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Steffen Grebe

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ABSTRACT

Boreal evergreen conifers are important for Northern countries and have functioned for centuries as main drivers of the economy. Nowadays, the attention has shifted to the sustainability of the boreal forests, their protection against ever increasing biodiversity loss and highlighting their irreplaceable role as carbon sinks in climate change mitigation. Climate change drastically changes the growth environment of boreal forests, which exerts a serious threat for the acclimation capacity to new environmental condition. As photosynthesis is the key process to sustain plant growth and biomass production, but also the most vulnerable process upon environmental changes, I decided to focus my PhD thesis on boreal evergreen conifer species, in particular the members of the Pinaceae family including pine and spruce. In current genome and molecular level photosynthesis research, the members of Pinaceae are drastically underrepresented, as the research has almost exclusively been based on few and only distantly related model species. Therefore, I aimed to further characterize the photosynthetic machinery of members of Pinaceae and investigate their seasonal regulation mechanisms necessary for successful overwintering and subsequent spring restoration of photosynthesis. Thereby also paving the way for a better understanding of photosynthesis across different scales, which become more and more accessible with new advances in remote-sensing technologies.

The key findings of my thesis work include the elucidation of the unique subunit composition of the photosynthetic apparatus of Pinaceae across the land plants with the help of a custom build mass spectrometry database. Furthermore, the identification of specific and highly dynamic thylakoid protein phosphorylations, particularly the triple phosphorylation of the LHCB1 and multiple phosphorylations PSBS proteins as prerequisites for the sustained thermal energy dissipation, allowed building a new model conferring photoprotection for spruce during winter and spring. And at last, the derivation of new in vivo parameters to disentangle the seasonal dynamics of PSI and PSII, suggesting a re-evaluation of the role of cyclic electron flow in conifer photoprotection.

KEYWORDS: Conifers, Pinaceae, photosynthesis, winter acclimation, LHC, PSBS, sustained thermal energy dissipation, cyclic electron flow

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TIIVISTELMÄ

Boreaaliset ikivihreät havupuumetsät ovat elintärkeitä pohjoiselle luonnolle ja ne ovat myös toimineet vuosisatojen ajan talouden vetureina pohjoismaissa. Nykyään huomio on siirtynyt yhä enemmän metsien kestävyyteen eli biologisen monimuotoisuuden sälyttämiseen ja metsien korvaamattomaan roolin ilmastonmuutoksen hillinnässä hiilinieluina. Ilmastonmuutos vaikuttaa voimakkaasti boreaalisten metsien kasvuympäristöön, mikä uhkaa vakavasti niiden sopeutumiskykyä. Fotosynteesi on keskeisin prosessi kasvien kasvun ja biomassan tuotannon ylläpitämisessä. Fotosynteesi on kuitenkin myös hyvin haavoittuva prosessi ympäristöolosuhteiden muuttuessa epäsuotuisimmiksi. Tästä syystä päätin keskittyä väitöskirjassani boreaalisten ikivihreiden havupuulajien, erityisesti Pinaceae-suvun männyn ja kuusen fotosynteesikoneiston kykyyn sopeutua ympäristöolosuhteiden muutoksiin. Nykyisessä genomi- ja molekyylitason fotosynteesitutkimuksessa Pinaceae-suvun jäsenet ovat aliedustettuina.

Tästä syystä olen selvittänyt tarkemmin kuusen ja männyn fotosynteesikoneiston rakennetta ja fotosynteesin toiminnan vuodenaikaisia säätelymekanismeja, jotka ovat välttämättömiä onnistuneelle talvehtimiselle ja sitä seuraavalle fotosynteesin palautumiselle keväällä. Säätelymekanismien molekyylitason ymmärtämistä tarvitaan myös nopeasti kehittyvien kaukokartoitusteknologioiden tulosten fysiologisen merkityksen tulkinnassa.

Väitöskirjatyöni tärkeimpiin tuloksiin kuuluu Pinaceae-heimon fotosynteesikoneiston ainutlaatuisen alayksikkökoostumuksen selvittäminen näille lajeille räätälöimäni massaspektrometriatietokannan avulla. Lisäksi ympäristöolosuhteiden muutokseen dynaamisesti reagoivien tylakoidiproteiinien fosforylaatioin, erityisesti LHCB1:n kolmoisfosforylaation sekä PSBS-proteiinin monipaikkaisen fosforylaation tunnistaminen sekä vuosirytmi olivat tärkeitä uusia havaintoja. Biofysikaalisiin mittaustuloksiini pohjautuen kehitin myös uusia in vivo -parametreja, joiden avulla PSI:n ja PSII:n kausittainen dynamiikka ja dynamiikan takana toimivat molekyylimekanismit voidaan erottaa toisistaan. Tutkimustyöni avulla on mahdollista kehittää malli siitä, miten havupuiden fotosynteesikoneiston sopeutumiskykyä ilmastonmuutoksen aiheuttamiin haasteisiin voitaisiin parantaa.

