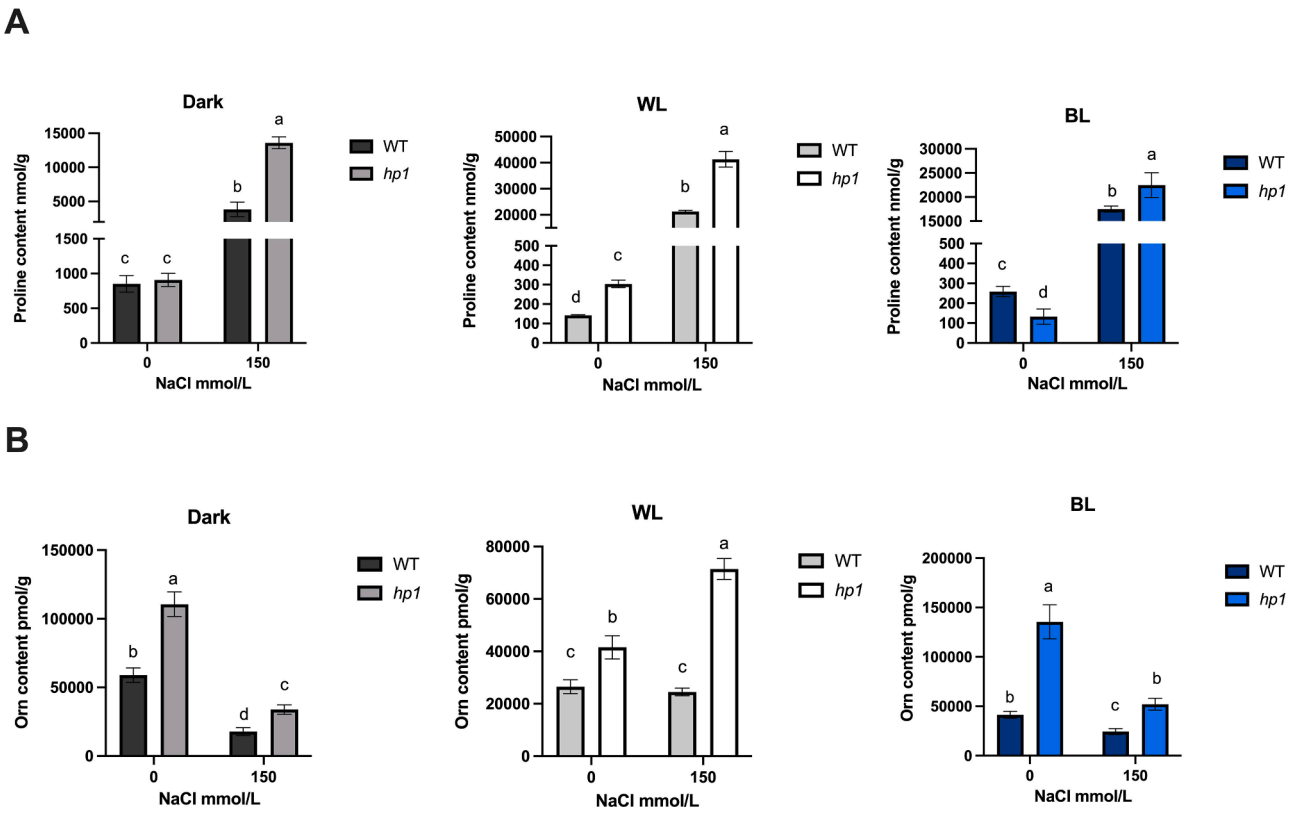

Fig. 8. Proline (Pro) and Ornithine (Orn) accumulation in *Solanum lycopersicum* cv. Rutgers (WT) and *hp1(high pigment 1)* mutant in dark, WL, and BL conditions exposed to salt stress.
Level of Pro (A) and Orn (B) in WT and *hp1* 7 DAG old plants (whole seedlings) in the absence or presence of NaCl (150 mmol/L), grown in the dark and under WL and BL conditions. Values are the mean ± SD of ± 6 technical replicates expressed in pmol/g FW. Different letters indicate statistically significant differences (Welsh ANOVA with Dunnett correction or for non-parametric data, multiple Mann-Whitney test, $p < 0.05$); Pro, proline; Orn, ornithine; FW, fresh weight; SD, standard deviation.

complexes such as CUL4-DDB1 and CDD (COP10-DDB1-DET1), involved in repressing light signalling by promoting the degradation of positive regulators (Schroeder et al., 2002; Chen et al., 2010). The loss of DDB1 function altered plant responses to light, resulting in a specific phenotype and changes in hormone and metabolic profiles. Our results revealed a strong interaction between light and ABA during salt stress. Enhanced light signalling in the *hp1* mutant leads to elevated ABA signalling and alterations in ABA biosynthesis, while the effect is more pronounced under BL conditions. This altered light-ABA interaction in *hp1* plants likely modulates the accumulation of stress-related metabolites and alters the plant's sensitivity to salt conditions. Dark-grown *hp1* plants showed a similar hypocotyl length as WT plants. In contrast, the *hp1* mutant displayed significantly shorter hypocotyl than WT under WL, with more obvious inhibition of growth under BL. This specific *hp1* phenotype in response to light is consistent with the results of previous works (Liu et al., 2004; Hunziker et al., 2022).

The stronger inhibitory effect of BL on hypocotyl elongation aligns with the earlier reported role of CRYs and PHOTs in regulating this process (Folta and Spalding, 2001). In our study, the BL condition was applied at a lower intensity (10 μmol m^{-2} s^{-1}) compared to WL (100 μmol m^{-2} s^{-1}) to avoid stress responses under continuous illumination, as higher BL intensities are known to trigger CRY-mediated ROS production (Consentino et al., 2015) and significant chloroplast avoidance responses (Ko et al., 2020). Additionally, the *hp1* phenotype parallels other photomorphogenic mutants, including CRY1 and CRY2 overexpression lines (Lin et al., 1998; Giliberto et al., 2005) and the *det1* (*de-etiolated 1*) mutant (Ganpudi and Schroeder, 2013).

A comparison of our tomato *hp1* mutant with *Arabidopsis ddb1* mutants reported in other studies reveals key differences. The tomato genome contains only a single *DDB1* gene, while *Arabidopsis* possesses two homologs (*DDB1A* and *DDB1B*) (Lieberman et al., 2004; Bernhardt et al., 2010). In *Arabidopsis* mutants deficient in one of the *DDB1* genes, the remaining copy may compensate for the lost function; therefore, these mutants showed no detectable changes in phenotype. However, the *Arabidopsis* double mutant *ddb1a/ddb1b* is lethal (Bernhardt et al., 2010), making tomato *hp1* a valuable model for studying the complete loss of DDB1 functions in photomorphogenesis.

Our salt stress growth experiments showed that *hp1* plants are potentially stress-tolerant, similar to findings in the tomato *7B-1* mutant demonstrating BL-specific tolerance to mannitol-induced osmotic stress (Fellner and Sawhney, 2002). The *hp1* shoots were salt-tolerant under BL and displayed minimal growth inhibition by NaCl under WL conditions. Under WL and BL, salinity slightly reduced root growth in *hp1* plants, whereas WT roots were insensitive to salt stress under the same light conditions. This differential response is likely due to the elevated accumulation of ABA in the *hp1* plant relative to WT. It's correlated with the earlier-described ABA inhibitory role in root growth. Several studies indicate that high ABA concentrations inhibit root growth by suppressing cell division and cell expansion through core signaling components (PYR/PYL receptors, SnRK2s, and PP2Cs), while also activating NADPH oxidases AtrbohD and AtrbohF to drive ROS production. ABA further disrupts growth by reducing auxin levels, downregulating auxin transport genes (AUX1, PIN1, PIN3, PIN4, and PIN7), and impairing auxin signalling (Li et al., 2017; Sun et al., 2018). Ethylene biosynthesis has also been shown to be required for this inhibitory effect (Luo et al., 2014).

