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Doctoral Programme in Technology

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ABSTRACT

Light is the primary source of energy for life on Earth. Photosynthesis is a process that converts light into chemical energy, producing sugars for living organisms. However, variations in the intensity or quality of light can be detrimental to photosynthetic organisms. To cope with these challenges, photosynthetic organisms have evolved sophisticated mechanisms to allow them to adjust the gene expression, physiology and metabolism in response to rapid changes in light conditions. These adjustments are initiated from photosynthesis and occur on short timescales and help to protect the organisms from potential damage while maintaining efficient energy production. Although acclimation to light stress, such as high light (HL) conditions, has been extensively studied, the specific roles of the light energy transducing photosystems, PSII and PSI, have remained unclear. The aim of this study was to further investigate the role of photosystems and to identify the types of signaling cascades they initiate in response to light stress. I used a PSII-deficient strain of *Synechocystis* sp. PCC 6803 to study the effects of PSII deficiency on thylakoid organization and gene expression. I also used *Arabidopsis thaliana* exposed to a light treatment that specifically inhibits PSI, to study the signaling cascades generated by compromised PSI activity. In addition, I investigated the signaling networks during recovery of plants from HL stress.

The absence of PSII leads to higher expression of genes encoding PSII components and repair proteins. Lack of PSII also leads to the accumulation of unassembled CP43 and CP47 proteins, higher PSI monomer to trimer ratio, and higher respiration. These results indicate that the PSII loss induces similar effects as the exposure of cells to HL, suggesting that PSII loss and HL-induced PSII photoinhibition trigger analogous signaling pathways, albeit with differences in the extent of photoinhibition and pigment damage.

I also provide a detailed analysis of the transcriptomic responses induced by PSI photoinhibition in plants. I show that PSI photoinhibition triggers the release of Fe from PSI FeS clusters, leading to an accumulation of excess Fe, an effect seen only under HL stress. Fe overload in chloroplast specifically upregulates genes in nucleus involved in iron homeostasis and sequestration, such as *FERRITIN* genes, highlighting a unique response to excess Fe stress. The Fe signaling pathway is distinct from the broader oxidative stress response observed under HL, which impacts both PSII and PSI and involves ROS production. Additionally, I show that CO_2 deprivation induces the expression of genes associated with oxylipin signaling, including those involved in flavonoid synthesis.

My study culminates in the complexity of the recovery from HL stress. I show that oxidative stress induced by HL treatment leads to the accumulation of jasmonic acid (JA) during both HL and the recovery phase. JA in turn induces the accumulation of antioxidants such as glutathione (GSH) and ascorbate (AsA), which scavenge the reactive oxygen species (ROS) generated by HL stress. These findings indicate that recovery from HL stress involves more than simply reversing the effects of HL stress but involves a coordinated response involving JA-mediated antioxidant accumulation to counteract the oxidative stress sustained during HL stress.

KEYWORDS: High light, Jasmonate, Photoinhibition, Photosystem I and II, Recovery, ROS, Signaling

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TIIVISTELMÄ

Valo on maapallon elämän tärkein energianlähde. Fotosynteesi on prosessi, joka muuttaa valoenergian kemialliseksi energiaksi ja tuottaa sokereita eliöiden elämän ylläpitämiseen. Valon määrän tai laadun vaihtelut voivat kuitenkin olla haitallisia fotosynteettisille eliöille. Selviytyäkseen näistä haasteista fotosynteettiset eliöt ovat kehittäneet mekanismeja, joiden avulla fotosynteesi pystyy sopeutumaan vaihteleviin valo-olosuhteisiin. Nämä mekanismit indusoituvat nopeasti ja suojelevat fotosynteettisiä eliöitä valon aiheuttamilta vaurioilta, samalla pyrkien säilyttämään mahdollisimman tehokkaan energian muutostehokkuuden. Vaikka sopeutumista valon määrässä tapahtuviin muutoksiin, kuten äkilliseen kirkkaaseen valoon, on tutkittu laajasti, valoenergiaa kemialliseksi energiaksi välittävien rakenteiden (PSI ja PSII) merkitys valosopeutumissa on edelleen epäselvä. Tämän tutkimuksen tavoitteena oli tunnistaa signaalinsiirtoreittejä, jotka indusoituvat valomäärän muuttuessa ja vaikuttavat geenien ilmenemiseen. Muutos geenien ilmenemisessä puolestaan aloittaa solun puolustus- ja sopeutumisreaktiot. Väitöskirjatyössäni selvitin PSII-kompleksin puuttumisen vaikutusta syanobakteerin (*Synechocystis* sp. PCC 6803) tylakoidikompleksien rakenteeseen ja geenien ilmenemiseen. Lisäksi tutkin lituruohon (*Arabidopsis thaliana*) altistumista valokäsittelylle, joka erityisesti vaurioittaa PSI-kompleksia, ja altistuksen synnyttämiä signaaleja sekä vaikutuksia geenien ilmenemiseen. Tutkin myös signalointiverkostoja kasvien kirkkaan valon aiheuttaman stressin aikana sekä erityisesti valostressistä toipumisen aikana.

PSII:n puuttuminen johtaa PSII-komponentteja ja korjausproteiineja koodaavien geenien aktivoitumiseen, irrallisten CP43- ja CP47-proteiinien kertymiseen tylakoidimembraaneihin, sekä PSI-monomeeri/trimeeri-suhteen kasvuun ja voimakkaampaan soluhengitykseen. Nämä tulokset osoittavat, että PSII:n puuttuminen indusoi samanlaisia vaikutuksia kuin solujen altistuminen kirkkaalle valolle, mikä viittaa siihen, että PSII:n menetys ja kirkkaan valon aiheuttama PSII:n fotoinhibitio laukaisevat analogisia signalointireittejä.

Lituruoholla tehdyt kirkkaan valon altistuskokeet osoittivat, että PSI:n fotoinhibitio laukaisee rautaionin (Fe) vapautumisen PSI:n FeS-keskuksista, mikä johtaa ylimääräisen Fe:n kerääntymiseen viherhiukkaseen. Fe:n ylikuormitus lisää spesifisesti raudan homeostaasiin ja varastointiin osallistuvien geenien ilmenemistä. Ylimääräisen Fe:n indusoima singnaalinsiirtoreitti eroaa kirkkaan valon aiheuttamasta laajemmasta oksidatiivisesta stressivasteesta, joka tuottaa reaktiivisia

happiyhdisteitä ja vaikuttaa molempiin valoreaktiokomplekseihin (PSII ja PSI). Lisäksi tutkin ilman hiilidioksidi-pitoisuuden vaikutusta kasvien fotosynteesiin ja havaitsin, että hiilidioksidin puute indusoi oksilipiini-välitteisen geenien ilmenemisen, erityisesti flavonoidisynteesiin osallistuvien geenien ilmeneminen kasvaa.

Tutkiessani lituruohon selviytymistä kirkkaan valon aiheuttamasta stressistä havaitsin, että valon aiheuttama oksidatiivinen stressi johtaa jasmonihapon (JA) kertymiseen sekä kirkkaassa valossa että palautumisvaiheen aikana. JA indusoi antioksidanttien, kuten glutationin ja askorbaatin kerääntymistä soluun. Nämä puolestaan poistavat valostressin tuottamia reaktiivisia happilajeja. Havaintoni osoittavat, että toipuminen valostressistä on erillinen aktiivinen prosessi, joka vaatii omat signalointimekanismit spesifisten geenien ilmenemiseksi, eikä tapahdu palautumisolosuhteisiin siirrettäessä pelkkänä valostressin yhteydessä indusoituvien geenien ilmenemisen palautumisena normaalitasolle.

ASIASANAT: Fotosynteesin fotoinhibitio, Jasmonaatit, ROS, Signalointi, Stressistä palautuminen, Valoreaktio I ja II, Valostressi

Table of Contents

Abbreviations

·OH	Hydroxyl radical
$^1O_2$	Singlet oxygen
ABA	Abscisic acid
AR	Antibiotic resistant *Synechocystis* sp. PCC 6803 strain
AsA	Reduced ascorbate
CAT	Catalase
CBB	Calvin-Benson-Basham cycle
CEF	Cyclic electron flow
Chl	Chlorophyll
COI1	Coronatine insensitive 1
Cyt b_6f	Cytochrome b6f Complex
D1	Reaction center protein of PSII
D2	Reaction center protein of PSII
DHA	Oxidized ascorbate
F0	Minimal PSII fluorescence yield, dark-acclimated sample
Fd	Ferredoxin
FER	Ferritin
FeS	Iron-sulfur cluster
FL	Fluctuating light
Fm	Maximal PSII fluorescence yield, dark-acclimated sample
FtsH	A protease involved in PSII repair
Fv	Variable fluorescence
GL	Growth light
GSH	Reduced glutathione
GSSG	Oxidized glutathione
GST	Glutathione s-transferase
H_2O_2	Hydrogen peroxide
HL	High light (5-10 times higher intensity than growth light)
HSP	Heat shock protein
HY5	Elongated hypocotyl 5
ISP	Rieske iron-sulfur protein
JA	Jasmonic acid
JAZ	Jasmonate zim-domain containing protein, JA signaling repressor
LHCA	Gene encoding LHCII protein
LHCB	Gene encoding LHCI protein
LOX	Lipoxygenase
NPQ	Non-photochemical quenching

$O_2^{\bullet-}$	Superoxide anion
OEC	Oxygen Evolving Complex
OPDA	12-oxo-phytodioneic acid
P680	PSII reaction center chlorophyll
P700	PSI reaction center chlorophyll
PBS	Phycobilisomes
PC	Plastocyanin
PETC	Photosynthetic electron transport chain
PGR5	Proton gradient regulator 5
PGRL1	PGR5-LIKE 1
PHY	Phytochrome
Pm	Maximum P700 Oxidation
pmf	Proton motive force
PQ	Plastoquinone
PS	Photosystem
PSI-PI	PSI photoinhibition treatment
RCA	RuBisCO activase
RES	Reactive electrophile species
ROS	Reactive oxygen species
RuBisCO	Ribulose-1,5-bisphosphate carboxylase/oxygenase
SA	Salicylic Acid
SCF	SKP1-CUL1-F-box protein, E3 ubiquitin ligase complex
STN7	Serine/threonine-protein kinase 7
TAP38	Thylakoid-associated phosphatase 38
TF	Transcription factor
ΔpH	Proton gradient across the thylakoid membrane

List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

I Kılıç, M., Gollan, P. J., Lepistö, A., Isojärvi, J., Sakurai, I., Aro, E. M., Mulo, P. Gene expression and organization of thylakoid protein complexes in the PSII-less mutant of Synechocystis sp. PCC 6803. *Plant Direct*, 2022; 6: e409.

II Kılıç, M., Käpylä, V., Gollan, P. J., Aro, E.-M., Rintamäki, E. PSI photoinhibition and changing CO_2 levels initiate retrograde signals to modify nuclear gene expression. *Antioxidants*, 2023; 12: 1902.

III Kılıç, M., Gollan, P. J., Aro, E.-M., Rintamäki, E. Jasmonic acid signaling and glutathione coordinate plant recovery from high light stress. *Manuscript*, 2024.

1 Introduction

Photosynthesis converts solar energy into chemical energy, sustaining all life on earth. The organic matter produced through photosynthesis serves as the basis of the ecosystems, providing fuel for heterotrophic organisms at different trophic levels. Solar energy, harnessed through photosynthetic organisms, enables the conversion of atmospheric carbon dioxide (CO_2) into organic compounds. This process is significant, given that approximately 50% of the plant biomass is composed of carbon (Bert and Danjon, 2006; Ma et al., 2018). Oxygen (O_2), a byproduct of photosynthesis, contributes significantly to atmospheric composition, supporting the aerobic respiration in living organisms. Both eukaryotic and prokaryotic O_2 evolving organisms play critical roles in shaping the composition of atmospheric gases, contributing to the dynamic equilibrium of Earth's atmosphere.

1.1 Oxygen-evolving photosynthesis

In cyanobacteria, no specific organelle for photosynthesis exists. Instead, photosynthesis occurs in the cytoplasm, where the thylakoid membranes are located and most of the carbon fixation reactions occur. Additionally, carboxysomes, where concentration of CO_2 takes place, are found in the cytoplasm. Cyanobacterial thylakoid membranes exist in various arrangements including radial, coiled and parallel sheets. Thylakoid membranes in *Synechocystis* sp. PCC 6803 (hereafter *Synechocystis*) form layers parallel to the plasma membrane (Mareš et al., 2019) and they serve a dual function by housing components of both the respiratory and photosynthetic electron transport chains (PETC). PETC and respiratory electron transport share several components, including the plastoquinone (PQ) pool, cytochrome b_6f (Cyt b_6f) and plastocyanin (PC) (Lea-Smith et al., 2016; Nikkanen et al., 2021). The shared components coordinate the electron flow between respiration and photosynthesis, allowing cyanobacteria to efficiently manage electron flow, optimize energy utilization, and adapt to varying environmental conditions (Lea-Smith et al., 2016; Nikkanen et al., 2021). Cyanobacteria have singular thylakoid membranes concentrically organized inside the cell, and the photosystem (PS) II and PSI complexes are not strictly segregated to different thylakoid domains (Pfeil et al., 2014; Liu, 2016). The light harvesting structures of cyanobacteria, the

phycobilisomes (PBS), are large soluble pigment-protein complexes that attach primarily to the PSII complexes on the cytoplasmic side of the thylakoid membrane with phycoerythrin (PE), phycocyanin (PCy) and allophycocyanin (APC) as main light-harvesting pigments (Zilinskas and Greenwald, 1986; Lea-Smith et al., 2016; Calzadilla and Kirilovsky, 2020; Pan et al., 2020). The cyanobacterial genome consists of several copies of circular DNA molecules and the genomic size varies from 1 to 9 Mb (Hess, 2011). The absence of a membrane structure around the genome simplifies the influence of metabolites, such as reactive oxygen species (ROS) on gene expression.

In contrast to prokaryotic cyanobacteria, eukaryotic plant and algae cells have evolved chloroplasts, derived from endosymbiosis with an ancient cyanobacterium. Chloroplasts carry out photosynthesis, converting light energy into chemical energy in the form of nicotinamide adenine dinucleotide phosphate (NADPH) and ATP. Chloroplasts have their own DNA and ribosomes, allowing them to partially govern their own protein synthesis. However, most of the genes encoding structural and functional components of the chloroplast are localized in the nucleus. Both plants and cyanobacteria use the two photosystems, PSII and PSI, for light-activated electron transport from water to $NADP^+$. However, the plant thylakoid membrane network is heterogeneous, consisting of the stacked (appressed) grana structures that predominantly accommodate the membrane-embedded PSII complexes together with the chlorophyll (Chl) and carotenoid-containing light-harvesting complexes (LHC) II, whereas PSI and LHCI are located in the non-appressed stroma thylakoids (Anderson, 2002; Mullineaux, 2005; Suorsa et al., 2015; Grebe et al., 2020).

1.1.1 Photosynthetic electron transport

Photosynthesis begins with the absorption of photons by pigments in PSs or in the surrounding LHCs (Figure 1). In PSII reaction center (RC), the excitation energy is used to transfer electrons from the primary donor P680 to pheophytin (Pheo), then to the primary acceptor, plastoquinone Q_A, and finally to the secondary acceptor plastoquinone Q_B. After receiving the second electron, Q_B binds two protons from chloroplast stroma to form PQH_2, which is released to the PQ pool inside the thylakoid membrane. Meanwhile, the electrons released from P680 are replaced by electrons taken from water by the oxygen evolving complex (OEC). PQH_2 transfers protons to the lumen and electrons to Cyt b_6f, which donates them to PC. In PSI RC, P700 undergoes another round of photon absorption, culminating in the transfer of electrons to ferredoxin (Fd), an iron-sulfur protein (Sonoike et al., 1995; Tiwari et al., 2016), while PC donates electrons to the $P700^+$. Fd transfers electrons to $NADP^+$, converting it to NADPH. This type of electron transport is called linear electron flow (LEF). At the same time, as electrons move through the PETC, protons are pumped across the thylakoid membrane by Cyt b_6f, creating a proton motive force (pmf)

across the thylakoid membrane. OEC also contributes to the pmf by releasing protons from water splitting in the lumen. Pmf drives the ATP synthesis by ATP synthase, an enzyme partially embedded in the thylakoid membrane.