KEYWORDS: Havupuut, Pinaceae, fotosynteesi, talvenkestävyys, LHC, PSBS, pitkäaikainen valoenergian hävittäminen lämpönä, syklinen elektroninsiirto

Table of Contents

Abbreviations

AEF	alternative electron flow
ATPase	chloroplastic ATP synthase
CBB cycle	Calvin-Benson-Bassham cycle
CEF	cyclic electron flow
CO_2	carbon dioxide
Cytbf	cytochrome-b6f complex
e^-	electron
ETC	electron transport chain
ETR	electron transport rate
Fd	ferredoxin
FNR	ferredoxin:NAD(P)H oxidoreductase
Fv/Fm	maximum quantum efficiency of photochemistry of photosystem II
Gya	billion years ago
H^+	proton
H_2O_2	hydrogen peroxide
LEF	linear electron flow
LHCI	light harvesting antenna complex of photosystem I
LHCII	light harvesting antenna complex of photosystem II
L-LHCII	loosely bound light harvesting antenna trimer of photosystem II
lpBN-PAGE	large pore blue-native polyacrylamide gel electrophoresis
Mya	million years ago
$NAPD^+$	oxidized nicotinamide-adenine-dinucleotide-phosphate
NAPDH	reduced nicotinamide-adenine-dinucleotide-phosphate
NDH1	NAD(P)H dehydrogenase 1
NPQ	non-photochemical quenching of chlorophyll-*a* fluorescence
O_2	molecular oxygen
OEC	oxygen evolving complex
P680	reaction center of PSII
P700	reaction center of PSI
PC	plastocyanin
PGR5	proton gradient regulation 5

PGRL1	pgr5-like photosynthetic phenotype 1
PMF	proton motive force
PQ	plastoquinone (oxidized)
PQH2	plastoquinol (reduced)
PSI	photosystem I
PSII	photosystem II
PTOX	plastid terminal oxidase
qE	energy-dependent quenching
qI	photoinhibitory-dependent quenching
qZ	zeaxanthin-dependent quenching
RC	reaction center
ROS	reactive oxygen species
FLV	c-type flavodiiron protein
sc	supercomplex
SDS-PAGE	sodium dodecyl sulfate polyacrylamide gel electrophoresis
S-LHCII	strongly bound light harvesting antenna trimer of photosystem II
M-LHCII	moderately bound light harvesting antenna trimer of photosystem II
VDE	violaxanthin de-epoxidase
Y_I	effective quantum yield of PSI photochemistry
Y_{II}	effective quantum yield of PSII photochemistry
Y_{loss}	non-photochemical “loss” of energy due to PSI photoinhibition
Y_{NA}	PSI acceptor-side limitation
Y_{ND}	PSI donor-side limitation
Y_{NO}	PSII quantum yield of non-regulatory energy dissipation
YNPQ	PSII quantum yield of regulatory non-photochemical quenching
ZE	zeaxanthin epoxidase
β-DM	n-dodecyl β-D-maltoside
ΔETR	difference in electron transport rate of photosystem I and II
ΔpH	proton gradient
ΔP_m	maximal redox active fraction of photosystem I, max. P700 oxidation
$\Delta P_m/\Delta P_{mR}$	maximal PSI activity
ΔΨ	electric potential

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 Grebe, S., Trotta, A., Bajwa, A.A., Suorsa, M., Gollan, P.J., Jansson, S., Tikkanen, M., and Aro, E.-M. The unique photosynthetic apparatus of Pinaceae: analysis of photosynthetic complexes in Picea abies. *Journal of Experimental Botany*, 2019; 70: 3211–3225.

II Grebe, S., Trotta, A., Bajwa, A.A., Mancini, I., Bag, P., Jansson, S., Tikkanen, M., and Aro, E.-M. Specific thylakoid protein phosphorylations are prerequisites for overwintering of Norway spruce (Picea abies) photosynthesis. *Proceedings of the National Academy of Sciences of the United States of America*, 2020; 117: 17499–17509.