The involvement of BL-mediated signalling in salt stress responses we further investigated using the *cry1acry2* double mutant, which lacks

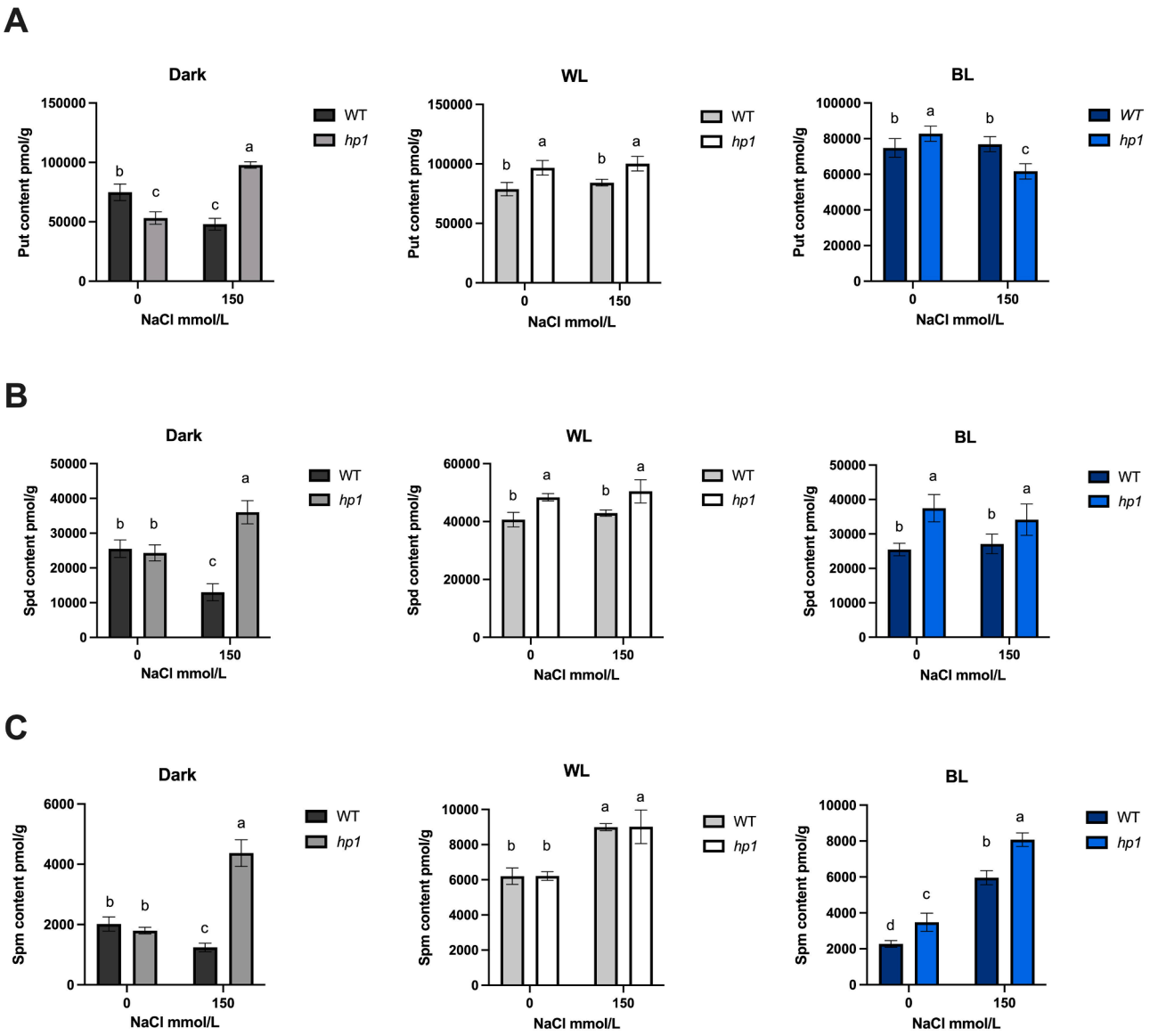

Fig. 9. Level of polyamines in *Solanum lycopersicum* cv. Rutgers (WT) and *hp1* (*high pigment 1*) in dark, WL and BL conditions exposed to salt stress.
Level of Put (A), Spd (B) and Spm (C) in WT and *hp1* 7 DAG old plants (whole seedlings) in the absence or presence of NaCl (150 mmol/L), grown in the dark and under WL and BL conditions. Values are the mean ± SD of ± 6 technical replicates expressed in pmol/g FW. Different letters indicate statistically significant differences (ANOVA with Tukey test or Welch ANOVA, $p < 0.05$); Put, putrescine; Spd, spermidine; Spm, spermine; FW, fresh weight; SD, standard deviation.

functional BL receptors (CRY) (the results are presented in the Supplementary material). *Cry1acry2* plants showed increased sensitivity to salt stress, particularly under light conditions (WL, BL) and at higher NaCl concentrations (150, 200 mmol/L NaCl). This aligns with previous studies reporting enhanced sensitivity of *crya1cry2* mutant to cold stress, as well as increased salt sensitivity in *cry1a* mutant tomato plants (Li et al., 2021; Dong et al., 2025). These contrasting results between *hp1* and *cry1acry2* further support the specific role of BL in plant adaptation to salt stress.

Previous research on *hp1* plants focused primarily on the fruit, confirming enhanced pigment accumulation in *hp1* fruits (Lieberman et al., 2004; Pal et al., 2019; Wang et al., 2019). In our study, we measured pigment levels (chlorophyll, carotenoids) in 7 DAG old seedlings treated with 150 mmol/L NaCl under WL and BL. The experiment revealed that under BL, the *hp1* mutant had raised photosynthetic pigment levels, which remained stable during salt stress, whereas in WT, pigment content varied between control and salt conditions. However, in WL as well as in BL, the carotenoid level was higher in *hp1* than in WT plants, regardless of the stress conditions. These results underline the positive role of BL photoreceptors in regulating pigment biosynthesis. Previous research reported an involvement of CRY1 and CRY2 in photosynthetic pigment accumulation (López-Figueroa and Niell, 1988; Giliberto et al., 2005; D'Amico-Damião et al., 2021). The possible reason for the BL-enhanced effect on chlorophyll metabolism lies in the modulation of the key catabolic genes. BL specifically upregulates *AtCLH2* via CRY1, whereas *AtCLH1* responds to both BL and RL through cryptochrome-phytochrome cooperation (Banas et al., 2011). WL may balance these signalling pathways in *hp1* plants, masking the pronounced effects observed under monochromatic BL due to mixed wavelengths.