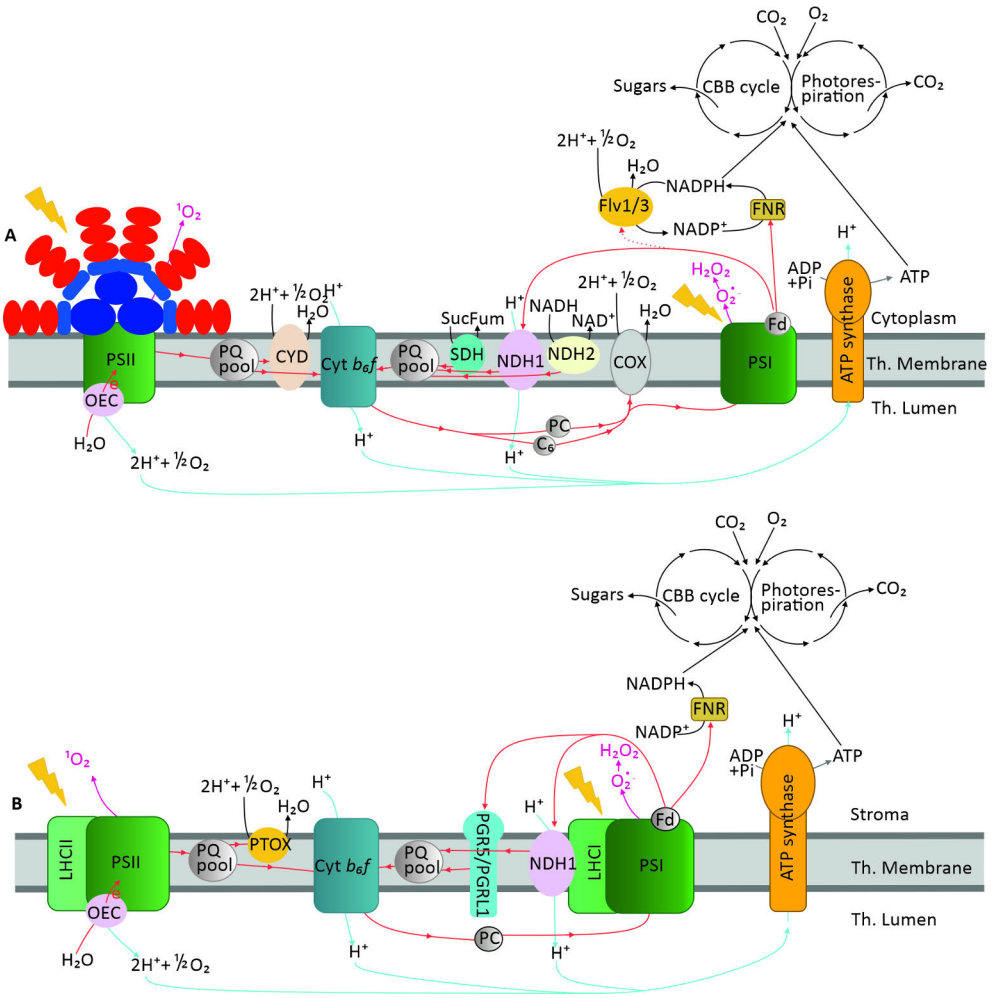

Figure 1. PETC in cyanobacteria and chloroplasts. **A**) Cyanobacterial PETC including respiratory complexes. **B**) Chloroplast PETC. NADPH PLASTOQUINONE OXIDOREDUCTASE 1 (NDH-1), NADH PLASTOQUINONE OXIDOREDUCTASE 2 (NDH-2), PROTON GRADIENT REGULATOR 5 / PGR5-LIKE 1 (PGR5/PGRL1), SUCCINATE PLASTOQUINONE OXIDOREDUCTASE (SDH), CYTOCHROME BD QUINOL OXIDASE (CYD), CYTOCHROME-C OXIDASE (COX), PLASTID TERMINAL OXIDASE (PTOX), FLAVODIIRON (Flv), FERREDOXIN-NADP$^+$-OXIDOREDUCTASE (FNR), CALVIN-BENSON-BASHAM (CBB) CYCLE. Red lines indicate electron transfer while cyan lines indicate proton transfer. NADPH and ATP are produced by the PETC to energize CBB cycle and photorespiration. Cyanobacterial SDH, NDH2 and CYD enzymes alongside a PQ pool are also found in the cytoplasmic membrane.

1.1.2 Structure and function of PSII

PSII exists as a dimer, each monomer consisting of approximately 20 subunits in the thylakoid membrane of both plants and cyanobacteria (Guskov et al., 2009; Graça et al., 2021). PSII RC complex binds, on the luminal side, the OEC, which is composed of a manganese cluster and associated OEC proteins. P680 is excited by light energy absorbed by Chls or carotenoids of the PSII internal Chl binding proteins (CP) such as CP43 and CP47, or by the external PBS and LHCII antenna in cyanobacteria and plants, respectively. Plant PSII RC complex has the D1 and D2 proteins encoded by *PsbA* and *PsbD* genes, while in many cyanobacteria, like *Synechocystis*, the D1 protein is encoded by three *PsbA* genes and D2 is encoded by *PsbD* (Mulo et al., 2009; Lu, 2016). D1 and D2 proteins of the PSII RC complex bind all electron carriers participating in electron transport from water to PQ. These RC proteins are surrounded by CP43 and CP47, encoded by *PsbC* and *PsbB* genes, respectively (Lu, 2016). Extrinsic proteins like PsbO, PsbP, and PsbR, stabilize the OEC, enhancing its functionality (De Las Rivas et al., 2007).

In plants, PSII is associated with the chl a/b and carotenoid binding LHCII antenna. LHCII consists of the LHCB4 (CP29), LHCB5 (CP26), and LHCB6 (CP24) proteins, often referred to as minor LHCII antenna complexes, and trimeric assemblies of the LHCB1, LHCB2, and LHCB3 proteins called the major LHCII antenna (Boekema et al., 1999). Minor antenna proteins are crucial not only for their role in light harvesting but also for stabilizing the PSII-LHCII supercomplex (Boekema et al., 1999; Minagawa and Tokutsu, 2015). The LHCII trimers efficiently capture and transfer light energy to the PSII core complex, significantly enhancing its light absorption cross-section, crucial for optimal photosynthesis. LHCII does not only function in energy transfer to PSII, but also has an important role in photoprotection, and regulation of the distribution of excitation energy between PSII and PSI.

PSII photochemical efficiency can be assessed by calculation of the ratio of variable fluorescence (F_v) to maximum fluorescence (F_m), known as F_v/F_m (Krause and Weis, 1991). F_m represents the maximum fluorescence level when all PSII RCs are closed, while F_V indicates the variable fluorescence level under light conditions, and it is calculated by subtracting the minimal fluorescence level (F_0) from Fm. F_v/F_m value provides a direct measure of the maximum PSII photochemistry, offering insights into the efficiency with which PSII converts light energy into chemical energy. Monitoring changes in F_v/F_m is crucial for assessing plant stress responses, environmental impacts, and overall photosynthetic efficiency.

1.1.3 Structure and function of Cyt *b*$_6$*f*

Cyt *b*$_6$*f*, a homodimer, transfers electrons from PSII to PSI during oxygenic photosynthesis. The structure of the Cyt *b*$_6$*f* complex is comprised of several subunits, including Cyt b6, Cyt f, the Rieske iron-sulfur protein (ISP) containing a [2Fe-2S] cluster and the subunit IV. Hemes in Cyt *b6*, Cyt *f* and 2Fe-2S cluster in ISP serve to transfer electrons through the Cyt *b*$_6$*f* complex. These subunits are encoded by *PetA*, *PetB*, *PetC* and *PetD* genes, respectively. PetG, PetM and PetN are structural subunits of Cyt *b*$_6$*f* and encoded by genes with same names as the proteins (Schwenkert et al., 2007; Lan et al., 2021).

Integral to the Cyt *b*$_6$*f* complex is the Q cycle, a process that couples electron transfer with generation of a higher proton gradient. In Q cycle, a PQH_2 molecule binds to the Q_0 site of Cyt *b*$_6$*f* and releases two protons into the lumen, and transfers one electron via 2Fe-2S cluster to heme f in Cyt *f*. This electron is transferred to the PC while the other electron is recycled and moves through *b* type hemes (bp and bn) of Cyt *b* to the Qi site of Cyt *b*$_6$*f* on the stromal side. When a second PQH_2 molecule delivers its electrons to Cyt *b*$_6$*f*, one of the electrons is again transported to the Qi site. After having received two electrons at the Qi site, the doubly reduced PQ molecule then binds two new protons from stroma and transfers them to lumen.

1.1.4 Structure and function of PSI

Functional PSI is a monomer in plants but a trimer in cyanobacteria (Ben-Shem et al., 2003a; Ben-Shem et al., 2003b; Grotjohann and Fromme, 2005). Functioning as a PC-Fd oxidoreductase, PSI orchestrates the conversion of light energy into reducing power in the form of NADPH. P700, a specialized pair of Chl a molecules, serves as the primary electron donor within the RC. When illuminated by light, Chls and carotenoids in the LHCI antenna and in the internal antenna of PSI absorb the photons and direct the light energy to P700. This process leads to electron transfer from P700 to three 4Fe-4S (FeS) clusters (FX, FA, and FB) via secondary electron acceptors A0 (Chl a), and A1 (phylloquinone Q). The FeS clusters transfer electrons to the soluble carrier Fd (Ben-Shem et al., 2003a; Grotjohann and Fromme, 2005).

PSI proteins are encoded by genes with the same names. PsaA and PsaB proteins form the RC and the central core of the PSI complexes, binding the cofactors (P700, A0, A1, and FX) involved in electron transfer from P700 to FX. Peripheral proteins surrounding the RC include PsaC on the stromal side, which binds the FA and FB clusters, as well as PsaD and PsaE that together with PsaC participate in binding of Fd (Fromme et al., 2001; Ben-Shem et al., 2003a; Grotjohann and Fromme, 2005). PsaC plays a critical role as a linker, connecting the RC to external electron acceptors, while PsaD and PsaE contribute to the structural integrity of PSI, aiding in the efficient transfer of electrons (Fromme et al., 2001; Grotjohann and Fromme,

2005). Additionally, PSI is associated with LHCI antenna, represented by the LHCA1-6 proteins. LHCA1-4 form a 'crescent' shaped antenna around PSI in *Arabidopsis thaliana,* collecting and directing light energy to P700 RC and inducing charge separation in P700 (Nelson and Junge, 2015), while the LHCA5-6 bind PSI to the NDH-1 complex, being important in PSI cyclic electron flow.

PSI photochemical efficiency is a critical indicator of the efficiency with which photosynthesis converts light energy into chemical energy. PSI efficiency can be assessed by absorbance change of P700 at 830 nm as an indicator of stable charge separation within PSI. Maximum P700 oxidation (P_m) reflects the maximum efficiency of PSI. Monitoring changes in P_m is a valuable tool for understanding the functionality of PSI and its role in PETC (Tiwari et al., 2016; Tikkanen and Grebe, 2018).

1.1.5 Structure and function of ATP synthase

The ATP synthase enzyme is composed of several protein subunits arranged in the thylakoid membrane. ATP synthase consists of a catalytic head region, known as the F1 complex, which protrudes into chloroplast stroma (Lawrence et al., 2011). This F1 complex is connected to F0 complex embedded within the thylakoid membrane by gamma (γ) and epsilon (ε) subunits. F0 complex acts as a rotor while γ and ε subunits act as a central stalk connecting F0 to the F1 complex during ATP synthesis. The outer stalk comprised of "b" subunits anchors the F1 subunit to the "a" subunit embedded in thylakoid membrane. The F0 complex comprises a ring of protein C subunits that facilitate the movement of protons from lumen to the stroma. This movement of protons causes rotation of the F0 complex that induces conformational changes in the F1 complex, enabling the synthesis of ATP from ADP and inorganic phosphate (Pi).

1.2 Regulation mechanisms of photosynthetic light reactions

To mitigate the detrimental effects of excessive light energy, plants have evolved protective mechanisms such as non-photochemical quenching (NPQ). NPQ is a photoprotective mechanism utilized by photosynthetic organisms to dissipate excess absorbed light energy as heat in PSII. There are several components of NPQ including the main forms of energy-dependent quenching (qE) and zeaxanthin-dependent quenching (qZ). The qE component of NPQ is initiated by protonation of the PSII subunit S (PsbS) upon acidification of thylakoid lumen (Roach and Krieger-Liszkay, 2012; Croce, 2015). It is proposed that PsbS promotes NPQ either by influencing LHCII oligomerization that enhances the probability of formation of a quenching conformation (Horton et al., 1991; Mullineaux et al., 1993; Müller et al.,

2001; Strand and Kramer, 2014), or by directly binding carotenoid pigments and positioning it close to peripheral Chl molecules, creating a quenching center (Niyogi et al., 2005; Croce, 2015). qZ component, linked to the accumulation of zeaxanthin in HL, is activated by protonation of VIOLAXANTHIN DE-EPOXIDASE (VDE) in the lumen upon increase in thylakoid acidification. Once activated, VDE catalyzes the de-epoxidation of violaxanthin, converting it into zeaxanthin, which contributes to the energy dissipation within the LHCIIs. NPQ dissipates the excess light energy as heat and thereby prevents the accumulation of ROS, preserving the structural and functional integrity of PETC (Baroli et al., 2004; Dall'Osto et al., 2012; Roach and Krieger-Liszkay, 2012; Roach et al., 2020).

Under stress conditions such as HL, Cyt b_6f plays a regulatory role in photosynthesis (Tikhonov, 2014; Tikhonov, 2018; Malone et al., 2021). In HL, the thylakoid lumen becomes highly acidic as the proton gradient across the thylakoid membrane (ΔpH) increases. This acidity leads to the protonation of the His128 (in spinach) residue of ISP that is involved in binding of the 2Fe-2S cluster (Hasan et al., 2013; Tikhonov, 2018; Malone et al., 2021). The protonation of ISP by ΔpH inhibits the deprotonation of PQH_2, and consequently slows the electron flow through Cyt b_6f towards PSI.

State transitions in photosynthesis optimize energy utilization of PSs (Mullineaux and Emlyn-Jones, 2005; Minagawa, 2011; Tikkanen et al., 2012). State transitions refer to adjustments in the organization of the light harvesting to optimize light energy distribution between PSs by reversible phosphorylation of LHCII proteins (Bellaflore et al., 2005). In State 1, LHCII proteins are not phosphorylated, and they mainly serve the PSII. In state 2, LHCII proteins are phosphorylated by SERINE/THREONINE-PROTEIN KINASE 7 (STN7), which leads to association of the loosely bound P-LHCII with PSI to enhance excitation energy transfer to PSI (Bellaflore et al., 2005; Pesaresi et al., 2009). Conversely, dephosphorylation of phosphorylated LHCII proteins by THYLAKOID-ASSOCIATED PHOSPHATASE 38 (TAP38) results in its dissociation from PSI and reassociation with PSII, thus redirecting excitation energy towards PSII (Pribil et al., 2010). State transitions ensure efficient light capture and utilization under light intensities limiting photosynthesis.

In LEF, the major route of electrons in photosynthesis is from water to $NADP^+$. However, electrons can also take an alternative route in cyclic electron flow (CEF), deviating from the linear path. In CEF, the electrons, after passing through PSI to Fd, return to the PETC either via PGR5/PGRL1-dependent or via NDH-1-dependent pathway (Munekage et al., 2002; Suorsa et al., 2016; Rantala et al., 2020; Wang et al., 2020; Zhang et al., 2020; Ma et al., 2021a). This alternative route allows the re-entry of electrons into PETC at PQ pool, and they move through the Cyt b_6f complex and via PC back to PSI, contributing to the establishment of the pmf across the

thylakoid membrane. Notably, the ability to divert electrons into CEF provides flexibility to the photosynthetic machinery, enabling plants to fine-tune the balance between ATP and NADPH production based on their energetic and metabolic needs (Bernát et al., 2011; Kramer and Evans, 2011; Suorsa et al., 2016; Ma et al., 2021a). This regulatory mechanism is crucial for optimizing energy utilization and maintaining the delicate equilibrium required for efficient photosynthesis.

Alternative electron flow (AEF), also known as water-water cycle, contributes to photoprotection under high light (HL) stress (Park et al., 1996; Ware et al., 2020). AEF is called water-water cycle because it uses the electrons gained from water by OEC at PSII to reduce O_2 to water on PSI acceptor side. AEF acts as a scavenging mechanism for ROS generated during photosynthesis. AEF plays a role in mitigating oxidative stress, reinforcing the resilience of plants in fluctuating environmental conditions (Asada, 1999; Miyake, 2010). AEF starts with reduction of O_2 to superoxide radical ($O_2^{\bullet-}$) at PSI acceptor side. The $O_2^{\bullet-}$ is disproportionated spontaneously or by SUPEROXIDE DISMUTASE (SOD) to hydrogen peroxide (H_2O_2) and O_2. H_2O_2 can induce cell damage by generating hydroxyl radicals (·OH) via the nonenzymatic Fenton reaction. H_2O_2 is reduced to water with the help of antioxidant enzymes.

1.3 Photoinhibition of PSs

Light is a substrate for PSII, but PSII photochemical efficiency also decreases in light and the decline is more severe under stress conditions like HL resulting in PSII photoinhibition (Tyystjärvi and Aro, 1996; Tikkanen et al., 2014; Huang et al., 2016). The D1 protein in PSII RC gets photodamaged and is then degraded by FTSH proteases and replaced with a newly synthesized D1 protein. Several theories on the cause of PSII photoinhibition have been proposed. i) Linear electron flow in PSII is blocked on the acceptor side of PSII resulting in overreduction of PSII components that leads to the oxidation of PSII proteins (Keren et al., 1997). ii) Electron flow is blocked on the donor side of PSII that leads to increase in lifetime of $P680^+$, which causes oxidative damage to D1 protein because $P680^+$ is a very strong oxidant (Tyystjärvi, 2008; Wei et al., 2011). iii) Manganese is released from Mn cluster and $P680^+$ cannot be re-reduced by OEC (Hakala et al., 2005; Tyystjärvi, 2008; Wei et al., 2011), which leads to oxidative damage to PSII RC. Replacement of the D1 protein by a new copy is called PSII repair cycle that requires the chloroplast protein synthesis. PSII photoinhibition is measurable when the damage to D1 protein exceeds the repair process. ROS has an extra effect on PSII photoinhibition, since it has been reported that also the PSII repair process is sensitive to ROS (Nishiyama et al., 2004; Nishiyama et al., 2006; Murata et al., 2007; Nishiyama et al., 2011).

PSI is susceptible to photoinhibition when the PSI acceptor side capacity is overwhelmed due to unregulated electron flow in PETC (Suorsa et al., 2012; Kanazawa et al., 2017). This is exemplified by PSI photoinhibition in *coupling factor quick recovery* (*cfq)* mutant with increased ATP synthase activity, and the *pgr5* mutant, both of which fail to build up ΔpH quick enough to activate ΔpH-dependent NPQ or ΔpH-dependent regulation of the Cyt b_6f complex (Suorsa et al., 2012; Gollan et al., 2017; Kanazawa et al., 2017). This failure in regulation leads to high rate of electron flow to PSI, quickly saturating PSI acceptor side and causing formation of ROS, which react with reduced iron (Fe) in the FeS clusters of PSI, destroying these clusters (Sonoike et al., 1995; Tiwari et al., 2016). This type of PSI photoinhibition has been observed in chilling-sensitive plant leaves exposed to low temperatures (Sonoike, 1996; Zhang and Scheller, 2004). This is attributed to accumulation of electrons in PETC at low temperature, because the lowering of temperature decreases the activity of stromal enzymes, particularly the Calvin-Benson-Basham (CBB) cycle enzymes, while the electron flow in light reactions is relatively temperature-independent (Zhang and Scheller, 2004; Liu et al., 2018; Lempiäinen et al., 2022). Recovery of PSI from photoinhibition is very slow, because no sophisticated mechanism for replacement of damaged proteins and co-factors has evolved, and membrane lipid rigidification further impairs the recovery process at low temperatures (Lima-Melo et al., 2019; Lempiäinen et al., 2022).

PSI photoinhibition can also be induced by exposing plants to various regimes of artificial fluctuating light (FL) (Tikkanen and Grebe, 2018). Photoinhibition of PSI by artificial FL operates on the principle of overreducing the intermediate electron carriers in PETC without activating the protective mechanisms such as NPQ. This is achieved by exposing plants first to red light, which preferentially excites PSII resulting in overreduced electron transporters between PSII and PSI. Subsequently, a saturating light is applied to channel these electrons through PSI, leading to sudden saturation of the PSI acceptor side and generation of ROS, which results in damaged FeS clusters (Tikkanen and Grebe, 2018; Lempiäinen et al., 2022).

PSI damage causes decline in CO_2 assimilation and starch accumulation as well as ROS production (Gollan et al., 2017; Lima-Melo et al., 2019; Lempiäinen et al., 2022). Photoinhibition of PSI is detrimental to plants because restoring the PSI activity can take days or longer, unlike the repair of damaged PSII, which occurs within minutes or hours (Kudoh and Sonoike, 2002; Lima-Melo et al., 2019; Lempiäinen et al., 2022). PSI photoinhibition can be prevented, or minimized, by using 3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) to block electron transfer from PSII, using lincomycin to block PSII repair, or producing transgenic plants with high NPQ (Havaux and Davaud, 1994; Han et al., 2010; Huang et al., 2016).

1.4 CO_2 assimilation and photorespiration

ATP and NADPH generated in photosynthetic light reactions serve as the energy source for the CBB cycle, which converts CO_2 into organic compounds, forming the basis for the synthesis of sugars and all other essential organic molecules crucial for plant growth and development. RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE/OXYGENASE (RuBisCO) binds CO_2 to ribulose bisphosphate (RuBP) molecules in the first reaction of CBB cycle, to form 3-phosphoglyceric acid (3PGA). 3PGA is converted to 1,3-bisphosphoglycerate (1,3-BPG) by PHOSPHOGLYCERATE KINASE (PGK) using ATP. 1,3-BPG is reduced to glyceraldehyde-3-phosphate (G3P) by G3P DEHYDROGENASE (GAPDH) using NADPH generated by the light reactions of photosynthesis. One of 6 G3P molecules produced in CBB cycle is used in carbohydrate synthesis, while the rest of the G3P molecules are used to produce ribulose-5-phosphate (Ru5P) in several enzymatic steps involving FRUCTOSE-1,6-BISPHOSPHATASE (FBPase) and SEDOHEPTULOSE-1,7-BISPHOSPHATASE (SBPase) and several other enzymes. PHOSPHORIBULOKINASE (PRK) converts Ru5P to RuBP, the starting molecule for the cycle. The regeneration RuBP ensures the continuous operation of the CBB cycle.

Regulation of RuBisCO activity is a pivotal aspect of photosynthetic CO_2 fixation, with RUBISCO ACTIVASE (RCA) playing a crucial role in the activation process of RuBisCO upon illumination. In darkness, the catalytic site of RuBisCO enzyme exists in inactivated form. Activation of RuBisCO enzyme in light requires the carbamylation of a specific Lys residue in the catalytic site of RuBisCO by CO_2 and Mg^{2+}, which stabilizes the carbamate formed in the first reaction (Shan et al., 2011; Waheeda et al., 2023). However, RuBP binds to the inactive catalytic site and prevents the activation reaction by CO_2 and Mg^{2+} upon illumination. RCA, an ATP-dependent enzyme that co-evolved with RuBisCO, acts as a catalytic chaperone to overcome this limitation by promoting the dissociation of inhibitory RuBP from the catalytic site and allowing the binding of CO_2 to the specific RuBisCO Lys residue (Jensen, 2000; Waheeda et al., 2023). Notably, studies in rice reveal that overexpression of RCA significantly improves crop yield, underlining the role of RCA in RuBisCO activation (Qu et al., 2021; Feng et al., 2023). Moreover, the regulatory complexity extends to isoforms of RCA, such as the redox-sensitive α-isoform and the redox-insensitive β-isoform, with their abundance varying across species like tobacco and *Arabidopsis* (Elizabete Carmo-Silva and Salvucci, 2013; Waheeda et al., 2023).

The chloroplast redox state also plays a role in regulating the activity of key enzymes involved in the CBB cycle (Michelet et al., 2013). Enzymes such as PRK, PGK, GAPDH, FBPase and SBPase which are activated by light, undergo thiol

oxidation in darkness, rendering them inactive (Lemaire et al., 2007; Michelet et al., 2013). However, upon exposure to light, THIOREDOXINs (TRX) reduce the oxidized disulfide bonds within these enzymes, thereby activating them (Nikkanen and Rintamäki, 2019). Moreover, the activity of CBB enzymes, particularly GAPDH and PRK, is modulated by CP12 proteins (Wedel et al., 1997). CP12 proteins typically contain cysteines capable of forming two disulfide bonds. When CP12 becomes oxidized, it binds to GAPDH, leading to the formation of a GAPDH/CP12/PRK complex (Wedel et al., 1997; Del Giudice et al., 2015). Within this complex, the activities of both GAPDH and PRK are significantly suppressed. The assembly of GAPDH/CP12/PRK complex is likely favored in darkness due to the oxidation of the TRX pool. However, the dissociation of the GAPDH/CP12/PRK complex and the subsequent restoration of GAPDH and PRK enzyme activities occur rapidly upon the action of reduced TRXs. The activation of CBB cycle enzymes by TRXs enables efficient regulation of the enzyme activity in response to changes in the cellular redox state, ensuring optimal functioning of the CBB cycle under FL conditions.

Photosynthesis efficiency is challenged by photorespiration, a metabolic pathway competing with CBB cycle. In photorespiration, RuBisCO fixes O_2 instead of CO_2, resulting in consumption of ATP without formation of organic compounds for storage of energy. In photorespiration, phosphoglycolate produced in oxygenation reaction of RuBisCO is processed to form PGA with the concomitant release of CO_2 and consumption of ATP. This process compromises the overall efficiency of CO_2 fixation, but it can also protect PETC components by preventing formation of ROS (Heber et al., 1996; Rivero et al., 2009; Fernie and Bauwe, 2020; Shi et al., 2022). Photorespiration also produces H_2O_2 in peroxisomes during conversion of glycolate to glyoxylate by GLYCOLATE OXIDASE (GOX). H_2O_2 is eliminated by reduction by CATALASE (CAT) to water and O_2.

1.5 Photosynthesis as a sensor of environmental stress

Plants, as stationary organisms, are intimately linked to their environment, rendering them vulnerable to changes in both abiotic and biotic factors that can impact their photosynthetic processes. Beyond its conventional role as a process converting light energy into chemical energy, photosynthesis can serve as a sensor for environmental changes due to its sensitivity to variations in abiotic (light, temperature, CO_2 levels, water availability) and biotic factors (Fey et al., 2005; Gollan and Aro, 2020; Jan et al., 2022). Chloroplast biogenesis and various stress types induce changes in both the photochemical reactions within the PETC and in the activity of CBB cycle enzymes (Figure 2) (Miller et al., 2010; Zhang et al., 2018; D'Alessandro et al.,

2019; Moore et al., 2022). Intermediates in Chl biosynthesis, PSII, PQ pool, PSI and CO_2 concentration are the key components of the photosynthesis involved in sensing environmental stress (Tikkanen et al., 2014; Singh et al., 2015; Pathak et al., 2017; Hernández-Verdeja and Strand, 2018; Lima-Melo et al., 2021). Altered function of these components initiates several signaling pathways that regulate gene expression both in the chloroplast and in the nucleus, which regulate the expression of genes involved in plant development, metabolisms, redox balance of the cell, defense, and senescence (Améras et al., 2003; Qi et al., 2015; Chan et al., 2016; Gollan and Aro, 2020). These signals include intermediates of metabolic processes as well as ROS and ROS-induced redox modifications. The convey of information to the nucleus through these signals is known as retrograde signaling. (Gollan et al., 2015; Hernández-Verdeja and Strand, 2018; Mielecki et al., 2020). This study focuses on the effect of changes in light intensity and spectrum on the photosynthetic machinery and the consequent signals to regulate the gene expression.

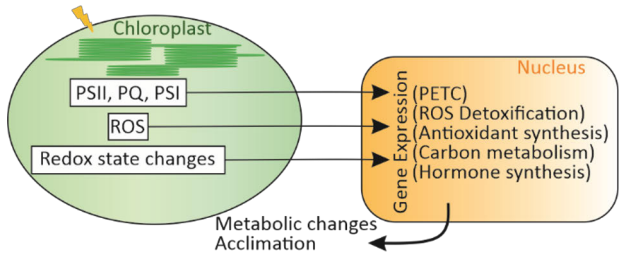

Figure 2. Light-induced retrograde signals initiated in chloroplast and their influence on nuclear gene expression. Light induces the production of ROS, or changes in redox states of electron carriers in PETC. The signals initiated in chloroplasts modify the expression of genes involved in PETC, ROS detoxification and antioxidant synthesis, carbon metabolism as well as hormone synthesis. The altered gene expression in nucleus results in activation of protective metabolism against the stress and acclimation to changed environmental conditions.

1.5.1 Regulation of light-induced gene expression by light receptors

Plants possess sophisticated mechanisms to sense and respond to light, crucial for their growth, development, and acclimation. The main photoreceptors involved in these processes are PHYTOCHROMEs (PHY) and CRYPTOCHROMEs (CRY), each regulating gene expression and physiological responses to light signals. PHYs are activated upon exposure to red light and translocate to the nucleus, where they initiate the phosphorylation and subsequent degradation of PHY INTERACTING FACTORS (PIF) which repress the expression of light induced genes (Pham et al., 2018). CRYs undergo conformational changes in flavin molecules upon absorption of blue light, changing its apoprotein structure (Wang et al., 2014). Active PHYs and

CRYs disrupt the activity of CONSTITUTIVELY PHOTOMORPHOGENIC 1 (COP1) by binding to SUPPRESSOR OF PHYA-105 1 (SPA1) within the COP1/SPA1 complex (Kleine et al., 2007; Pham et al., 2018). This interaction leads to the translocation of COP1 out of the nucleus, which prevents the degradation of transcription factors (TF) such as ELONGATED HYPOCOTYL 5 (HY5) allowing for the accumulation of HY5 and subsequent activation of light-responsive genes (Guo et al., 2021; Bian et al., 2022). HY5 is a major TF that has a direct and indirect regulatory influence on the expression of hundreds of genes during light-induced development of Arabidopsis seedlings (Sibout et al., 2006; Kleine et al., 2007; Lee et al., 2007). HY5 binds to the promoters of light-regulated genes, including those involved in biosynthesis of Chl and other pigments, photosynthetic complexes, as well as sulfur and Fe uptake during chloroplast biogenesis (Shin et al., 2013; Toledo-Ortiz et al., 2014; Gangappa and Botto, 2016; Guo et al., 2021). HY5 controls nuclear gene expression also in mature plants under several environmental stresses, like HL or FL (Gonzalez et al., 2008; Shin et al., 2013; Jiang et al., 2020). It also coordinates the function of the multimeric transcription complex MYB–bHLH–WD repeat (MBW) that activates the anthocyanin synthesis genes (Gonzalez et al., 2008; Ma et al., 2021b; Yan et al., 2021; Li et al., 2022).