A defect in the DBB1 protein increased the mutant plant's response to light. Consequently, we decided to analyse the expression of the *HY5* and *PIF4* genes, which encode key transcription factors controlling light signalling (Toledo-Ortiz et al., 2014). HY5 is a central positive regulator of photomorphogenesis, coordinating light-responsive development and stress adaptation (Nawkar et al., 2017; Xiao et al., 2022). Our results showed that the *hp1* mutant upregulated *HY5* expression under light conditions, particularly in response to BL. These outcomes indicate *hp1*

hypersensitivity to light, due to an amplified light signalling pathway, consistent with phenotypic and pigment changes. In dark-growing plants, the transcription factor *HY5* is degraded by COP1, an E3 ubiquitin ligase, through regulated complexes involving the DDB1 protein (Chen et al., 2010; Xu et al., 2014), suggesting that a defect in this protein may alter *HY5* expression. Interestingly, *HY5* transcript levels declined under salt stress in *hp1* and WT plants, with a more pronounced reduction in *hp1* relative to the basal level. This may reflect the plant's transition from growth to stress adaptation. Elevated *HY5* expression under BL supports previous discoveries that BL promotes HY5 accumulation via CRY1-COP1 interactions (Osterlund et al., 2000; Liu et al., 2011). Unexpectedly, WT plants showed higher *HY5* transcripts in the dark relative to light (WL, BL), possibly as a preparatory transcriptional mechanism for rapid photomorphogenetic responses upon light exposure.

The PIF4 is a negative regulator of phytochrome signalling that promotes gene expression to inhibit photomorphogenesis (Choi and Oh, 2016). Dark-grown *hp1* plants displayed upregulated *PIF4* gene under control conditions compared to the WT. However, under salt stress, transcript levels markedly decreased in the *hp1* mutant, whereas the expression slightly increased in WT plants grown in the dark. This altered *PIF4* expression is likely due to the loss of DDB1 protein, which typically interacts with the COP1-SPA ubiquitin ligase complex to regulate PIF4 stability in the dark (Ponnu and Hoecker, 2021). During salt conditions, the disrupted regulatory system fails to properly coordinate stress signalling with photomorphogenic pathways, resulting in opposite transcriptional responses between dark-grown *hp1* and WT plants. In *hp1* plants exposed to BL, we observed slightly higher *PIF4* expression under control conditions, which correlated with published literature indicating that cryptochromes directly interact with PIF4 to regulate plant growth under BL. Moreover, the CRY1–PIF4 complex is a key mechanism for BL-controlled temperature-responsive growth (Ma et al., 2016; Pedmale et al., 2016). Furthermore, we analysed the expression of the *ABI5* gene encoding a key transcription factor in ABA signalling. Our data revealed that the enhanced light signalling pathway in the *hp1* plants may have influenced ABA signalling, possibly through HY5 – ABI5 interaction (Chen et al., 2008; Bhagat et al., 2021). According to Yadukrishnan & Datta (2021), ABI5 may act as a major convergence point in the interaction between light and ABA under abiotic stress. We found that *ABI5* gene was upregulated in *hp1* plants compared to WT, especially under BL. Zhou et al. (2018) suggest that CRY1 may modulate ABA signalling via the HY5–ABI5 regulon. To further support the role of BL in regulating *ABI5* expression, we measured *ABI5* transcript levels in the *cry1cry2* double mutant under identical conditions. Consistent with *ABI5* the upregulation observed in *hp1* plants, we showed that *cry1cry2* plants exhibited reduced *ABI5* transcript levels compared to WT under all light conditions (dark, WL, and BL), particularly under salt stress. The most pronounced downregulation was observed under BL, confirming the specific role of CRY-mediated BL perception in modulating ABA signalling through ABI5 regulation under salt stress.

Altered ABA signalling in the *hp1* mutant was also supported by expression of key ABA regulators *SnRK2.2* (positive ABA regulator) and *PP2C2* (negative ABA regulator). In the dark, *SnRK2.2* and *PP2C2* expression was reduced in the *hp1* plants compared to WT. Conversely, under WL and BL, *hp1* plants exhibited higher transcript levels of *SnRK2.2*, indicating enhanced activation potential of ABA signalling. At the same time, the upregulation of *PP2C2* transcript level in *hp1* under WL and BL, particularly during salt stress, reflects amplified negative feedback control of ABA signalling in the mutant. This coordinated modulation of both positive and negative ABA regulators is consistent with the elevated *ABI5* expression observed in *hp1* plants exposed to WL and BL.

ABA quantification in tomato WT and *hp1* seedlings provides insight into distinct light-dependent accumulation patterns in plant responses to salt stress, which correlate with the gene expression results of *NCED1* and *CYP707A3*. Under dark conditions, salt-stressed WT plants had ABA levels through coordinated upregulation of *NCED1* and *CYP707A3*. In contrast, salt-stressed etiolated *hp1* mutant accumulated elevated ABA due to reduced *CYP707A3* expression, effectively limiting degradation and promoting accumulation. WL surprisingly decreased ABA content in both genotypes; salt stress does not affect *NCED1* expression in WT and *hp1* plants, and *CYP707A3* was downregulated only in salt-stressed *hp1* plants compared to basal expression. In contrast, BL enhanced ABA levels in WT plants via salt-induced *NCED1* upregulation, while the *CYP707A3* transcript level remained unchanged. Under BL, salt stress substantially increased ABA accumulation in *hp1* relative to the basal level, driven by enhanced *NCED1* expression and a simultaneous marked decrease in *CYP707A3* expression. These results indicate that *hp1* plants have altered both ABA synthesis and catabolism pathways in a light-dependent manner, correlated with enhanced light and ABA signalling networks, and thus with the observed tolerance of *hp1* shoots to salinity.

We further validated these findings by measuring ABA content and the expression of *NCED1* and *CYP707A3* genes in the *cry1cry2* double mutant under the same conditions. In the dark, salt stress induced significantly higher ABA accumulation in *cry1acry2* compared to WT, driven by a pronounced increase in *NCED1* expression, while *CYP707A3* transcript levels were reduced across all light conditions under salt stress. However, under WL and BL, salt-stressed *cry1acry2* plants maintained lower ABA levels than WT, consistent with reduced *NCED1* expression regardless of salt treatment. These results suggest that CRYs may play a key role in regulating ABA homeostasis under salt stress by modulating both biosynthesis and catabolism pathways in a light-dependent manner, supporting the importance of BL signalling in plant adaptation to salinity.

In our experiments, we observed that in the absence of salt stress, BL induced the accumulation of ACC in *the hp1* mutant, but not in the WT. These data align with earlier research, reporting light-mediated regulation of ethylene biosynthesis through alterations in ACS and ACO gene expression, affecting ACC content (Harkey et al., 2019). Under BL, exposure to salt stress resulted in a decline in ACC levels in WT plants, while this reduction was substantially stronger in the *hp1* mutant. Thus, *hp1* mutant tolerance to salt stress in BL is associated with lower ethylene accumulation. These results are in good correlation with observations that exogenous ABA reduced ACC levels in both WT and *hp1* plants in the dark and under BL conditions, with the reduction more pronounced in the *hp1* mutant under BL. The data indicate that BL mediates ABA-induced inhibition of ethylene biosynthesis. Previous publications reported that ABA and ethylene interact antagonistically or synergistically, depending on various environmental factors (Ghassemian et al., 2000; LeNoble et al., 2004; Li et al., 2019). A study by Li et al. (2011) supported the idea that the interaction between ABA and ACC depends on light conditions, and HY5 modulates both biosynthesis pathways.