1.5.2 ROS production, scavenging, and signaling in light

PSs generate ROS (Figure 1), which in addition to inducing oxidative stress, can react with secondary messengers transferring the signal forward. There are four ROS types formed in PETC, including singlet oxygen ($^1O_2$) produced mainly in PSII, $O_2^{\bullet-}$ at PSI acceptor side, H_2O_2 via dismutation of $O_2^{\bullet-}$ by SOD, and ·OH formed by the Fenton reaction, a chemical reaction that involves the reduction of H_2O_2 by ferrous iron (Fe^{2+}) (Khorobrykh et al., 2020).

$^1O_2$ is highly reactive due to paired electrons with antiparallel spins in the same orbital, which makes it more reactive than molecular O_2 with parallel electron spins in two different orbitals (Dogra and Kim, 2019; Khorobrykh et al., 2020). $^1O_2$ can accept electrons from other molecules, making it very reactive towards electron-rich compounds, such as protein thiols (Liu and Liu, 2015; Dogra and Kim, 2019; Dmitrieva et al., 2020). $O_2^{\bullet-}$ has one unpaired electron, making it inherently reactive because they seek to pair the unpaired electron by reacting with other molecules. H_2O_2 is a strong oxidizing agent as it can accepts electrons from other molecules and donate oxygen atoms to them. It also contains a peroxide bond (O-O single bond), which is relatively weak and can easily break, leading to the formation of highly reactive ·OH due to an unpaired electron in its structure. Fenton reaction produces Fe^{3+} from Fe^{2+}, as an electron is used to reduce H_2O_2. Ferritin is a cellular protein that can store iron in a safe, non-reactive form by oxidizing Fe^{2+} to Fe^{3+}. By storing iron in a Fe^{3+} state, ferritins effectively reduce the pool of free Fe^{2+}, limiting the

substrate available for the Fenton reaction and consequently decreasing the production of harmful ·OH (Sági-Kazár et al., 2022).

When plants are exposed to HL, one of the responses is the increased formation of $^1O_2$. Carotenoids and tocopherols are the most important antioxidants that protect plant cells from $^1O_2$-induced damage, and prevent lipid peroxidation in thylakoids by breaking free-radical chain reactions (Farmer and Mueller, 2013; Dmitrieva et al., 2020). For instance, $^1O_2$ scavenging by β-carotene results in formation of β-cyclocitrol (β-CC), a compound that induces the expression of nuclear genes including the genes involved in synthesis of PQ, anthocyanin and flavonoids, and methionine (Ramel et al., 2012; Ramel et al., 2013; Schmitt et al., 2014; Shumbe et al., 2014; Dmitrieva et al., 2020).

H_2O_2, which is mostly produced on the acceptor side of PSI, has lower reactivity than $^1O_2$, which means that it may travel longer distances to induce responses. H_2O_2 can traverse cellular membranes, thus affecting other cellular organelles than the one where it was synthetized. It participates in redox signaling by activating or inhibiting specific target proteins that may be involved in initiating the defense and acclimation processes (Gechev et al., 2002; Vanderauwera et al., 2005; Lv et al., 2019). It can diffuse from the chloroplast to the nucleus either through membranes, facilitated by structures known as stromules that enable close contact between chloroplast and nucleus, or it may also diffuse via aquaporins (Borisova et al., 2012; Bienert and Chaumont, 2014; Caplan et al., 2015). H_2O_2 has been shown to influence the expression of hundreds of genes including *HEAT SHOCK PROTEINS* (*HSP*) involved in protein folding and repair, ROS detoxification genes, like *GLUTATHIONE S-TRANSFERASEs* (*GST)*, *CAT2*, ASCORBATE PEROXIDASE 1 (*APX1),* and *APX2* and TFs like *HEAT SHOCK FACTORS (HSF*) and multiple *N-TERMINAL REGION CONTAINING* (*NAC*) genes (Vanderauwera et al., 2005; Hieno et al., 2019). Thereby H_2O_2 produced as a result of HL exposure initiates signals leading to scavenging of ROS and to better acclimation to HL stress.

H_2O_2 also causes oxidative damage in the chloroplast by reacting with lipids and proteins among others, especially under HL. Oxidative damage caused by H_2O_2 can be reversed by molecular and enzymatic antioxidant systems (Figure 3). H_2O_2 can interact, for example, with thiol containing compounds such as cysteine residues of proteins, leading to the formation of disulfide bonds and sulfenic acid (-SOH) that modifies the function of target proteins. These proteins can also undergo S-glutathionylation in the presence of glutathione (GSH). The reversibility of disulfide bonds, sulfenylation, and methionine sulfoxidation is catalyzed by TRXs and GLUTAREDOXINs (GRX) (Meyer et al., 2008). Oxidized proteins can be reduced by TRXs, which are subsequently reduced by Fd. Alternatively, oxidized proteins can be reduced by GRXs, which are reduced by GSH, which in turn is regenerated by GLUTATHIONE REDUCTASE (GR) using NADPH as a source of reducing

power. H_2O_2 can be reduced to water by antioxidant enzymes like PEROXIREDOXINs (PRX), APXs or GLUTATHIONE PEROXIDASEs (GPX), which use either TRX, NADPH-DEPENDENT CHLOROPLAST THIOREDOXIN REDUCTASE C (NTRC), ascorbate (AsA) or GSH as electron sources (Figure 3) (Foyer and Noctor, 2011; Noshi et al., 2016; Zhang et al., 2016). GSH also reduces the oxidized ascorbate (DHA), forming oxidized glutathione (GSSG), which is reduced by NADPH generated through photosynthesis.

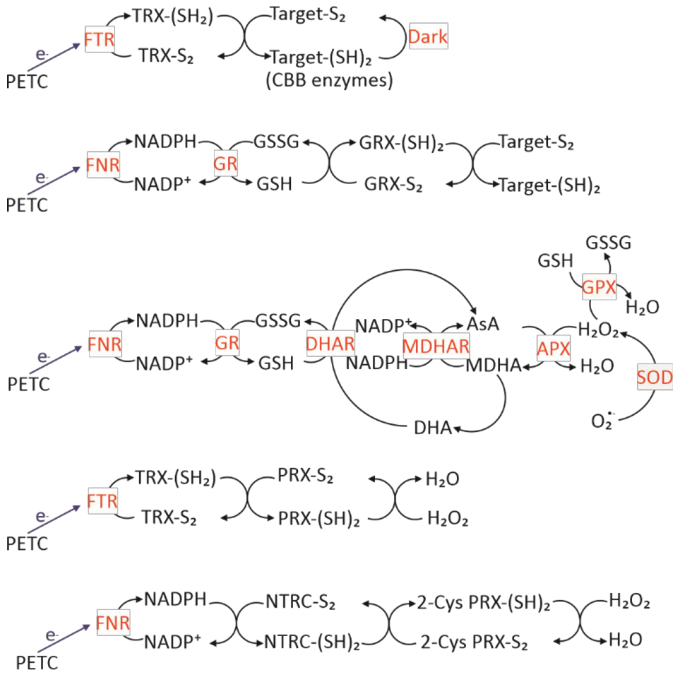

Figure 3: Regulation of redox sensitive proteins and ROS scavenging in the chloroplast. TRXs and GRXs receive electrons from PETC via FERREDOXIN-THIOREDOXIN REDUCTASE (FTR) and GSH, respectively. Reduced PRXs and 2-Cys PRXs scavenge H_2O_2. NADPH acts as the source of the electrons for NTRC and GSH-AsA cycle for detoxification of ROS. DEHYDROASCORBATE REDUCTASE (DHAR), MONODEHYDROASCORBATE REDUCTASE (MDHAR).

1.5.3 Other signals originating from photosynthesis to control gene expression in changing light intensities

Location of the PQ pool as an intermediary electron transporter between PSII and PSI makes its redox state sensitive to changes in PSII and PSI activities (Surpin et al., 2002; Pfannschmidt et al., 2009). Both oxidized and reduced PQ pool have been suggested to be integral to photosynthetic redox control affecting chloroplast and nuclear gene expression (Figure 2) (Pfannschmidt et al., 1999; Fey et al., 2005;

Borisova-Mubarakshina et al., 2019). PQH_2 has been associated with expression of several genes, including chloroplast genes encoding PSII and PSI proteins such as *PsbA*, *PsaA*, and *PsaB* (Pfannschmidt et al., 1999; Allen, 2015). Reduced PQ also initiates pathways that regulate the size of the LHCII antenna (Frigerio et al., 2007; Kouřil et al., 2013). However, elevated H_2O_2 content under HL was suggested to be responsible for the decrease in the PSII antenna size, not the PQ redox state (Borisova-Mubarakshina et al., 2015). It has been suggested that also the STN7 kinase potentially serves as the bridge connecting the redox state of the PQ pool and the regulation of photosynthesis-related gene expression (Bellaflore et al., 2005; Pesaresi et al., 2009; Chan et al., 2016).

Also, the variations in CO_2 levels indirectly affect the PETC gene expression via the activity of the CBB cycle. A decrease in CO_2 limits the RuBisCO carboxylation reaction, causing over-reduction of PETC components. Conditions limiting CO_2 uptake such as drought and salinity stress prompt stomatal closure and reduce the efficiency of CBB cycle (Agurla et al., 2018; Orzechowska et al., 2021). Stomatal closure reduces water loss but also limits CO_2 uptake, affecting photosynthetic efficiency. This leads to an accumulation of NADPH, causing over-excitation of the photosynthetic apparatus and production of ROS. Antioxidant systems are upregulated to scavenge ROS, preventing damage to thylakoid membranes (Miller et al., 2010; Geng et al., 2016). Photorespiration, on the other hand, is enhanced under low CO_2 conditions, ultimately aiding in the regeneration of RuBP and recycling of CO_2 which leads to the mitigation of oxidative stress within the plant cells (Laxa and Fromm, 2018; Fernie and Bauwe, 2020; Shi et al., 2022). An increase in CO_2 may enhance photosynthetic rates but, at high CO_2 levels can also lead to stomatal closure, thereby limiting CO_2 uptake (Xu et al., 2016; Lima-Melo et al., 2021). Additionally, increased CO_2 concentration may affect the expression of genes related to light harvesting and the abundance of PETC proteins (Pan et al., 2018; Foyer and Noctor, 2020).

1.5.4 Light induced oxylipin signaling

The modulation of gene expression in response to light also involves hormones as their levels may change in response to light intensity, contributing to the signaling pathways that influence gene expression. Stress such as severe or long HL stress (Alsharafa et al., 2014; Dietz, 2015), or the combination of heat stress and HL treatment (Balfagón et al., 2019) induce the formation of oxylipins. These signaling molecules are derived from polyunsaturated fatty acids (PUFA) and are generated through the activation of lipases that release PUFAs from plastid membranes. Oxylipins, such as 12-oxo-phytodieonic acid (OPDA) and jasmonic acid (JA), play a pivotal role in retrograde signaling under different stress types in plants. The synthesis of OPDA, initiated by the release of α-linolenic acid (a type of PUFA),

involves a series of enzymatic steps, including LIPOXYGENASE (LOX), ALLENE OXIDE SYNTHASE (AOS), and ALLENE OXIDE CYCLASE (AOC) enzymes (Figure 4). OPDA synthesis occurs in chloroplasts, and it is exported to the cytosol through JASSY, a JA transporter (Guan et al., 2019). OPDA is then exported from cytosol to peroxisome where it is converted to JA by OPDA REDUCTASE 3 (OPR3) and the subsequent β-oxidation steps.

Production of $^1O_2$ in chloroplast has been shown to increase oxylipin biosynthesis (Krieger-Liszkay, 2005; Fischer et al., 2012). PSII photoinhibition, inducing $^1O_2$ formation, led to the induction of *LOX*, *AOS*, *AOC* and *OPR3* genes involved in oxylipin biosynthesis (Op Den Camp et al., 2003; Ramel et al., 2013). Arabidopsis mutants (*flu* and *ch1*), characterized by accumulation of Chl biosynthesis intermediates and deficient Chl biosynthesis, respectively, exhibit elevated levels of $^1O_2$ (Op Den Camp et al., 2003; Ochsenbein et al., 2006; Przybyla et al., 2008; Ramel et al., 2013). These mutants had high levels of oxylipins as well as increased expression of oxylipin responsive genes (Op Den Camp et al., 2003; Ochsenbein et al., 2006; Przybyla et al., 2008; Ramel et al., 2013). Both ROS-induced lipid peroxidation and LOX–dependent lipid peroxidation were stimulated by HL in *ch1* mutants (Ramel et al., 2013). PSI photoinhibition has been shown to cause a decrease in the ROS production as the rate of electron flow through PSI declines (Gollan et al., 2017; Lima-Melo et al., 2021). Therefore, OPDA production by lipid peroxidation is also suppressed, leading to the repression of oxylipin-responsive gene expression implying that PSI photoinhibition exerts a negative effect on the oxylipin signaling pathway (Ramel et al., 2012; Gollan et al., 2017; Lima-Melo et al., 2019; Gollan and Aro, 2020).

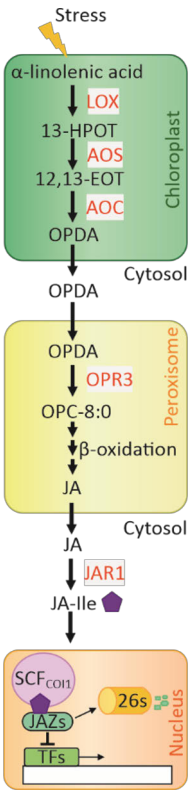

Figure 4: Jasmonic acid (JA) biosynthesis and signaling. OPDA synthesis takes place in the chloroplast, from where it is transported to the peroxisome and used for JA synthesis. In the cytosol, JA is activated by binding to Isoleucine amino acid forming JA-Ile, which moves into the nucleus, where it forms a complex with JA receptor, the COI1 protein. SCF^{COI1}-JA-Ile complex ubiquitinates JASMONATE ZIM-DOMAIN (JAZ) repressor proteins. Polyubiquitinated repressor proteins are recognized and degraded by the 26S proteasome, and the transcription factors are released, enabling the expression of JA-responsive genes. For enzymes in OPDA and JA synthesis, see the text above. JA-RESISTANT 1 (JAR1), 13-Hydroperoxy linolenic acid (13-HPOT), 12S, 13S-epoxy-linolenic acid (12,13-EOT).

OPDA can influence oxylipin signaling by binding to CYCLOPHILIN 20-3 (CYP20-3), a redox sensitive protein, to form the cysteine synthase complex (CSC), which synthesizes free cysteine. Cysteine is a sulfur containing amino acid used in the synthesis of GSH by Γ-GLUTAMYLCYSTEINE SYNTHETASE (γ-GCS) and GLUTATHIONE SYNTHETASE (GS) (Laxa et al., 2007; Liu et al., 2020) enzymes, resulting in an enhancement of the antioxidant capacity of the cells (Park et al., 2013). Interestingly, CYP20-3 knockout plants are sensitive to HL stress and the PSII repair cycle is inhibited (Pan et al., 2018).

Both OPDA and JA induce the expression of genes involved in lipid and antioxidant metabolisms, influencing the redox balance in cells and helping plants tolerate the stresses (Sasaki-Sekimoto et al., 2005; Mueller et al., 2008). OPDA is classified as reactive electrophile species (RES) because its structure contains unsaturated carbonyl bonds in cyclopentanone ring. The reactive cyclopentanone ring of OPDA can be inactivated by glutathionylation in the reaction catalyzed by GST enzymes, such as GST PHI 8 (GSTF8) and GST Tau 19 (GSTU19), which induce the formation of GS-OPDA conjugate (Mueller et al., 2008; Dixon and Edwards, 2009; Dixon et al., 2010; Skipsey et al., 2011). GS-OPDA conjugates are

transported to the vacuole, where they are degraded by GAMMA-GLUTAMYL TRANSPEPTIDASE 4 (GGT4) enzyme (Grzam et al., 2007; Ohkama-Ohtsu et al., 2007; Ohkama-Ohtsu et al., 2011).

JA is activated by binding to isoleucine (Ile) amino acid (Figure 4). JA-Ile regulates gene expression via ubiquitin-dependent signaling pathway. In this pathway, JA-Ile binds to its receptor CORONATINE INSENSITIVE 1 (COI1), forming the biologically active JA-COI1 complex. COI1 is a key component of the SCF (SKP1-CUL1-F-box protein) E3 ubiquitin ligase complex. Binding of JA-Ile to SCF complex triggers ubiquitination and subsequent degradation of JAZ repressor proteins, which are negative regulators of JA-responsive TFs (Chini et al., 2007; Thines et al., 2007). JA signaling contributes to the HL acclimation by upregulating transcriptional expression of GST genes and upregulating the production of antioxidants such as GSH and AsA, which scavenge the ROS (Sasaki-Sekimoto et al., 2005; Gollan and Aro, 2020). However, the pathway for GSH accumulation in response to JA is not known. JA also regulates the expression of genes encoding proteins engaged in anthocyanin synthesis, senescence, as well as its own biosynthesis, and genes that repress JA signaling (Xiang and Oliver, 1998; Shan et al., 2009; Zhou and Memelink, 2016).

1.5.5 Hormonal crosstalk in light signaling

SA and abscisic acid (ABA) hormones, produced in chloroplasts, are also involved in light signaling. SA is a crucial signaling molecule in plants, known for its involvement in expression of hundreds of defense genes against biotic and abiotic stresses (Wang et al., 2006; Blanco et al., 2009; Lv et al., 2015; Ding et al., 2018; Chen et al., 2020). HL stress induces SA biosynthesis, which in turn triggers signals aimed at mitigating photodamage and maintaining cellular homeostasis (Lv et al., 2015; Chen et al., 2020). SA orchestrates the activation of antioxidant defense mechanisms, including the upregulation of enzymes such as SOD, CAT, and PRXs, which scavenge the ROS generated under HL conditions (Mateo et al., 2006; Qu et al., 2018). Additionally, SA regulates the expression of HSPs that enhance plant tolerance to HL (Mateo et al., 2006; Blanco et al., 2009; Sangwan et al., 2022). SA-deficiency impaired the capability to acclimate to HL (Mateo et al., 2006) since SA plays an important role in alleviating photoinhibition under HL (Chen et al., 2020; Moustakas et al., 2022).

ABA-mediated signaling pathways are activated in response to various abiotic stresses, including HL, to regulate stomatal closure, thereby reducing water loss and maintaining cellular hydration status (Weatherwax et al., 1996; Hsu et al., 2021; Segarra-Medina et al., 2023). SA and ABA pathways are often interconnected, with SA positively regulating ABA biosynthesis and ABA enhancing SA signaling under stress conditions (Figure 5) (Parwez et al., 2022). Moreover, JA signaling pathways

can interact with SA and ABA pathways to modulate defense responses (Fujita et al., 2006). Key components in this crosstalk include TFs like JAZs, MYC2, NONEXPRESSER OF PR GENES 1 (NPR1), which participate in the interplay between SA, ABA and JA pathways, influencing both plant growth and defense mechanisms (Mou et al., 2003; Dombrecht et al., 2007; Aleman et al., 2016; Chen et al., 2021). ABA receptor PYRABACTIN RESISTANCE-LIKE 6 (PYL6) functions like COI1 and negatively regulates the activity of MYC2, a JA TF, in an ABA-dependent manner (Aleman et al., 2016). On the other hand, JA signaling can inhibit SA accumulation through modulation of NAC TFs, which regulate the activity of SA biosynthesis genes (Figure 5) (Zheng et al., 2012; Yang et al., 2019).

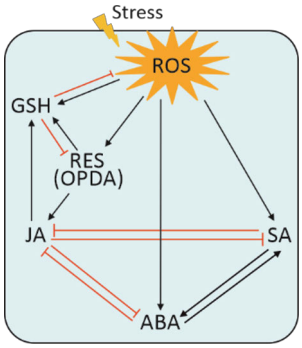

Figure 5. Crosstalk between ROS, OPDA, JA, SA, and ABA hormones under light stress (such as HL). Upon accumulation of ROS due to the stress, the plant hormones (OPDA, JA, SA and ABA) accumulate and initiate signaling pathways. JA has an antagonistic relationship with SA and ABA. SA promotes ABA accumulation, while ABA enhances SA signaling. OPDA and JA also induce the accumulation of GSH, which scavenges ROS and RES (OPDA).

Crosstalk between ROS, oxylipins and ABA may also be mediated by the SAL1/PAP pathway. 3′-phosphoadenosine 5′-phosphosulfate (PAPS) is a precursor for 3'-phosphoadenosine 5'-phosphate (PAP) that is degraded by 3'(2'),5'-BISPHOSPHATE NUCLEOTIDASE (SAL1) enzyme (Rodríguez et al., 2010). Oxidation of SAL1 by H_2O_2 causes a formation of intra and intermolecular disulfide bonds in the enzyme protein leading to its inactivation (Estavillo et al., 2011; Chan et al., 2016), resulting in PAP accumulation. PAP is transferred to the nucleus where it inactivates EXORIBONUCLEASEs (XRN) that degrades the RNA substrates and allows the accumulation of RNA transcripts (Estavillo et al., 2011). SAL1/PAP pathway has been implicated in the expression of 25% of HL responsive genes (Estavillo et al., 2011). SAL1 loss-of-function mutant has been shown to have a higher expression of *LOX2* gene and elevated JA levels (Rodríguez et al., 2010). PAP accumulation leads to sulfur starvation (Lee et al., 2012), which induces the expression of JA synthesis genes as well as JA-responsive genes (Hirai et al., 2003; Maruyama-Nakashita et al., 2003). This is in accordance with other studies, which show that JA induces the expression of genes of the sulfur reduction pathway and PAPS biosynthesis pathway, and that sulfur starvation enhances the expression of

JA synthesis and responsive genes (Jost et al., 2005; Sasaki-Sekimoto et al., 2005; Lee et al., 2012). OPDA accumulation in response to light stress is also associated with increased PAP levels (Kopriva, 2013). OPDA that induces GSH accumulation in plastids, may activate ADENOSINE 5′-PHOSPHOSULFATE KINASE (APK), which synthesizes PAPS that is then converted to PAP in the cytosol (Kopriva, 2013).

2 Aims of the Study

Photosynthetic signaling plays an important role in the induction of light-stress responses and during the following recovery phase under optimal conditions. However, there is still limited understanding regarding the origins of signals triggered by modifications of light quality and quantity as well as the impact of these signals on global gene expression and metabolite levels. Especially the recovery phase after HL treatment has been less investigated. It is unclear whether this phase is simply a relaxation of the gene expression and metabolism to the pre-HL stress levels, or if recovery-specific gene expression and metabolism are needed to rebalance the redox state of the cell after HL treatment.

This project aims to:

I Investigate how the lack of PSII affects the accumulation and organization of thylakoid protein complexes and the changes in gene expression in the cyanobacterium *Synechocystis* sp. PCC 6803.

II Explore the influence of PSI-acceptor-side components on PSI susceptibility to light damage, and to investigate the changes in global gene expression under various CO_2 concentrations in control and PSI photoinhibited leaves of *Arabidopsis thaliana*.

III Elucidate the signaling mechanisms and the role of metabolites involved in the recovery phase from short-term HL stress in *Arabidopsis thaliana*.

3 Materials and Methods

3.1 Materials and growth conditions

A glucose tolerant *Synechocystis* sp. PCC 6803 AR strain, with the *PsbA1* and *PsbA3* genes inactivated by antibiotic resistance cassettes (Mäenpää et al., 1993), was used as the background control strain. The PSII-less strain is a variant of the AR strain with an additional spontaneous mutation in Val219 codon of the *PsbA2* gene, thereby inactivating also the third *PsbA2* gene in Synechocystis genome (Paper I). The PSII-less strain was grown on BG-11 agar plates under continuous light of 50 µmol photons m^{-2} s^{-1}, and 32°C in the presence of 5-mM glucose, 10-µM DCMU, and antibiotics (spectinomycin 10 µg/ml, streptomycin 5 µg/ml, kanamycin 5 µg/ml, and chloramphenicol 2.5 µg/ml) (Mulo et al., 1997). Liquid cultures for experiments were grown without DCMU in 50 ml batches and shaken at 90 rpm.

Wild type (WT) plants of *Arabidopsis thaliana* (L.) Heynh. Columbia (Col-0) ecotype were grown under an 8 h photoperiod at 100 µmol photons m^{-2} s^{-1} (growth light; GL) with POWERSTAR HQI-T 400 W/D metal halide lamps (OSRAM GmbH, Munich Germany) as the light source at 23°C and 60% relative humidity. Six-week-old plants were used for experiments.

To analyze the signaling cascade initiated in chloroplast, WT and *coi1* mutants of *Arabidopsis thaliana* were illuminated at HL (1000 µmol photons m^{-2} s^{-1}) for 60 min and subsequently at growth light (GL) (100 µmol photons m^{-2} s^{-1}) for 60 min for recovery. *Coi1-1* and *coi1-2* mutant lines at Col-0 background were obtained from The Nottingham Arabidopsis Stock Centre (NASC, Nottingham, UK, N68754 and N68755).

To analyze the effect of the specific PSI photoinhibition treatment (PSI-PI) (Tikkanen and Grebe, 2018), on global gene expression under various CO_2 concentrations, WT plants of *Arabidopsis thaliana* were moved from growth conditions to the treatment chamber. The plants were allowed to stabilize for 10 min in chamber conditions prior to the specific PSI-PI light treatment (Paper II Figure 1). A single PSI-PI treatment cycle consisted of 30 s of GL followed by three repeated cycles of 5 s of red light (660 nm, 35 µmol photons m^{-2} s^{-1}) and 1 s of intense white light (1000 µmol photons m^{-2} s^{-1}) using programmable LED lamps (Heliospectra, Göteborg, Sweden). Plants were subjected to PSI-PI treatment or to GL treatment

for 3 h at 0 ppm, 100 ppm, 400 ppm, and 1000 ppm CO_2 concentrations using an air-tight chamber (Paper II Figure 1).

3.2 Extraction of proteins from cyanobacteria and BN-SDS-PAGE analysis

Protein extraction from control and mutant Synechocystis strains followed the protocol outlined by (Zhang et al., 2009). In brief, the total proteins and thylakoid-associated proteins were extracted and separated using 12% (w/v) SDS-PAGE containing 6 M urea. Proteins were then electrotransferred onto a PVDF membrane and immunodetected, using specific antibodies, as described in Paper I. For blue native (BN)-PAGE, protein solubilization was carried out according to the method described in (Zhang et al., 2012), using 1.5% dodecyl maltoside, and without the addition of protease inhibitors in the washing buffer. BN-PAGE was conducted following the procedure described by (Järvi et al., 2011), and protein separation in the second dimension was performed according to (Mustila et al., 2016). Identification of protein spots on BN/SDS-PAGE gels was performed according to (Herranen et al., 2004) and (Zhang et al., 2004).

3.3 Estimation of respiration and photosynthetic activity in cyanobacteria

O_2 uptake of the cell culture, using a Clark-type Hansatech oxygen electrode (Hansatech, King's Lynn, UK), was recorded for 5 min in darkness to determine the respiration rate. Subsequently, the same culture was exposed to 1000 μmol photons m^{-2} s^{-1} for 5 min to measure the rate of O_2 evolution in light. PSI activity was evaluated by measuring O_2 uptake in the presence of 10 μM DCMU, 0.1 mM methyl viologen (MV), 50 μM 2,6-dichlorophenolindophenol (DCPIP), 1 mM ascorbate, and 50 μM NaN_3 for 5 minutes under 1000 μmol photons m^{-2} s^{-1}.

3.4 Biophysical analysis of cyanobacteria

Absorption spectra of the cells were obtained using the OLIS CLARiTY 17 spectrophotometer (Olis, Athens, GA, USA). The spectra underwent double normalization at 440 and 750 nm following the method outlined by (Luimstra et al., 2018). 77 K fluorescence emission spectra measurements were conducted with QEPro spectrometer (Ocean Optics, Orlando, FL, USA) using 580-nm monochromatic light as described in Paper I.

3.5 Biophysical measurements of plants

The plant leaves, pre-incubated in darkness for 20 min, were used for simultaneous measurements of chl a fluorescence and P700-oxidation signals using the Dual-

PAM-100 (Walz, Effeltrich, Germany) (Paper II and III). Photochemical efficiency of PSII was quantified as the ratio of variable to maximum fluorescence (F_v/F_m). Maximum oxidation of P700 (P_m) was determined after far-red illumination followed by a saturating pulse. The fraction of open PSII RCs (qL) was calculated following the methodology described by (Kramer et al., 2004), which involved estimating the minimum fluorescence in light (F0') using the approach proposed by (Oxborough and Baker, 1997) .

To determine the quantum yields of photosystems at different light intensities, the leaves were exposed to illumination at 25, 50, 100, and 500 μmol photons m^{-2} s^{-1} for 3 minutes before the measurements (Paper II). The yield of functional PSI centers (Y(I)), yield of donor-side limitation (Y(ND)), and yield of acceptor-side limitation (Y(NA)) in Paper II were calculated by normalizing the P_m for each leaf sample using the average P_m value of the GL samples at 400 ppm CO_2 as a reference P_m (PmR). This normalization effectively eliminates the contribution of damaged PSI RCs to Y(I), Y(ND), and Y(NA). The photochemical quantum yield of PSII (Y(II)), yield of non-photochemical quenching (Y(NPQ)), and yield of nonregulated energy dissipation (Y(NO)) were calculated according to the methodology proposed by (Genty et al., 1989).

3.6 Stomatal aperture measurement

Leaves were detached and promptly pressed onto Affinis Precious Polyvinylsiloxane resin (Coltene, Cuyahoga Falls, OH, USA) for imprinting and the stomatal aperture was estimated as described in Paper II.

3.7 Analysis of metabolites

Analysis of the metabolites were done as described in Paper II and III. Briefly, plant leaves were flash-frozen in liquid nitrogen and ground to a fine powder, followed by extraction with methanol or other specified solvents depending on the target metabolite. For ultra-performance liquid chromatography (UPLC) analysis, methanol extracts were prepared and analyzed by the Turku Metabolomics Centre, allowing precise quantification of hormones, and the glutathione-OPDA conjugate. Additionally, specialized assays were performed to measure specific stress-related metabolites, including H_2O_2, glutathione, ascorbate, and sugars and starch levels.

3.8 RNA isolation and analysis

Total RNA from Synechocystis was extracted using the hot phenol method and converted to cDNA (Tyystjärvi et al., 2001) (Paper I) and sent to the Finnish Functional Genomics Centre at Turku Bioscience (Turku, Finland) for single-ended library preparation and sequencing of RNA libraries with the Illumina HiSeq2500

platform. RNA-seq reads were aligned using Strand NGS 2.7 software (Agilent, Santa Clara, CA, USA) with the reference genome and annotations from GCA_000340785.1 (GenBank assembly accession). Before alignment, the first three 3′ nucleotides were removed. Quantification of the aligned reads was performed using the DESeq R package. Three independent biological replicates were analyzed.