We also examined how the regulation of ethylene biosynthesis affects ABA levels under the same light conditions using ACC and AVG treatments. Modulation of ethylene biosynthesis resulted in limited effect on ABA levels in the dark and WL conditions in both genotypes, whereas more pronounced responses were observed in WT and *hp1* plants exposed to BL, indicating that BL strongly modulates the crosstalk between these pathways. The *hp1* plants treated by AVG showed higher ABA accumulation compared to the control condition than WT, which is consistent with enhanced light signalling in *hp1*, which likely amplifies ABA accumulation when ACC production is suppressed. We suggest that BL may enhance ABA responsiveness to altered ethylene biosynthesis, leading to increased ABA levels under AVG and ACC treatment. Overall, these findings indicate that ABA-ethylene crosstalk is dynamically regulated and strongly influenced by various environmental conditions.

The crosstalk was further supported by the observation that modulation of ethylene biosynthesis through ACC and AVG treatments influenced ABA accumulation in a light-dependent manner during salt stress. In the dark, ACC and AVG treatments had no effect on ABA

content under salt stress in WT and *hp1* plants, whereas under WL and BL, both treatments generally increased ABA levels. However, this effect was absent in *hp1* plants under BL, suggesting that the ABA response in *hp1* may already operate at maximum capacity, with enhanced light signalling potentially limiting further ABA accumulation when ethylene biosynthesis is modulated under salt stress.

Additional insight into the light-dependent regulation of ACC metabolism was provided by treatments with exogenous ACC and the ethylene biosynthesis inhibitor AVG, which revealed altered regulation of ACC metabolism in *hp1* plants. In the dark and WL conditions, *hp1* accumulated significantly higher ACC levels than WT compared to their respective controls, while under BL, these differences between genotypes were no longer observed. Conversely, AVG treatment in plants under BL resulted in a more pronounced reduction of ACC content in *hp1* relative to the basal levels than in WT, indicating enhanced sensitivity of ethylene biosynthesis to BL signalling in this mutant.

Amplified light signalling and ABA levels in the mutant *hp1* most likely affect the content of stress-related compounds, including phenolic compounds, proline, and polyamines. Proline functions as an osmolyte and an antioxidant, scavenging reactive oxygen species under stress conditions (El Moukhtari et al., 2020). Salt stress increased proline levels in both genotypes under all tested light conditions, while the most pronounced proline accumulation was observed under WL. Our data are consistent with the previously described regulatory role of light in proline metabolism, mediated through HY5-induced expression of *P5CS1* and suppression of *PDH1* (Hayashi et al., 2000; Kovács et al., 2019). Salt-stressed *hp1* plants exhibited elevated proline levels compared to WT under dark and light conditions, particularly in WL, which was linked to higher *P5CS1* expression. Moreover, the results align with other studies demonstrating the essential role of light in salt-induced proline accumulation (Kovács et al., 2019; Kovtun et al., 2019). Additionally, we analysed proline content in the *cry1acry2* tomato double mutant to support the role of light signalling in proline accumulation. *Crya1cry2* showed an opposite pattern in response to salt stress in the dark compared to WL and BL conditions. In the dark, *cry1acry2* plants exhibited higher proline levels than WT under salt stress, whereas in WL and BL, proline content was significantly reduced relative to WT. It's correlated with results obtained in *hp1* indicating that enhanced light signalling promotes proline synthesis, while impaired BL perception in *crya1cry2* compromises this response.

Proline synthesis occurs via glutamate and Orn pathways (Meena et al., 2019). Therefore, we measured Orn levels in WT and *hp1* plants. Our *hp1* mutant showed elevated Orn levels compared to WT under all tested conditions. The effects of light (WL, BL) and dark conditions on Orn metabolism varied during salt stress. Both BL and dark led to reduced Orn levels in salt-stressed plants of both genotypes, with the decrease being more pronounced in the *hp1* mutant. In contrast, we observed a different pattern of Orn accumulation in WT and *hp1* plants grown in WL. While WT plants maintained stable Orn levels under salt conditions, *hp1* plants experienced an increase in Orn accumulation under salt stress. The obtained results support the hypothesis that enhanced light signalling in *hp1* plants affects proline synthesis pathways.

The *hp1* mutant also produced higher levels of phenolic compounds than WT under both WL and BL in control conditions, supporting an enhanced antioxidant defence in *hp1* plants. However, during salt stress, only *hp1* plants grown in BL showed a higher content of phenolic compounds compared to WT plants, whereas no difference was observed between genotypes under WL. These data are consistent with research confirming BL's role in regulating the accumulation of phenolic compounds under stress conditions via CRYs (Brelsford et al., 2019; Rai et al., 2019), which directly interact with PIF4 and PIF5 transcription factors to modulate stress-responsive phenolic biosynthesis (Pedmale et al., 2016).

In addition to the above-mentioned substances, polyamines represent another important group in plants' defence against stress. Arg and also Orn are precursors for polyamines (Put, Spd, and Spm). Our results demonstrated that the *hp1* had enhanced accumulation of all analysed polyamines (Put, Spd, Spm), which can boost stress tolerance. It is associated with a higher content of Arg and Orn in *hp1* plants relative to WT under both tested light conditions. Under control conditions, WL stimulated Put levels exclusively in *hp1* mutant compared to dark-grown plants. Spd and Spm content raised under WL in both genotypes, with an increase under BL specific to *hp1* plants. This data supports the earlier report that in tomato, polyamines are accumulated more under light (WL, BL) than in the dark (Santa-Cruz et al., 1998). Salt stress mostly didn't affect levels of Put and Spd, while only Spm level increased under light (WL, BL), especially in BL conditions with consistently higher Spm content in *hp1* plants. Research on wheat plants revealed that BL upregulated key genes for polyamine biosynthesis, whereas red light had opposing effects on the expression of these genes (Pál et al., 2022). Surprisingly, in the dark, salinity reduced polyamine content in WT, whereas it increased its amount in the *hp1* mutant. The data indicate that the mutant confers improved stress tolerance mechanisms even under dark conditions.

Based on observed changes in the accumulation of proline and polyamines, we suggest that enhanced light signalling in *hp1* regulates multiple stress-related metabolic pathways through shared precursors, such as Orn, contributing to improved stress adaptation.

5. Conclusions

This study demonstrates that the tomato *hp1* mutant provides a unique model for studying light-ABA interactions during salt stress. Through impaired DDB1 function, *hp1* plants exhibit amplified light signalling that coordinates ABA biosynthesis, ethylene precursor modulation, and accumulation of protective metabolites, including proline, polyamines, and phenolic compounds. The pronounced effects under BL confirm the essential role of specific light wavelengths in stress adaptation mechanisms. Our results indicate that enhanced interactions between HY5 and ABI5 in *hp1* plants may create a regulatory hub that integrates light perception with hormonal stress responses. Additionally, light coordinates multiple metabolic pathways via shared metabolic precursors such as Orn and Arg. These findings suggest that manipulating signalling components, like DDB1, presents a potential strategy for enhancing salt tolerance in crop breeding programs. Future research should investigate the molecular details of DDB1-mediated regulation of these pathways and determine whether similar mechanisms exist in other crop species facing salt stress.