From plant leaves, RNA for RNAseq was isolated using an innuPREP plant RNA isolation kit (Analytik Jena, Jena, Germany) according to the manufacturer's instructions (Paper II and III). RNA was converted to cDNA with the Bio-Rad iScript cDNA Synthesis Kit (Bio-Rad, Hercules, CA, USA) according to the manufacturer instructions. The cDNA samples were sent to the BGI Europe Genomic Center (Copenhagen, Denmark) for sequencing. The raw sequence reads from each replicate were quantified with Salmon (v0.12) (Patro et al., 2017) software using *Arabidopsis thaliana* genome assembly TAIR10 cDNA sequences as the reference (Paper II and III). Analyses of differential gene expression were carried out with the DESeq2 R package (v3.16) (Love et al., 2014). Differentially expressed genes (DEG) were annotated using the *Arabidopsis thaliana* genome annotation (TAIR 10.49.gtf). Genes with combined read counts lower than 10 were eliminated before differential expression analyses were performed. Genes with $-1 \geq \log 2\ (FC) \geq 1$ were selected for gene enrichment analyses. Gene enrichment analysis was performed with http://geneontology.org/ (accessed on 10 January 2023) software (Ashburner et al., 2000; Thomas et al., 2022; Aleksander et al., 2023). The gene lists for heatmaps were compiled manually based on GO terms or the published literature.

For qPCR, iScript™ cDNA Synthesis Kit (Biorad, Hercules, CA, USA) was used to synthesize cDNA (Paper III). Prior to use, the resulting cDNA solution underwent a fivefold dilution with water. RT-qPCR assays were done as described in Paper II using a Biorad iq5 real time PCR machine (Biorad, Hercules, CA, USA).

Isoform switch analysis was performed using IsoformSwitchAnalyzeR (Vitting-Seerup et al., 2019), a specialized software tool as described in Paper III.

3.9 Statistical analysis

Statistical significance between different samples was evaluated using a one-way ANOVA with the post hoc Tukey HSD Calculator (https://astatsa.com/OneWay_Anova_with_TukeyHSD/ accessed on 30 April 2024).

4 Results

4.1 PSII absence changed the expression of genes associated with PSII, altered the thylakoid organization and led to higher respiration in Synechocystis

Gene expression, thylakoid organization, pigment content, and electron transport in *Synechocystis* were investigated in the AR control and PSII-less strains to elucidate the effects of the loss of PSII activity on the expression, abundance and function of the thylakoid membrane complexes.

Surprisingly, the complete loss of PSII function resulted in only a very small total number of DEGs (Paper I Table 1). These DEGs included upregulated *slr0228* gene, an FtsH-type protease associated with PSII maintenance (Komenda et al., 2006), as well as the *PsbA2*, *PsbA3*, and *PsbD2* genes encoding PSII components. *sll1471* gene, encoding the CpcG2 (CpcL) linker protein, mostly found in the type of PBS associated with PSI (Kondo et al., 2007), showed significant downregulation (Paper I Table 1).

At protein level, the analyses of thylakoid protein complexes showed that CP43 and CP47 were present as unassembled proteins in the PSII-less mutant (Paper I Figure 2b). The levels of the PBS linker protein CpcL and orange carotenoid protein (OCP) showed no difference in accumulation (Paper I Figure 1), whereas the abundance of phycocyanin protein (PCy) in the PBS complex was notably lower in the PSII-less strain, while allophycocyanin (APC) showed no difference to the control strain (Paper I Figure 1). However, the absence of difference in PCy protein level had no major effect on the pigment composition of the PSII-less strain, as the absorption of PCy pigment was similar in both strains (Paper I Figure 3a). However, a slight blue-shift in the peak of PCy was observed in the PSII-less cells, indicating possible differences in PBS composition between the control and PSII-less mutant (Paper I Figure 3a). In addition, the PSII-less mutant had higher carotenoid and lower Chl absorbance compared to the control (Paper I Figure 3a). The PSII-less mutant also showed differences to the control strain in organization of the respiratory complexes as the absence of PSII function led to a higher level of Cyt b_6f (Paper I

Figure 1 and 2). Finally, the measurements of O_2 evolution rates demonstrated higher respiration rates in the PSII-less mutant compared to the control (Paper I, Figure 2b).

PSI activity and abundance also changed in the absence of PSII and was reflected in lower PsaB level (Paper I Figure 2b) and 50% decrease in the PSI activity in comparison to control (Paper I Figure 3b). Additionally, the ratio of PSI monomers to PSI trimers was higher in the mutant, with a small proportion of PSI dimers also observed (Paper I Figure 2). The NDH-1 complex (Paper I Figure 2A) and its individual subunits (Paper I Figure 2B), were found only in the PSII-less strain, apparently due to their higher abundance than in the control strain. The levels of PSI acceptor side proteins (Fd, FNR, RbcL subunit of RuBisCO, Flv3) and AtpB were similar between the PSII-less mutant and the control (Paper I Figure 1). Additionally, the fluorescence peak at 725 nm, emitted from PSI, was significantly lower in the PSII-less strain compared to control strain (Paper I Figure 3c).

These results revealed that the loss of PSII activity in cyanobacteria led to minimal changes in gene expression but significantly impacted thylakoid organization, pigment composition, and electron transport, particularly by increasing the abundance of respiratory complexes and reducing PSI activity.

4.2 Impact of PSI photoinhibition on global gene expression in plant leaves

Next, I investigated how the compromising of the PSI function influences photosynthetic processes and nuclear gene expression in plant leaves. A PSI-specific photoinhibition (PSI-PI) treatment, with consecutive changes of light quality and quantity (Tikkanen and Grebe, 2018), was employed here, since it inhibits specifically PSI activity with only minor effect on PSII activity (Paper II Figure 2) (Lempiäinen et al., 2022). PSI-PI treatment relies on overreducing the PETC intermediates between PSII and PSI without activating the protective mechanisms. It was achieved by illuminating the plants first with red light that is preferentially absorbed by PSII, and then giving a saturating light to channel those electrons to PSI to cause its photoinhibition. This method was employed across varying CO_2 levels to investigate whether changes in CO_2 concentration, a major sink of electrons from PSI, either exacerbate or alleviate PSI photoinhibition and thereby affect the signaling pathways induced by PSI photoinhibition.

4.2.1 Susceptibility of PSI to specific photoinhibition treatment is not dependent on CO_2 concentration

PSI-PI treatment for 3 h reduced the P_m by approximately 50% across all CO_2 concentrations tested, while PSII photochemical efficiency (F_v/F_m) declined by less than 10% (Paper II Figure 2), demonstrating the PSI specificity of this specific light

treatment. Surprisingly, the CO_2 concentrations lower than the air-level (400 ppm) did not exacerbate PSI photoinhibition, while elevated CO_2 did not protect PSI from photoinhibition (Paper II Figure 2A). Functional PSI centers exhibited approximately 50% lower quantum yields (Y(I)) in PSI-PI treated plants at lower light intensities compared to control plants (Paper II Figure 3A). However, under HL, Y(I) of PSI-PI exposed leaves did not differ from control plants (Paper II Figure 3). The acceptor side limitation (Y(NA)) of functional PSI centers was substantially higher in PSI-PI leaves compared to controls under all conditions (Paper II Figure 3A). PSI-PI treatment caused approximately a 20% decrease in the proportion of open PSII centers (qL) (Paper II Figure 2C) under all CO_2 conditions. Additionally, PSI-PI treatment induced a ~50% decrease in PSII photochemistry (Y(II)) and corresponding increases in non-regulated energy dissipation (Y(NO)) and regulated energy dissipation (Y(NPQ)) under illumination of 50 and 100 µmol photons m^{-2} s^{-1} (Paper II Figure 3B). Importantly, changes in CO_2 concentration had minimal effect on the functional parameters of PSI and PSII either in GL or in PSI-PI treated plants (Paper II Figure 3). This suggests that susceptibility of PSI to photoinhibition is independent of CO_2 concentration.

Furthermore, compared to GL plants, PSI-PI treatment did not significantly affect the accumulation of glucose or fructose in leaves exposed to atmospheric or lower CO_2 concentrations (Paper II Figure 4A and B). However, PSI-PI-treated leaves exhibited significantly higher amounts of these sugars at a high CO_2 concentration of 1000 ppm (Paper II Figure 4A and B). PSI-PI treatment also caused a notable reduction of about 40 to 50% in starch content at 400 and 1000 ppm CO_2 (Paper II Figure 4D). The stomatal aperture index was slightly but significantly higher in PSI-PI leaves in the absence of CO_2, while at 1000 ppm CO_2, the stomatal aperture index was significantly lower in both the control and PSI-PI treated leaves compared to all other conditions (Paper II Figure S1).

4.2.2 Changes in global gene expression induced by varying CO_2 concentrations

The effects of elevated CO_2 on plant photosynthetic processes, growth and gene expression have been extensively investigated, whereas much less is known about the effects of CO_2 concentrations lower than those found in the present atmosphere. All CO_2 concentrations tested in the experiment resulted in significant changes in gene expression, with only a 10% overlap between the CO_2 treatments in GL-treated plants (Paper II Figure 5A and B) and a 7% overlap in PSI-PI treated plants (Paper II Figure 5C and D). CO_2 deprivation induced a large number of DEGs, particularly the genes involved in the biosynthesis of secondary metabolites such as flavonoids and anthocyanins derived from phenylalanine were affected (Paper II Table 1). In particular, the lack of CO_2 induced the upregulation of genes encoding key enzymes

in flavonoid synthesis, such as CHALCONE SYNTHASE (CHS) and DIHYDROFLAVONOL 4-REDUCTASE (DFR), as well as TFs regulating flavonoid biosynthesis genes (Paper II Table 1). Low CO_2 (100 ppm) also significantly altered gene expression, with distinct DEGs compared to atmospheric CO_2 with minimal overlap in highly upregulated or downregulated genes (Paper II Figure 5). Elevated CO_2 only slightly altered gene expression in GL plants compared to atmospheric CO_2 (Paper II Figure 5). Overall, the change in CO_2 concentration resulted in a small number of overlapping DEGs, indicating unique responses to each treatment condition.

To elucidate the source of chloroplast-generated retrograde signals triggered by changes in CO_2 concentration, we analyzed the expression of genes known to respond to potential initiators of chloroplast signaling, including ROS and oxylipins. At 0 ppm and 1000 ppm CO_2, the majority of oxylipin- and JA-responsive genes were upregulated in both GL- and PSI-PI-treated leaves, suggesting a major role for oxylipins and/or JA as signaling molecules under these conditions (Paper II Figure 7). However, only about 50% of genes responding to $^1O_2$ or H_2O_2 were induced, suggesting a lesser involvement in signaling (Paper II Figure 7). At 100 ppm CO_2, neither $^1O_2$ nor JA signaling could explain the gene expression changes, with only a few genes upregulated in response to oxylipins and H_2O_2.

4.2.3 PSI-PI treatment upregulates genes involved in Fe homeostasis, CEF, CBB cycle and photorespiration

PSI-PI treatment was effective in identifying metabolic pathways and signaling cascades affected by PSI photoinhibition, as it allowed identification of DEGs that respond specifically to PSI, when PSII is only weakly inhibited. Analysis of DEGs targeted by PSI-PI treatment revealed several pathways related to the processes on the acceptor side of PSI (Paper II Figure 6). PSI-PI treatment caused moderate upregulation of the genes encoding leaf-type Fds (FD1 and FD2), which serves both LEF and CEF in PETC (Paper II Figure 6). Furthermore, CEF genes encoding components of the chloroplast NDH complex, and the PGR proteins were upregulated, indicating that PSI-PI treatment appears to activate a signaling cascade that enhances electron flow from FD to the PQ pool, to safeguard the PSI.

Additionally, PSI-PI treatment consistently upregulated the expression of key enzymes involved in other processes that accept electrons from PSI, such as the CBB cycle and photorespiration (Paper II Figure 6B and S3). Genes involved in RuBP carboxylation/oxygenation (RuBisCO, RCA), triose phosphate production (GAP), and RuBP regeneration (RPI, TKL1, PRK) showed increased expression in response to PSI-PI treatment (Paper II Figure 6B and S3). In addition, the *CP12-2* gene was upregulated by PSI-PI treatment, facilitating the initiation of the CBB cycle upon light activation. In the photorespiration pathway, peroxisomal enzymes showed

higher expression in PSI-PI-treated leaves compared to control leaves. The peroxisomal *CAT2* gene, involved in H_2O_2 scavenging, showed significant induction by PSI-PI treatment (Paper II Figure 6B and S3). Moreover, genes encoding enzymes involved in the processing photorespiratory amino acid intermediates, which are responsible for glycerate production in the final phase of photorespiration, were upregulated in response to PSI-PI treatment (Paper II Figure 6B and S3). Notably, genes encoding peroxisomal enzymes unrelated to photorespiration did not respond to PSI-PI treatment, indicating specificity in the modification of the gene expression induced by PSI photoinhibition (Paper II Figure 6B and S3). Additionally, genes encoding mitochondrial enzymes involved in photorespiration, particularly those catalyzing serine production from glycine (*GLDP1*, *GLDP2*), were upregulated by PSI-PI treatment (Paper II Figure 6B and S3). Genes involved in starch and sucrose synthesis, or degradation did not show clear differential expression patterns in response to PSI-PI treatment (Paper II Figure 6B and S4). Despite the reduction in starch accumulation at atmospheric and elevated CO_2 concentrations due to PSI-PI treatment, the expression of genes encoding chloroplast starch synthesis remained unchanged (Paper II Figure S4).

PSI photoinhibition has been shown to be caused by the damage to FeS clusters in PSI (Tiwari et al., 2016). Interestingly, among the prominent DEGs induced by PSI-PI treatment were the genes encoding proteins involved in Fe homeostasis. 22 genes encoding proteins involved in Fe metabolism were differentially expressed in PSI-PI-treated leaves (Paper II Table 2). The genes induced by PSI-PI treatment included those encoding FERRITIN proteins (FER1, 3, and 4) and other proteins involved in Fe transport and storage (Paper II Table 2) (Mukherjee et al., 2006; Nechushtai et al., 2012; Sági-Kazár et al., 2022). Furthermore, PSI photoinhibition repressed the expression of genes previously shown to be induced by Fe deficiency in plants such as those involved in Fe uptake (*FEP1* and *2*) (Paper II Table 2). This data suggests that a release of Fe from photoinhibited PSI centers initiates a retrograde signal that, in turn, regulates nuclear gene expression involved in Fe homeostasis and in PSI acceptor side metabolism (Paper II Figure 8).

Genes encoding components of light signaling pathways also showed differential expression in response to PSI-PI treatment (Paper II Table 3). The upregulated genes belong to the group of genes that promote the light signaling cascades in plants, (e.g., *HY5*, *HYH*, *COL2*, *ARF*, *AT5G18404*, *SIG5*), whereas the repressed genes are known to maintain the metabolism found in dark-adapted cells (e.g., *RPGE1*,*3*,*4*; *PIF2*,*6*; *SIB1*) (Paper II Table 3). PSI-PI treatment also upregulated the chloroplast-localized *SIG5* gene, which controls plastid gene expression via the plastid-encoded RNA polymerase (PEP), indicating that the plastid gene expression is also affected by the treatment. Reduced expression of suppressors of photomorphogenesis and photosynthetic gene expression (*PIF2*, *PIF6*, *RPGEs*) potentially releases

GOLDEN2-LIKE (*GLK*) TFs, targets of RPGE regulation (Waters et al., 2009), from inhibition, thereby promoting the expression of light-responsive genes.

Taking these results together, it is apparent that PSI-PI treatment activates the expression of nuclear genes involved in metabolic pathways that use electrons derived from PSI, thereby increasing electron flow in LET and promoting the formation of pmf that protects PSI from photoinhibition. Additionally, this artificial treatment of varying light quality and quantity affects light signaling pathways, promoting genes associated with light acclimation while downregulating the genes that repress the light responses.