Funding

The presented work was supported by Internal Grant Agency of Palacký University (IGA_PrF_2025_019; IGA_PrF_2026_013 and IGA_PrF_2026_14), by the "Biorefining and circular economy for sustainability" (TN02000044) grant, by the "SMART Plant Biotechnology for Sustainable Agriculture" (CZ.02.01.01/00/23_020/0008497) project of the ERDF Programme Johannes Amos Comenius and by ERC Synergy project "Unravelling Spatio-temporal Auxin Intracellular Redistribution for Morphogenesis" (STARMORPH, reg. no. 101166880).

CRediT authorship contribution statement

Petra Bublavá: Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Data curation, Conceptualization. **Kateřina Cermanová:** Writing – review & editing, Methodology, Investigation, Data curation. **Michal Karady:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Conceptualization. **Martin Fellner:** Writing – review & editing, Validation, Supervision, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors thank Hana Svobodová, Hana Vylíčilová, and Veronika Krbečková for technical assistance. We thank C. M. Rick (Tomato Genetics Resource Center, University of California, Davis, USA) for providing seeds of the *hp1* mutant. We thank E. Fantini (ENEA, Rotondella (Matera), Italy) and E. Heuvelink (Wageningen University & Research, Wageningen, The Netherlands) for providing seeds of *cry1a-cry2* mutant.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.stress.2026.101439.

Data availability

Data will be made available on request.

References

Ahmad, M., Cashmore, A.R., 1993. HY4 gene of *A. thaliana* encodes a protein with characteristics of a blue-light photoreceptor. Nature 366 (6451), 162–166. https://doi.org/10.1038/366162a0.

Banas, A.K., Łabuz, J., Sztatelman, O., Gabrys, H., Fiedor, L., 2011. Expression of enzymes involved in chlorophyll catabolism in Arabidopsis is light controlled. Plant Physiol. 157 (3), 1497–1504. https://doi.org/10.1104/pp.111.185504.

Benlloch-González, M., Romera, J., Cristescu, S., Harren, F., Fournier, J.M., Benlloch, M., 2010. K^+ starvation inhibits water-stress-induced stomatal closure via ethylene synthesis in sunflower plants. J. Exp. Bot. 61 (4), 1139–1145. https://doi.org/10.1093/jxb/erp379.

Bergougnoux, V., Hlaváčková, V., Plotzová, R., Novák, O., Fellner, M., 2009. The *7B-1* mutation in tomato confers a blue light-specific lower sensitivity to coronatine, a toxin produced by *Pseudomonas syringae* pv. tomato. J. Exp. Bot. 60 (4), 1219–1230. https://doi.org/10.1093/jxb/ern366.

Bernhardt, A., Mooney, S., Hellmann, H., 2010. Arabidopsis DDB1a and DDB1b are critical for embryo development. Planta 232 (3), 555–566. https://doi.org/10.1007/s00425-010-1195-9.

Bhagat, P.K., Verma, D., Sharma, D., Sinha, A.K., 2021. HY5 and ABI5 transcription factors physically interact to fine tune light and ABA signaling in Arabidopsis. Plant Mol. Biol. 107 (1–2), 117–127. https://doi.org/10.1007/s11103-021-01187-z.

Bhatnagar, A., Singh, S., Khurana, J.P., Burla, A., 2020. HY5-COP1: the central module of light signaling pathway. J. Plant Biochem. Biotechnol. 29 (4), 590–610. https://doi.org/10.1007/s13562-020-00623-3.

Blázquez, M.A., 2024. Polyamines: their role in plant development and stress. Annu. Rev. Plant Biol. 75 (1), 95–117. https://doi.org/10.1146/annurev-arplant-070623-110056.

Brelsford, C.C., Morales, L.O., Nezval, J., Kotilainen, T.K., Hartikainen, S.M., Aphalo, P. J., Robson, T.M., 2019. Do UV-A radiation and blue light during growth prime leaves to cope with acute high light in photoreceptor mutants of *Arabidopsis thaliana*? Physiol. Plant. 165 (3), 537–554. https://doi.org/10.1111/ppl.12749.

Cermanová, K., Bublavá, P., Darbandsari, M., Fellner, M., Novák, O., Karady, M., 2025. Metabolic network divergence: polyamine and ethylene biosynthesis dynamics in *Arabidopsis thaliana* and *Solanum lycopersicum*. Plant Stress 18, 101124. https://doi.org/10.1016/j.stress.2025.101124.

Chen, H., Xiong, L., 2008. Role of HY5 in abscisic acid response in seeds and seedlings. Plant Signal. Behav. 3 (11), 986–988. https://doi.org/10.4161/psb.6185.

Chen, H., Huang, X., Gusmaroli, G., Terzaghi, W., Lau, O.S., Yanagawa, Y., Zhang, Y., Li, J., Lee, J.H., Zhu, D., Deng, X.W., 2010. Arabidopsis CULLIN4-damaged DNA binding protein 1 interacts with constitutively photomorphogenic1-suppressor of PHYA complexes to regulate photomorphogenesis and flowering time. Plant Cell 22 (1), 108–123. https://doi.org/10.1105/tpc.109.065490.

Choi, H., Oh, E., 2016. PIF4 integrates multiple environmental and hormonal signals for plant growth regulation in Arabidopsis. Mol. Cells 39 (8), 587–593. https://doi.org/10.14348/molcells.2016.0126.

Consentino, L., Lambert, S., Martino, C., Jourdan, N., Bouchet, P.E., Witczak, J., Castello, P., El-Esawi, M., Corbineau, F., d'Harlingue, A., Ahmad, M., 2015. Blue-light dependent reactive oxygen species formation by Arabidopsis cryptochrome may define a novel evolutionarily conserved signaling mechanism. New Phytol. 206 (4), 1450–1462. https://doi.org/10.1111/nph.13341.

D'Amico-Damião, V., Dodd, I.C., Oliveira, R., Lúcio, J.C.B., Rossatto, D.R., Carvalho, R.F., 2021. Cryptochrome 1a of tomato mediates long-distance signaling of soil water deficit. Plant Sci. 303, 110763. https://doi.org/10.1016/j.plantsci.2020.110763.

Dong 董韩, H., Di 狄延翠, Y., Guo 国志信, Z., Lou 娄 世浩, S., Ji 嵇泽琳, Z., Wang 王梓晨, Z., Li 李鹏举, P., Zhou 周艳虹, Y., Yu 喻景权, J., Hu 胡超轶, C., 2025. The cryptochrome 1a-elongated hypocotyl 5 module regulates blue light-induced salt stress tolerance in tomato. Plant Physiol. 199 (3), kiaf538. https://doi.org/10.1093/plphys/kiaf538.

El Moukhtari, A., Cabassa-Hourton, C., Farissi, M., Savouré, A., 2020. How does proline treatment promote salt stress tolerance during crop plant development? Front. Plant Sci. 11, 1127. https://doi.org/10.3389/fpls.2020.01127.

Fantini, E., Sulli, M., Zhang, L., Aprea, G., Jiménez-Gómez, J.M., Bendahmane, A., Perrotta, G., Giuliano, G., Facella, P., 2019. Pivotal roles of cryptochromes 1a and 2 in tomato development and physiology. Plant Physiol. 179 (2), 732–748. https://doi.org/10.1104/pp.18.00793.

Fellner, M., Sawhney, V.K., 2002. The *7B-1* mutant in tomato shows blue-light-specific resistance to osmotic stress and abscisic acid. Planta 214 (5), 675–682. https://doi.org/10.1007/s004250100671.

Finkelstein, R.R., Gampala, S.S., Rock, C.D., 2002. Abscisic acid signaling in seeds and seedlings. Plant Cell 14 (Suppl), S15–S45. https://doi.org/10.1105/tpc.010441.

Finkelstein, R., Reeves, W., Ariizumi, T., Steber, C., 2008. Molecular aspects of seed dormancy. Annu. Rev. Plant Biol. 59, 387–415. https://doi.org/10.1146/annurev.arplant.59.032607.092740.

Finkelstein, R.R., Lynch, T.J., 2000. The Arabidopsis abscisic acid response gene ABI5 encodes a basic leucine zipper transcription factor. Plant Cell 12 (4), 599–609. https://doi.org/10.1105/tpc.12.4.599.

Folta, K.M., Spalding, E.P., 2001. Unexpected roles for cryptochrome 2 and phototropin revealed by high-resolution analysis of blue light-mediated hypocotyl growth inhibition. Plant J. 26 (5), 471–478. https://doi.org/10.1046/j.1365-313x.2001.01038.x.

Ganpudi, A.L., Schroeder, D.F., 2013. Genetic interactions of *Arabidopsis thaliana* damaged DNA binding protein 1B (DDB1B) with DDB1A, DET1, and COP1. G3 3 (3), 493–503. https://doi.org/10.1534/g3.112.005249.

Ghassemian, M., Nambara, E., Cutler, S., Kawaide, H., Kamiya, Y., McCourt, P., 2000. Regulation of abscisic acid signaling by the ethylene response pathway in Arabidopsis. Plant Cell 12 (7), 1117–1126. https://doi.org/10.1105/tpc.12.7.1117.

Giliberto, L., Perrotta, G., Pallara, P., Weller, J.L., Fraser, P.D., Bramley, P.M., Fiore, A., Tavazza, M., Giuliano, G., 2005. Manipulation of the blue light photoreceptor cryptochrome 2 in tomato affects vegetative development, flowering time, and fruit antioxidant content. Plant Physiol. 137 (1), 199–208. https://doi.org/10.1104/pp.104.051987.

Gondor, O.K., Tajti, J., Hamow, K.Á., Majláth, I., Szalai, G., Janda, T., Pál, M., 2021. Polyamine metabolism under different light regimes in wheat. Int. J. Mol. Sci. 22 (21), 11717. https://doi.org/10.3390/ijms222111717.

Gupta, N., Nath, U., 2020. Integration of light and hormone response during seedling establishment. J. Plant Biochem. Biotechnol. 29 (4), 652–664. https://doi.org/10.1007/s13562-020-00628-y.

Harkey, A.F., Yoon, G.M., Seo, D.H., DeLong, A., Muday, G.K., 2019. Light modulates ethylene synthesis, signaling, and downstream transcriptional networks to control plant development. Front. Plant Sci. 10, 1094. https://doi.org/10.3389/fpls.2019.01094.

Hayashi, F., Ichino, T., Osanai, M., Wada, K., 2000. Oscillation and regulation of proline content by P5CS and ProDH gene expressions in the light/dark cycles in *Arabidopsis thaliana* L. Plant Cell Physiol. 41 (10), 1096–1101. https://doi.org/10.1093/pcp/pcd036.

Huala, E., Oeller, P.W., Liscum, E., Han, I.S., Larsen, E., Briggs, W.R., 1997. Arabidopsis NPH1: a protein kinase with a putative redox-sensing domain. Science 278 (5346), 2120–2123. https://doi.org/10.1126/science.278.5346.2120.

Hunziker, J., Nishida, K., Kondo, A., Ariizumi, T., Ezura, H., 2022. Phenotypic characterization of high carotenoid tomato mutants generated by the target-AID base-editing technology. Front. Plant Sci. 13, 848560. https://doi.org/10.3389/fpls.2022.848560.

Jarillo, J.A., Ahmad, M., Cashmore, A.R., 1998. NPL1 (accession No. AF053941): a second member of the NPH serine/threonine kinase family of Arabidopsis (PGR98–100). Plant Physiol. 117, 719.

Jing, Y., Lin, R., 2020. Transcriptional regulatory network of the light signaling pathways. New Phytol. 227 (3), 683–697. https://doi.org/10.1111/nph.16602.

Karady, M., Hladík, P., Cermanová, K., Jiroutová, P., Antoniadi, I., Casanova-Sáez, R., Ljung, K., Novák, O., 2024. Profiling of 1-aminocyclopropane-1-carboxylic acid and selected phytohormones in Arabidopsis using liquid chromatography-tandem mass spectrometry. Plant Methods 20 (1), 41. https://doi.org/10.1186/s13007-024-01165-8.

Kendrick, R.E., Kerckhoffs, L.H.J., Van Tuinen, A., Koornneef, M., 1997. Photomorphogenic mutants of tomato. Plant Cell Environ. 20 (6), 746–751. https://doi.org/10.1046/j.1365-3040.1997.d01-109.x.

Ko, S.-S., Jhong, C.-M., Shih, M.-C., 2020. Blue light acclimation reduces the photoinhibition of *Phalaenopsis aphrodite* (moth orchid). Int. J. Mol. Sci. 21 (17), 6167. https://doi.org/10.3390/ijms21176167.

Kopittke, P.M., Menzies, N.W., Wang, P., McKenna, B.A., Lombi, E., 2019. Soil and the intensification of agriculture for global food security. Environ. Int. 132, 105078. https://doi.org/10.1016/j.envint.2019.105078.

Kovács, H., Aleksza, D., Baba, A.I., Hajdu, A., Király, A.M., Zsigmond, L., Tóth, S.Z., Kozma-Bognár, L., Szabados, L., 2019. Light control of salt-induced proline accumulation is mediated by elongated hypocotyl 5 in Arabidopsis. Front. Plant Sci. 10, 1584. https://doi.org/10.3389/fpls.2019.01584.

Kovtun, I.S., Efimova, M.V., Malofii, M.K., Kuznetsov, V.V., 2019. Tolerance of potato plants to chloride salinity is regulated by selective light. Dokl. Biol. Sci. 484 (1), 19–22. https://doi.org/10.1134/S0012496619010058.

LeNoble, M.E., Spollen, W.G., Sharp, R.E., 2004. Maintenance of shoot growth by endogenous ABA: genetic assessment of the involvement of ethylene suppression. J. Exp. Bot. 55 (395), 237–245. https://doi.org/10.1093/jxb/erh031.

Li, C., Zhang, W., Yuan, M., Jiang, L., Sun, B., Zhang, D., Shao, Y., Liu, A., Liu, X., Ma, J., 2019. Transcriptome analysis of osmotic-responsive genes in ABA-dependent and -independent pathways in wheat (*Triticum aestivum* L.) roots. PeerJ 7, e6519. https://doi.org/10.7717/peerj.6519.

Li, X., Chen, L., Forde, B.G., Davies, W.J., 2017. The biphasic root growth response to abscisic acid in Arabidopsis involves interaction with ehylene and auxin signalling pathways. Front. Plant Sci. 8, 1493. https://doi.org/10.3389/fpls.2017.01493.

Li, Y., Shi, Y., Li, M., Fu, D., Wu, S., Li, J., Gong, Z., Liu, H., Yang, S., 2021. The CRY2-COP1-HY5-BBX7/8 module regulates blue light-dependent cold acclimation in Arabidopsis. Plant Cell 33 (11), 3555–3573. https://doi.org/10.1093/plcell/koab215.