4.3 JA and GSH play pivotal roles in regulating gene expression in plants during the recovery process from HL treatment.

The effects of HL stress on expression of genes encoding protective processes and antioxidant metabolism in plants are well-studied (Hernández et al., 2004; Balfagón et al., 2019; Huang et al., 2019; Alvarez-Fernandez et al., 2021). On the contrary, our knowledge on differential gene expression during the recovery of plants from HL stress is much less investigated. In Paper III, I analyzed the global gene expression changes, stress hormones, and antioxidant levels in *Arabidopsis* leaves subjected to short-term HL stress and subsequent recovery to investigate the signaling pathways and role of photosynthesis in plant recovery from HL stress.

Transcriptome analysis of the plants revealed that there were more DEGs during the recovery than under the HL stress (Paper III Figure S1), indicating substantial changes in metabolic processes and signaling pathways during the recovery phase. The DEGs in HL and recovery were used for gene enrichment analysis, which showed that GO terms related to ROS significantly enriched during HL stress, whereas terms related to JA were enriched during both HL and recovery (Paper III Table S1). Based on these results, the involvement of JA in recovery was further investigated by determining the changes in the expression of genes known to be involved JA synthesis and signaling, as well as those known to respond to JA treatment. I also measured the abundance of metabolites such as ROS ($^1O_2$, H_2O_2), oxylipins (OPDA and JA), stress hormones (SA, ABA), and antioxidant levels to find out their involvement in processes induced by HL and recovery treatment.

The analyses revealed a peak in expression of $^1O_2$ responsive genes early in the recovery phase, while H_2O_2 responsive genes showed increased expression during HL but decreased expression during the recovery phase (Paper III Figure S2). Most genes involved in OPDA and JA biosynthesis, as well as the genes known to respond to OPDA and JA, showed upregulation later in HL and maintained high expression during the recovery phase (Paper III Figure 1). Metabolite analysis showed that H_2O_2 levels peaked in HL and the levels declined during recovery, paralleling with the

expression of H_2O_2-responsive genes, while lipid peroxidation levels, indicative of $^1O_2$ accumulation, increased slightly with recovery (Paper III Figure 8). As ROS are known to be involved in the accumulation of oxylipins, detached leaves were treated with H_2O_2 without HL treatment to investigate the interaction between ROS and oxylipins. Increased expression of JA responsive genes was observed during recovery from H_2O_2 treatment (Paper III Figure 3), supporting the hypothesis of ROS induced oxylipin accumulation (Hieno et al., 2019; Lv et al., 2019). To confirm that the genes upregulated during recovery were indeed JA-dependent, the expression of several recovery-sustained genes was measured in coi*1* mutants, which lack JA signaling. These genes were not upregulated during recovery in the mutants (Paper III Figure 4), indicating that JA is required to induce the expression. The explicit role of JA in the recovery processes was further supported by the increased accumulation of JA during the recovery (Paper III Figure 6) while OPDA levels paralleled H_2O_2 levels (Paper III Figures 6 and 8). Furthermore, a short duration of HL treatment, as little as two minutes, was shown to be sufficient for the induction of several JA-induced genes during recovery (Paper III Figure 6).

Both AsA and GSH levels also showed an increase in response to recovery condition (Paper III Figures 7 and 8). This correlated well with the expression of the genes involved in glutathione metabolism (Paper III Figure 2). Genes associated with GSH biosynthesis and recycling as well as with intracellular transport were mostly upregulated in both HL and the subsequent recovery phase (Paper III Figure 2). The expression levels of *GLUTATHIONE SYNTHETASE 2 (GSH2)*, which is responsible for catalyzing the biosynthesis of GSH by adding glycine (Gly) to y-Glu-Cys, increased during R60 (Paper III Figure 2). In addition, the genes involved in sulfur metabolism during the recovery phase showed parallel expression with JA-responsive genes (Sasaki-Sekimoto et al., 2005). Sulfur is assimilated to synthesize cysteine, which serves as a building block for GSH.

GSH may also control OPDA function in the cell by detoxifying its RES activity. GSTU catalyzes the conjugation of GSH with OPDA (GS-OPDA) (Paper III Figure 2) (Skipsey et al., 2011). Seven *GSTU* genes were upregulated in response to HL and recovery treatments (Paper III Figure 2). In addition, the expression of the *GGT4* gene was significantly increased by both HL and recovery treatments (Paper III Figure 2), suggesting that the GS-OPDA conjugate formed in the cytosol is likely transported to the vacuole for processing by GGT4 (Grzam et al., 2007; Ohkama-Ohtsu et al., 2007). Furthermore, the amount of GS-OPDA conjugate increased during the HL exposure and subsequently decreased during the recovery phase (Paper III Figure 7).

SA and ABA levels did not show significant changes in HL, and they both showed decreased abundance during the recovery phase (Paper III Figure 6). About half of the ABA responsive genes showed increased expression in HL, and at the

beginning of the recovery. However, the expression of SA responsive genes remained largely unchanged in both HL and recovery (Paper III Figure S3), although SA metabolite levels decreased during recovery (Paper III Figure 6).

These results show that plants undergo significant changes in gene expression and metabolite levels during recovery from HL stress. The accumulation of JA and antioxidants and the concomitant upregulation of JA-responsive genes suggest their critical role in plant recovery from HL stress.

4.4 Searching for the retrograde signals generated by light-induced stresses in the chloroplast

To identify the retrograde signals induced by HL (Paper III), PSI-PI treatment (Paper II), and changes in CO_2 concentrations (Paper II), the genes differentially expressed under these stresses were used for comparative metadata analysis (Table 1). The expression of the genes encoding photosynthetic components, light signaling, response to ROS, and genes involved in hormone synthesis and stress response were compared to find out what is the most important signal generated by these light-induced stresses (Paper II and III, Figure 6). Both the short-term HL treatment (Paper III) and the long-term HL treatment (3.5 h, data from (Alvarez-Fernandez et al., 2021)) were included to present HL stress in this analysis. In particular, I wanted to separate the signals initiated by HL alone from those generated by the PSI-PI treatment. If PSI-PI-responsive genes show similar or identical expressions in response to HL, this could indicate that the expression of these genes is simply a response to HL. The analysis showed that about 70% of genes induced by PSI-PI were also upregulated in response to HL3.5h treatment (Figure 6, Paper II Figure S6) (Alvarez-Fernandez et al., 2021), while most of the Fe homeostasis genes that were differentially expressed in PSI-PI treated plants, did not respond to the HL treatment (Paper II Table 2 and Figure S6). This shows that although the transcript profiles after PSI-PI treatment and HL have some similarities, PSI photoinhibition also had a specific and partially stronger effect on nuclear gene expression than HL alone. Additionally, many genes involved in CEF, CBB cycle, and photorespiration were highly upregulated in response to PSI-PI treatment, moderately upregulated in long-term HL stress, while only few genes were induced during short-term HL stress (Figure 6). This suggests that prolonged exposure to HL may induce photoinhibition in some PSI complexes. Further analysis using the Genevestigator database collaborates with this observation, by revealing that the transcriptomic changes induced by PSI-PI treatment were similar to those observed in plants subjected to a very strong increase in light intensity (Paper II Figure S7). Thereby, the similarity between the long-term HL treatment, strong HL treatment, and PSI-PI treatment may be due to the gradual photoinhibition of PSI.

Table 1. Responses of the genes differentially expressed in leaves exposed to different light stresses and different CO_2 concentrations presented in my doctoral thesis. The change in expression of responsive genes is scaled based on the number of genes with differential expression. For example, if more than 50% of genes show upregulation, the response is labeled as *high* or *up*. If 25-50% of genes show upregulation, it is labeled as *moderate* or *moderately up*. If less than 25% of the genes are upregulated, the response is labeled as *low* or *none*. HL60min and R60min data are from Paper III and from Figure 6; HL3.5h data is from (Alvarez-Fernandez et al., 2021); PSI-PI, No CO_2, Low CO_2, High CO_2 data are from Paper II and Figure 6. ND: Not determined.

	HL60min	**R60min**	**HL3.5h**	**PSI-PI**	**No CO_2**	**Low CO_2**	**High CO_2**
Light Signaling	Moderate	Low	Moderate	High	Low	Low	Low
$^1O_2$ Signaling	Moderate	High	ND	Low	High	Low	Low
H_2O_2 Signaling	High	Moderate	ND	Moderate	Moderate	Low	Low
OPDA Signaling	High	High	ND	Low	High	Low	Low
JA Signaling	High	High	ND	Low	High	Low	Low
Fe Signaling	Moderate	Low	Moderate	High	Low	Low	Low
PETC Genes	Down	Down	Down	None	Down	Up	Down
CEF Genes	None	Down	Moderately Up	Up	Down	Up	Down
CBB Genes	None	Down	Moderately Up	Up	Down	Up	Down
Photorespiration Genes	None	Down	Moderately Up	Up	Down	Up	Down

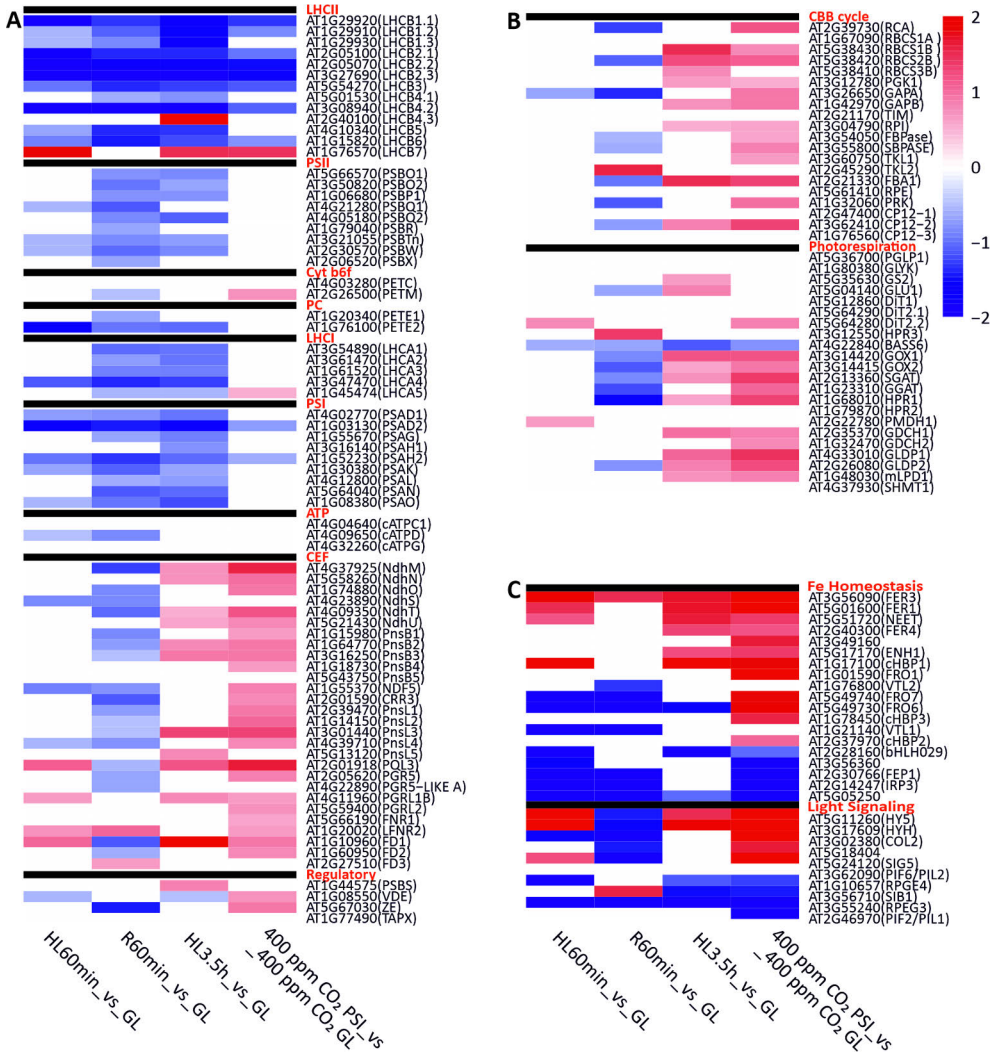

Figure 6. Comparison of the expression of genes encoding photosynthetic structures and genes involved in Fe homeostasis and light signalling under conditions studied in my thesis. **A**) PETC and CEF genes; **B**) genes encoding enzymes in CCB cycle and photorespiration; **C**) genes involved in light and Fe signaling. Data for HL60min and R60min is from paper III; data for HL3.5h is from (Alvarez-Fernandez et al., 2021); data for the PSI-PI at 400 CO_2 ppm is from paper II. Only significant values (-0.5≥ log_2FC ≥ 0.5 and P<0.05) are shown for PETC, CEF, CBB cycle and photorespiration genes, whereas only significant values (−1 ≥ log 2 (FC) ≥ 1 and P<0.05) are shown for light and Fe signaling genes. The names of the gene clusters are shown in bold red within the gene list in A and B.

In addition, the comparative analysis showed a clear similarity between the signaling in response to deprivation of CO_2 and recovery from HL treatment (Table 1). In particular, the involvement of $^1O_2$ and oxylipin signaling in these conditions

was very similar. Both conditions also caused a significant decrease in the expression of photosynthetic genes. This may suggest that both conditions lead to a release of $^1O_2$, which induces oxylipin accumulation.

5 Discussion

Photosynthetic apparatus utilizes light for energy production, but also detects environmental changes in light and translates them into signals in the form of metabolites. These signals influence the expression of the genes both inside the chloroplast and nucleus for adjusting the metabolism and physiology over short timescales of light changes, from seconds to minutes, or for inducing acclimation processes, if the changes last for longer time. However, these processes are not flawless and may have limitations that prevent complete protection against cellular damage, such as photoinhibition of PSII and PSI. Damage to these photosynthetic complexes can generate distinct signals that require separate investigation. While signaling in response to PSII photoinhibition caused by HL has been extensively studied, signaling induced by PSI photoinhibition alone appears to be less investigated. In this study, I focused on chloroplast retrograde signaling cascades separately induced by PSII photoinhibition or by PSI photoinhibition. I also investigated the recovery from HL stress to identify the signals important to restore redox balance after the short-term HL stress.

5.1 The loss of PSII in cyanobacteria has a similar impact on thylakoid complex organization and signaling as HL exposure.

The absence of PSII in cyanobacteria is fundamentally similar to PSII photoinhibition caused by HL stress, as both conditions result in nonfunctional PSII (Murata et al., 2007; Tyystjärvi, 2013). However, PSII loss is also distinct because HL exposure not only induces PSII photoinhibition but also leads to PSI photoinhibition, damages pigments, and results in ROS generation (Muramatsu and Hihara, 2012). Furthermore, absence of PSII differs from photoinhibition because, in the photoinhibited PSII, the pigments and core proteins (except D1 which is replaced by newly synthesized D1) remain mostly intact. These components can still capture energy and may lead to the generation of ROS (Dogra and Kim, 2019; Dmitrieva et al., 2020). In contrast, there is no assembly of PSII complexes in D1-deficient cyanobacteria, since PSII assembly starts with D1 (Lu, 2016; Zabret et al., 2021).

Although there were only a few DEGs in PSII-less cyanobacteria, it had a substantial impact on organization of thylakoid complexes (Paper I). The loss of PSII resembles HL-induced photoinhibition in various aspects, such as leading to a higher PSI monomer-to-trimer ratio (Paper I Figures 2a and 2b). In *Synechocystis* sp. PCC 6803, trimeric PSI is typically more abundant than monomeric PSI (Paper I Figure 2b) (Karapetyan et al., 1999), while stress conditions such as HL increase the monomer-to-trimer ratio (Wang et al., 2008; Kopečná et al., 2012). Alongside reduced PSI content and PSI monomerization, PSI activity may also be impacted by modifications in the PBS composition, evidenced by the blue shift in the PC absorption peak observed in the PSII-less mutant (Paper I Figure 3a). Decoupling of PBS also takes place in response to HL (Tamary et al., 2012), which protects PSII from photoinhibition. In *Synechocystis* sp. PCC 6803, PBS complexes contain one of two CpcG linker proteins. CpcL (encoded by *CpcG2* gene) is predominantly associated with PSI, while the CpcG1-PBS complex transfers energy to both photosystems (Kondo et al., 2007; Kondo et al., 2009). Despite strong downregulation of the *CpcG2* gene expression in the PSII-less mutant compared to control, no changes were detected in the accumulation of the CpcL protein (Paper I Table 1; Figure 1).