Li, Z., Zhang, L., Yu, Y., Quan, R., Zhang, Z., Zhang, H., Huang, R., 2011. The ethylene response factor AtERF11 that is transcriptionally modulated by the bZIP transcription factor HY5 is a crucial repressor for ethylene biosynthesis in Arabidopsis. Plant J. 68 (1), 88–99. https://doi.org/10.1111/j.1365-313X.2011.04670.x.

Liang, X., Zhang, L., Natarajan, S.K., Becker, D.F., 2013. Proline mechanisms of stress survival. Antioxid. Redox Signal. 19 (9), 998–1011. https://doi.org/10.1089/ars.2012.5074.

Lichtenthaler, H.K., 1987. Chlorophylls and carotenoids: pigments of photosynthetic biomembranes. Methods Enzymol. 148, 350–382. https://doi.org/10.1016/0076-6879(87)48036-1.

Lieberman, M., Segev, O., Gilboa, N., Lalazar, A., Levin, I., 2004. The tomato homolog of the gene encoding UV-damaged DNA binding protein 1 (DDB1) underlined as the gene that causes the high pigment-1 mutant phenotype. Theor. Appl. Genet. 108 (8), 1574–1581. https://doi.org/10.1007/s00122-004-1584-1.

Lin, C., Ahmad, M., Cashmore, A.R., 1996. Arabidopsis cryptochrome 1 is a soluble protein mediating blue light-dependent regulation of plant growth and development. Plant J. 10 (5), 893–902. https://doi.org/10.1046/j.1365-313x.1996.10050893.x.

Lin, C., Yang, H., Guo, H., Mockler, T., Chen, J., Cashmore, A.R., 1998. Enhancement of blue-light sensitivity of Arabidopsis seedlings by a blue light receptor cryptochrome 2. Proc. Natl. Acad. Sci. 95 (5), 2686–2690. https://doi.org/10.1073/pnas.95.5.2686.

Lin, Z., Li, Y., Wang, Y., Liu, X., Ma, L., Zhang, Z., Mu, C., Zhang, Y., Peng, L., Xie, S., Song, C.P., Shi, H., Zhu, J.K., Wang, P., 2021. Initiation and amplification of SnRK2 activation in abscisic acid signaling. Nat. Commun. 12 (1), 2456. https://doi.org/10.1038/s41467-021-22812-x.

Liu, B., Zuo, Z., Liu, H., Liu, X., Lin, C., 2011. Arabidopsis cryptochrome 1 interacts with SPA1 to suppress COP1 activity in response to blue light. Genes Dev. 25 (10), 1029–1034. https://doi.org/10.1101/gad.2025011.

Liu, Y., Roof, S., Ye, Z., Barry, C., van Tuinen, A., Vrebalov, J., Bowler, C., Giovannoni, J., 2004. Manipulation of light signal transduction as a means of modifying fruit nutritional quality in tomato. Proc. Natl. Acad. Sci. 101 (26), 9897–9902. https://doi.org/10.1073/pnas.0400935101.

Liu, Y., Singh, S.K., Pattanaik, S., Wang, H., Yuan, L., 2023. Light regulation of the biosynthesis of phenolics, terpenoids, and alkaloids in plants. Commun. Biol. 6 (1), 1055. https://doi.org/10.1038/s42003-023-05435-4.

López-Figueroa, F., Niell, F.X., 1988. Control de la síntesis de clorofila a por el fitocromo y criptocromo en la rodofícea *Corallina elongata* Ellis et Soland [control of chlorophyll a synthesis by phytochrome and cryptochrome in the red alga *Corallina elongata* Ellis et Soland]. Rev. Esp. Fisiol. 44 (3), 287–294.

Lou, Y.R., Ahmed, S., Yan, J., Adio, A.M., Powell, H.M., Morris, P.F., Jander, G., 2020. Arabidopsis ADC1 functions as an Nδ-acetylornithine decarboxylase. J. Integr. Plant Biol. 62 (5), 601–613. https://doi.org/10.1111/JIPB.12821.

Luo, X., Chen, Z., Gao, J., Gong, Z., 2014. Abscisic acid inhibits root growth in Arabidopsis through ethylene biosynthesis. Plant J. 79 (1), 44–55. https://doi.org/10.1111/tpj.12534.

Ma, D., Li, X., Guo, Y., Chu, J., Fang, S., Yan, C., Noel, J.P., Liu, H., 2016. Cryptochrome 1 interacts with PIF4 to regulate high temperature-mediated hypocotyl elongation in response to blue light. Proc. Natl. Acad. Sci. 113 (1), 224–229. https://doi.org/10.1073/pnas.1511437113.

Mahapatra, K., Dwivedi, S., Mukherjee, A., Pradhan, A.A., Rao, K.V., Singh, D., Bhagavatula, L., Datta, S., 2025. Interplay of light and abscisic acid signaling to modulate plant development. J. Exp. Bot. 76 (3), 730–745. https://doi.org/10.1093/jxb/erae192.

Males, J., Griffiths, H., 2017. Stomatal biology of CAM plants. Plant Physiol. 174 (2), 550–560. https://doi.org/10.1104/pp.17.00114.

Meena, M., Divyanshu, K., Kumar, S., Swapnil, P., Zehra, A., Shukla, V., Yadav, M., Upadhyay, R.S., 2019. Regulation of L-proline biosynthesis, signal transduction, transport, accumulation and its vital role in plants during variable environmental conditions. Heliyon 5 (12), e02952. https://doi.org/10.1016/j.heliyon.2019.e02952.

Murashige, T., Skoog, F., 1962. A revised medium for rapid growth and bio assays with tobacco tissue cultures. Physiol. Plant. 15 (3), 473–497. https://doi.org/10.1111/j.1399-3054.1962.tb08052.x.

Nawkar, G.M., Kang, C.H., Maibam, P., Park, J.H., Jung, Y.J., Chae, H.B., Chi, Y.H., Jung, I.J., Kim, W.Y., Yun, D.J., Lee, S.Y., 2017. HY5, a positive regulator of light signaling, negatively controls the unfolded protein response in Arabidopsis. Proc. Natl. Acad. Sci. 114 (8), 2084–2089. https://doi.org/10.1073/pnas.1609844114.

Ohkuma, K., Lyon, J.L., Addicott, F.T., Smith, O.E., 1963. Abscisin II, an abscission-accelerating substance from young cotton fruit. Science 142 (3599), 1592–1593. https://doi.org/10.1126/science.142.3599.1592.

Osterlund, M.T., Hardtke, C.S., Wei, N., Deng, X.W., 2000. Targeted destabilization of HY5 during light-regulated development of Arabidopsis. Nature 405 (6785), 462–466. https://doi.org/10.1038/35013076.

Pal, H., Kundu, A., Sahu, R., Sethi, A., Hazra, P., Chatterjee, S., 2019. Unraveling the metabolic behavior in tomato high pigment mutants (hp-1, hp-2dg, og) and non ripening mutant (rin) during fruit ripening. Sci. Hortic. 246, 652–663. https://doi.org/10.1016/j.scienta.2018.11.047.

Pál, M., Hamow, K.Á., Rahman, A., Majláth, I., Tajti, J., Gondor, O.K., Ahres, M., Gholizadeh, F., Szalai, G., Janda, T., 2022. Light spectral composition modifies polyamine metabolism in young wheat plants. Int. J. Mol. Sci. 23 (15), 8394. https://doi.org/10.3390/ijms23158394.

Pedmale, U.V., Huang, S.C., Zander, M., Cole, B.J., Hetzel, J., Ljung, K., Reis, P.A.B., Sridevi, P., Nito, K., Nery, J.R., Ecker, J.R., Chory, J., 2016. Cryptochromes interact directly with PIFs to control plant growth in limiting blue light. Cell 164 (1–2), 233–245. https://doi.org/10.1016/j.cell.2015.12.018.

Pérez-Arellano, I., Carmona-Alvarez, F., Martínez, A.I., Rodríguez-Díaz, J., Cervera, J., 2010. Pyrroline-5-carboxylate synthase and proline biosynthesis: from osmotolerance to rare metabolic disease. Protein Sci. 19 (3), 372–382. https://doi.org/10.1002/pro.340.

Pfaffl, M.W., 2001. A new mathematical model for relative quantification in real-time RT-PCR. Nucleic Acids Res. 29 (9), e45. https://doi.org/10.1093/nar/29.9.e45.

Ponnu, J., Hoecker, U., 2021. Illuminating the COP1/SPA ubiquitin ligase: fresh insights into its structure and functions during plant photomorphogenesis. Front. Plant Sci. 12, 662793. https://doi.org/10.3389/fpls.2021.662793.

Porra, R.J., 2002. The chequered history of the development and use of simultaneous equations for the accurate determination of chlorophylls a and b. Photosynth. Res. 73, 149–156. https://doi.org/10.1023/A:1020470224740.

Quail, P.H., Briggs, W.R., Chory, J., Hangarter, R.P., Harberd, N.P., Kendrick, R.E., Koornneef, M., Parks, B., Sharrock, R.A., Schafer, E., Thompson, W.F., Whitelam, G. C., 1994. Spotlight on phytochrome nomenclature. Plant Cell 6 (4), 468–471. https://doi.org/10.1105/tpc.6.4.468.

Rai, N., Neugart, S., Yan, Y., Wang, F., Siipola, S.M., Lindfors, A.V., Winkler, J.B., Albert, A., Brosché, M., Lehto, T., Morales, L.O., Aphalo, P.J., 2019. How do cryptochromes and UVR8 interact in natural and simulated sunlight? J. Exp. Bot. 70 (18), 4975–4990. https://doi.org/10.1093/jxb/erz236.

Saito, S., Hirai, N., Matsumoto, C., Ohigashi, H., Ohta, D., Sakata, K., Mizutani, M., 2004. Arabidopsis CYP707As encode (+)-abscisic acid 8′-hydroxylase, a key enzyme in the oxidative catabolism of abscisic acid. Plant Physiol. 134 (4), 1439–1449. https://doi.org/10.1104/pp.103.037614.

Santa-Cruz, A., Perez-Alfocea, F., Caro, M., Acosta, M., 1998. Polyamines as short-term salt tolerance traits in tomato. Plant Sci. 138 (1), 9–16. https://doi.org/10.1016/S0168-9452(98)00143-5.

Schroeder, D.F., Gahrtz, M., Maxwell, B.B., Cook, R.K., Kan, J.M., Alonso, J.M., Ecker, J. R., Chory, J., 2002. De-etiolated 1 and damaged DNA binding protein 1 interact to regulate Arabidopsis photomorphogenesis. Curr. Biol. 12 (17), 1462–1472. https://doi.org/10.1016/s0960-9822(02)01106-5.

Somers, D.E., Schultz, T.F., Milnamow, M., Kay, S.A., 2000. ZEITLUPE encodes a novel clock-associated PAS protein from Arabidopsis. Cell 101 (3), 319–329. https://doi.org/10.1016/s0092-8674(00)80841-7.

Sun, L.R., Wang, Y.B., He, S.B., Hao, F.S., 2018. Mechanisms for abscisic acid inhibition of primary root growth. Plant Signal. Behav. 13 (9), e1500069. https://doi.org/10.1080/15592324.2018.1500069.

Tardieu, F., Parent, B., Simonneau, T., 2010. Control of leaf growth by abscisic acid: hydraulic or non-hydraulic processes? Plant Cell Environ. 33 (4), 636–647. https://doi.org/10.1111/j.1365-3040.2009.02091.x.

Thompson, A.J., Jackson, A.C., Symonds, R.C., Mulholland, B.J., Dadswell, A.R., Blake, P.S., Burbidge, A., Taylor, I.B., 2000. Ectopic expression of a tomato 9-cis-epoxycarotenoid dioxygenase gene causes over-production of abscisic acid. Plant J. 23 (3), 363–374. https://doi.org/10.1046/j.1365-313x.2000.00789.x.

Toledo-Ortiz, G., Johansson, H., Lee, K.P., Bou-Torrent, J., Stewart, K., Steel, G., Rodríguez-Concepción, M., Halliday, K.J., 2014. The HY5-PIF regulatory module coordinates light and temperature control of photosynthetic gene transcription. PLoS Genet. 10 (6), e1004416. https://doi.org/10.1371/journal.pgen.1004416.

Vengosh, A., 2003. Salinization and saline environments. In: Holland, H.D., Turekian, K. K. (Eds.), Treatise on Geochemistry 9, pp. 1–35. https://doi.org/10.1016/B0-08-043751-6/09051-4.

Wang, A., Chen, D., Ma, Q., Rose, J.K.C., Fei, Z., Liu, Y., Giovannoni, J.J., 2019. The tomato high pigment1/damaged DNA binding protein 1 gene contributes to regulation of fruit ripening. Hortic. Res. 6, 15. https://doi.org/10.1038/s41438-018-0093-3.

Wu, W., Chen, L., Liang, R., Huang, S., Li, X., Huang, B., Luo, H., Zhang, M., Wang, X., Zhu, H., 2025. The role of light in regulating plant growth, development and sugar metabolism: a review. Front. Plant Sci. 15, 1507628. https://doi.org/10.3389/fpls.2024.1507628.

Xiao, Y., Chu, L., Zhang, Y., Bian, Y., Xiao, J., Xu, D., 2022. HY5: a pivotal regulator of light-dependent development in higher plants. Front. Plant Sci. 12, 800989. https://doi.org/10.3389/fpls.2021.800989.

Xu, D., Li, J., Gangappa, S.N., Hettiarachchi, C., Lin, F., Andersson, M.X., Jiang, Y., Deng, X.W., Holm, M., 2014. Convergence of light and ABA signaling on the ABI5 promoter. PLoS Genet. 10 (2), e1004197. https://doi.org/10.1371/journal.pgen.1004197.

Yadukrishnan, P., Datta, S., 2021. Light and abscisic acid interplay in early seedling development. New Phytol. 229 (2), 763–769. https://doi.org/10.1111/nph.16963.
Younis, M.E.-B., Hasaneen, M.N., Abdel-Aziz, H.M., 2010. An enhancing effect of visible light and UV radiation on phenolic compounds and various antioxidants in broad bean seedlings. Plant Signal. Behav. 5 (10), 1197–1203. https://doi.org/10.4161/psb.5.10.11978.
Zhou, T., Meng, L., Ma, Y., et al., 2018. Overexpression of sweet sorghum cryptochrome 1a confers hypersensitivity to blue light, abscisic acid and salinity in Arabidopsis. Plant Cell Rep. 37 (2), 251–264. https://doi.org/10.1007/s00299-017-2227-8.