Signaling in PSII-less cyanobacteria strain also appears to be similar to HL as it has been shown that the expression of *PsbA2*, *PsbA3*, and *PsbD2* and *FtsH* genes is upregulated in response to HL treatment (Sakurai et al., 2012). Oxidation of downstream PQ pool upon PSII photoinhibition may be the source of signal that regulates the expression of these genes as multiple studies have suggested that the redox state of the PQ pool regulates *PsbA* gene transcription (Pfannschmidt et al., 2009; Borisova-Mubarakshina et al., 2019). Histidine kinases might be involved in the PQ oxidation-induced signaling process (Srivastava and Shukla, 2021). RppA and Hik33 (DspA) are two kinases reported to sense the redox state of PQ pool and regulate the signal cascades leading to the induction of the genes encoding PSII subunits and proteins involved in PSII repair (Li and Sherman, 2000; Hsiao et al., 2004; Ge et al., 2017). Thus, it is plausible that the absence of PSII affects the redox state of the PQ pool with a consequent upregulation of the *PsbA2, PsbA3, PsbD2*, and *FtsH* gene expression, possibly through the action of histidine kinases (Paper I Table 1).

5.2 Deprivation of CO_2 initiates jasmonate signaling in plant leaves

Deprivation of CO_2 from plant leaves induced expression of several genes known to be upregulated by OPDA and JA signaling (Paper II Figure 7C and D). The upregulation of JA-responsive genes might be triggered by increased ROS production due to the over-reduction of the PETC, leading to JA synthesis

(Ochsenbein et al., 2006; Przybyla et al., 2008). Genes that responded strongly to absence of CO_2 encode enzymes and TFs involved in metabolic pathways for flavonoid production. These genes include 7 biosynthetic enzymes and 13 TFs (Paper II Table 1). This finding corroborates with recent report of increase in flavonoid levels in plants in the absence of CO_2 (Banerjee et al., 2019). R2R3-MYB TFs (MYB75, MYB90, MYB113, and MYB114) form a complex with GL3/EGL3/TT8 and TTG1 TFs (Borevitz et al., 2000; Gonzalez et al., 2008), which specifically activates enzymes involved in flavonoid synthesis and anthocyanin metabolism (Gonzalez et al., 2008; Liu et al., 2021). JA has been shown to mediate flavonoid accumulation by inducing the expression of *R2R3-MYB* genes (Li et al., 2020; Qi et al., 2011; Richter et al., 2023; Shan et al., 2009; Zhou & Memelink, 2016), and JA receptor mutants show deficiencies in MYB TFs (Shan et al., 2009). Based on these findings, it can be deduced that JA activates the genes encoding *R2R3-MYB/bHLH/WRKY* TFs (Araguirang and Richter, 2022), which induces genes involved in biosynthesis of flavonoids. Flavonoids, as effective ROS scavengers, protect the plant from oxidative stress.

5.3 PSI photoinhibition causes the release of Fe from PSI FeS clusters that activates iron signaling

PSI-PI treatment led to unique expression profiles that have not been reported earlier. PSI-PI treatment induced differential expression of 59 genes (Paper II Table 2). Twenty-four genes were related to plant Fe homeostasis (Paper II Table 2), consistent with damage to FeS clusters during PSI photoinhibition (Sonoike et al., 1995; Tiwari et al., 2016). Although PSI-PI treatment does not induce degradation of PSI subunits during treatment (Lempiäinen et al., 2022), damaged FeS cluster may release Fe from PSI complexes, leading to excess Fe stress in the chloroplast. Free Fe is dangerous to the cell, because it can result in the production of hydroxyl radicals via the Fenton reaction between H_2O_2 and Fe^{+2} (Khorobrykh et al., 2020). *FER* genes that were upregulated in PSI-PI treated leaves, are shown to be induced by Fe excess and other stresses (Ravet et al., 2009; Briat et al., 2010; Alvarez-Fernandez et al., 2021). FER proteins bind and sequester Fe, protecting cells from oxidative damage (Sági-Kazár et al., 2022). Furthermore, the other genes known to be induced by excess Fe and involved in transportation of Fe in the cell (like *NEET* and *FRO* genes), were upregulated in PSI-PI treated leaves (Paper II Table 2). Degradation of photodamaged PSI complex in *Chlamydomonas* has also been shown to induce FER protein accumulation (Busch et al., 2008), and in the *pgr5* mutant that is susceptible to PSI-PI, *FER* and the Fe transporter genes were induced by HL (Gollan et al., 2017). It is therefore feasible to propose that PSI damage releases Fe from PSI FeS clusters, initiating a signal from the chloroplast to the nucleus (Paper II Figure 8).

This signal upregulates genes involved in excess Fe, while repressing those genes known to be induced by Fe deficiency (Paper II Table 2 and Figure 8). The production of ·OH via Fenton reaction at the early phase of PSI-PI treatment (Tiwari et al., 2024) may initiate this cascade.

The effect of PSI-PI on nuclear gene expression partially mimics HL stress but is stronger and more selective (Table 1). HL alone damages PSI FeSA and FeSB clusters, while strong PSI photoinhibition damages also FeSX cluster (Tiwari et al., 2016; Tiwari et al., 2024), indicating severe excess Fe stress under PSI photoinhibition compared to light increase. PSI-PI also differs from HL stress, because HL induces ROS production and PSII photoinhibition (Andersson & Aro, 2001; Murata et al., 2007; Tyystjärvi & Aro, 1996), while PSI-PI treatment causes negligible effect on PSII and reduces the ROS production (Lima-Melo et al., 2019). Both treatments induce genes associated with excess Fe stress (Paper II Table 2, Figure S7), but HL lacks the specific repression of Fe-deficiency genes observed in PSI-PI-treated leaves (Table 1, Paper II Table 2) Click or tap here to enter text..

Additionally, PSI-PI treatment induces genes encoding PSI electron sinks more strongly than HL alone (Table 1, Paper II Figure 6) (Huang et al., 2019; Alvarez-Fernandez et al., 2021). The higher upregulation of genes involved in CEF, CBB cycle and photorespiration in PSI-PI-treated leaves compared to both short and long term HL treatment (Table 1), highlights the specificity of Fe signaling. A similar DEG profile of these processes was found in leaves exposed to HL at 100 times the growth light intensity, which is likely to cause strong PSI photoinhibition (Paper II Figure S7). Increased CEF activity in PSI-PI- treated leaves may contribute to the buildup of ΔpH across the thylakoid membrane, which in turn activates protective mechanisms such as NPQ or ΔpH-dependent regulation of the Cyt b_6f complex. Additionally, increased activity of CBB and photorespiration could act as electron sinks to mitigate formation of ROS that damage the FeS clusters of PSI.

PSI-PI treatment also affected regulators involved in light receptor signaling, inducing or repressing the specific genes involved in these processes (Paper II Table 3). The differential expression of these genes may be due to the red light contained in the PSI-PI treatment, or the genes may respond to the Fe signal coming from the chloroplast (Paper II Figure 8).

5.4 Plant recovery from HL stress involves jasmonate signaling and accumulation of glutathione

Signaling in response to HL treatment has been extensively studied (Rossel et al., 2002; Mullineaux et al., 2018; Huang et al., 2019; Gollan and Aro, 2020; Bobrovskikh et al., 2022), while the recovery from HL is usually overlooked. It may be assumed that any changes in gene expression and metabolism in response to

increased light intensity simply reverse when light intensity is decreased. However, my analysis shows (Paper III) that the recovery from HL stress is more complex, as the initial response to recovery involves the expression of distinct genes that were either upregulated already in response to HL treatment or newly induced when transferred to the recovery conditions.

Oxylipins, GSH and AsA were the most important metabolites induced by HL treatment and subsequent recovery. HL treatment is known to cause accumulation of H_2O_2 (Hernández et al., 2004; Mullineaux et al., 2006) that was also observed in the current study (Paper III Figure 8). On the other hand, H_2O_2 is scavenged by antioxidants, which was observed as an increase in the amount of GSSG and DHA in HL (Paper III Figures 7 and 8) (Yoshimura et al., 2000; Foyer and Noctor, 2011; Noshi et al., 2016), in order to mitigate oxidative stress. HL has also been shown to induce accumulation of OPDA (Paper III Figure 6) (Balfagón et al., 2019). Accordingly, the genes involved in OPDA and JA biosynthesis were induced during HL, but they continued to be upregulated during recovery, correlating with increased JA accumulation in leaves (Paper III Figure 2 and 6). Notably, OPDA levels decreased during recovery, probably because it is converted to JA and degraded in vacuole (Paper III Figures 3 and 6). The role of JA in recovery was confirmed by the lack of expression of selected recovery-sustained genes in JA receptor *coi1* mutants (Paper III Figure 4). Remarkably, a short HL treatment of two min was sufficient to upregulate some selected recovery-sustained genes, indicating that brief HL exposures, such as those caused by canopy movements, are enough to trigger JA accumulation for recovery (Paper III Figure 5).

The primary signal leading to JA accumulation during recovery phase is still unclear. H_2O_2 has been shown to induce JA biosynthesis (Hieno et al., 2019; Lv et al., 2019), but our data shows that H_2O_2 level returns to GL level within 15 min of recovery, whereas JA accumulation continued up to one hour (Paper III Figure 6). Furthermore, the expression of recovery-sustained genes was not directly upregulated by H_2O_2 treatment (Paper II Figure 3). This suggests that other ROS than H_2O_2 may trigger the JA accumulation in recovery phase. Induction of the genes responding to $^1O_2$ was highest in leaves recovered for 15 min from HL stress and the accumulation of TBARS, an indicator of lipid peroxidation, continued during recovery (Paper III Figures 8 and S2), suggesting that $^1O_2$ may be a source of ROS that maintain OPDA level in leaves during recovery. OPDA does not accumulate, because it is converted to JA in leaves.

The short-term HL treatment followed by subsequent recovery at GL demonstrates that GSH is an important antioxidant induced under recovery conditions. Oxylipins have been suggested to have a role in sulfur assimilation leading to the production of cysteines, which are building blocks of glutathione (Xiong et al., 2001; Jost et al., 2005; Sasaki-Sekimoto et al., 2005; Rodríguez et al.,

2010; Lee et al., 2012). JA has been shown to activate genes involved in sulfur metabolism, and GSH and AsA biosynthesis (Sasaki-Sekimoto et al., 2005), suggesting a correlation between JA signaling and antioxidant levels during recovery (Paper III Figures 2, 6-8). OPDA can also induce GSH production by binding to CYP20-3, which activates the cysteine synthase complex (CSC) (Park et al., 2013; Sun et al., 2017; Liu et al., 2020; Adhikari and Park, 2023). AsA, another important antioxidant, is linked to GSH metabolism through the ascorbate-glutathione cycle, which scavenges H_2O_2 (Foyer and Noctor, 2011; Noshi et al., 2016). AsA levels increased significantly during recovery (Paper III Figure 8), highlighting its importance in detoxifying ROS during recovery. I conclude that ROS causes the synthesis of OPDA and JA, which then induce GSH accumulation by inducing the genes involved in sulfur assimilation and GSH homeostasis during the recovery phase.

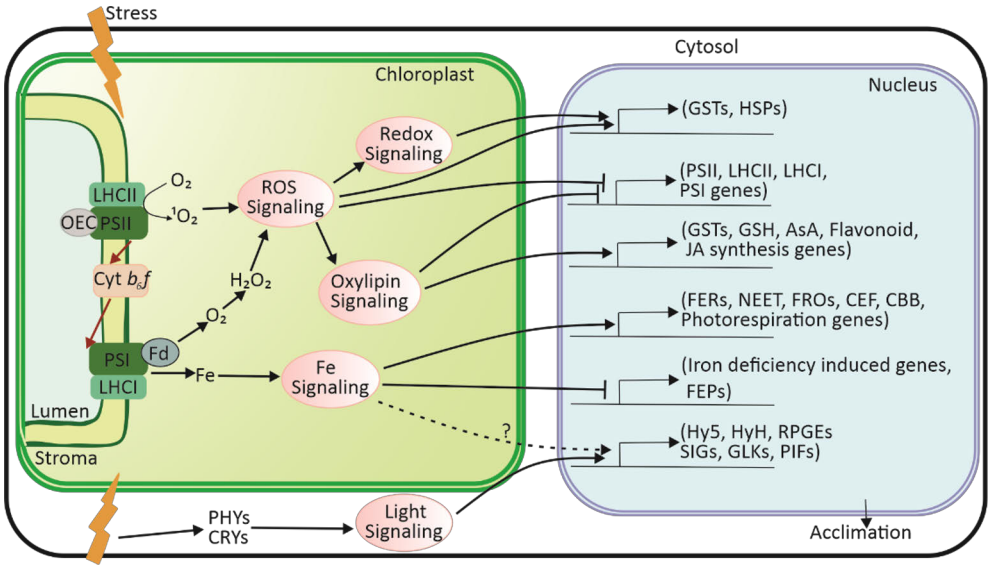

Figure 7. Light stress-induced signaling pathways, based on the findings of this thesis, reveal multiple response mechanisms. HL causes increased ROS generation by PSs, leading to changes in the redox state of the stroma, which can induce the expression of ROS-responsive genes, such as GSTs and HSPs, or repress the expression of PETC genes (PSII, LHCII, PSI and LHCI). In addition to their direct role in redox-state-induced gene expression, ROS can also promote the synthesis of oxylipins, such as OPDA and JA. The oxylipins, in turn, induce genes involved in antioxidant metabolism while further repressing PETC gene expression. HL or specific FL treatments can cause PSI photoinhibition, leading to the release of iron (Fe). This released Fe activates signaling cascades that induce the expression of genes involved in iron storage and transport, while repressing those involved in iron uptake. Additionally, Fe signaling can stimulate the expression of genes encoding proteins involved in CEF, CBB cycle and photorespiration, reducing electron pressure on PSI, thereby minimizing PSI photoinhibition. Alternatively, specific PSI-PI treatment used in Paper II may activate the PHY and CRY pathways, promoting the expression of genes involved in light signaling.

6 Conclusions

The aim of this work was to investigate the role of photosynthesis in regulating the plant acclimation to light stress. Photosynthesis serves as the origin of many signals that regulate the gene expression for acclimation. Damage to photosynthetic complexes or the lack of a complex can have multiple effects on the organization and function of thylakoid protein complexes and photosynthetic CO_2 fixation. My research reveals the intricate nature of plant responses to light-induced stress, emphasizing the essential roles of PSI, PSII, ROS, oxylipins, and antioxidants in stress acclimation and recovery from stress. The signaling pathways involved often overlap, illustrating how different stress types can activate similar responses. Signals like ROS, JA, and iron may be triggered by multiple stressors, leading to shared gene expression patterns and pathways. This overlap allows plants to effectively manage and adapt to complex environmental conditions (Figure 7).

Genes identified as responding to light stress can be used to engineer plants with enhanced resistance or manipulated to explore their role in plant acclimation and metabolism. Furthermore, these findings could form the basis for more in-depth analyses to determine whether the expression genes responding to these metabolites enhances plant resilience or yield. A deeper understanding of the dynamics under fluctuating light will provide valuable insights into plant resilience mechanisms and highlight potential targets for genetic and biotechnological strategies. This, in turn, will enable the manipulation of these pathways to develop crops with increased resistance to environmental stresses, thereby supporting sustainable agricultural productivity under challenging conditions.

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