III Grebe, S., Riikonen, A., Porcar-Castell, A. and Aro, E.-M. (2022). Cyclic electron transport or methodological artifact? Corrected PSI quantum yields disentangle the seasonal dynamics of PSII and PSI in overwintering boreal evergreens, *Manuscript*

1 Introduction

1.1 Oxygenic photosynthesis

Photosynthesis converts the light energy from the sun into chemical energy and is one of the oldest and important chemical reactions on earth, sustaining life as we know it today (Hohmann-Marriott and Blankenship, 2011). The most dominant form is the oxygenic photosynthesis, which comprises of two connected processes: the water-splitting/O_2-releasing light reactions along with the carbon reduction reactions. Light reactions convert light into chemical energy in the form of nicotinamide-adenine-dinucleotide-phosphate (NADPH) and adenosine-triphosphate (ATP) (Rochaix, 2011). In the carbon reduction, NADPH and ATP are used in the reactions of the Calvin-Benson-Bassham (CBB) cycle to assimilate atmospheric carbon-dioxide (CO_2) into organic compounds (Sharkey, 2019)

1.1.1 Evolution of oxygenic photosynthesis

The evolution of oxygenic photosynthesis is widely considered to be responsible for the rapid rise of atmospheric oxygen levels 2.5–2.3 billion years ago (Gya) (Lyons, Reinhard and Planavsky, 2014; Planavsky et al., 2021), which profoundly altered the redox state of the atmosphere and oceans, as well as the course of eukaryotic evolution (Hohmann-Marriott and Blankenship, 2011). However, the origin of oxygenic photosynthesis still remains elusive (Fischer, Hemp and Johnson, 2016; Sánchez-Baracaldo and Cardona, 2020), partly because the enzymatic capability of water-splitting might be older (>3.0 Gya, (Cardona, 2019; Cardona et al., 2019)) than the emergence of the earliest known oxygenic-photoautotrophic organisms, cyanobacteria (2.5–2.3 Gya, (Soo et al., 2014; Shih et al., 2017)).

Cyanobacteria, for hundred millions of years, remained the only group of oxygenic photoautotrophic organisms until 2.1 – 1.6 Gya (Sánchez-Baracaldo et al., 2017), when a cyanobacterium was engulfed by a heterotrophic eukaryote via endosymbiosis (Sagan, 1967; Gray, 2017). This engulfed ancient cyanobacterium, likely a *Gloemargarita* (Ponce-Toledo et al., 2017; Sánchez-Baracaldo et al., 2017), evolved over time into the first chloroplast, giving rise to the first phototrophic eukaryote, the algae (Archaeplastida). Around 1.6–1.4 Gya, the Archaeplastida further branched into the three ancient algae lines of glaucophytes, red algae

(rhodophytes) and green algae (chlorophytes) (Yoon et al., 2004; Parfrey et al., 2011). All Archaeplastida emerged from a single primary endosymbiotic event (Delwiche, Kuhsel and Palmer, 1995; Rodríguez-Ezpeleta et al., 2005; Price et al., 2012), while multiple secondary and tertiary endosymbiosis events gave rise to other algae groups, like e.g. Chlorarachniophytes and Euglenophytes from green algae as well as Haptophytes, diatoms and dinoflagellates from red algae (Reyes-Prieto, Weber and Bhattacharya, 2007; Archibald, 2009; Keeling, 2013).

1.1.2 Evolution of land plants (Embryophytes)

Before photosynthetic organisms transitioned to land, early evolution of photosynthesis took place exclusively in aquatic environments. This land transition is associated with the emergence of new traits like cell walls and alternating life cycles in algae (Harrison, 2017; Donoghue et al., 2021), but also required biochemical and physiological adaptations to various to new stress conditions (Holzinger and Pichrtová, 2016).

Although the terrestrial lifestyle likely evolved multiple times independently, all land plants (Embryophytes) derived from a single group of green algae, the Streptophytes/Charophytes (Delwiche and Cooper, 2015; de Vries and Archibald, 2018), which split from Chlorophytes more than 700 million years ago (Mya) (Becker, 2013). Recent phylogenomic analyses suggest that the closest common ancestor to land plants evolved from Zygnematophycae living in freshwater and terrestrial environments (Wickett et al., 2014; Cheng et al., 2019; One Thousand Plant Transcriptomes Initiative, 2019; Jiao et al., 2020), implicating that the terrestrial lifestyle in Streptophytes was potentially established before the emergence of land plants (Harholt, Moestrup and Ulvskov, 2016)

Land plants can be classified into three main linages with a phylogenetic sister relationship (Figure 1): early land plants (Bryophytes), vascular plants (Tracheophytes) and seed plants (Spermatophytes), including the gymnosperms (non-flowering plants) and angiosperms (flowering plants). Bryophytes emerged 515–470 Mya, which included hornworts (Anthocerotophyta), liverworts (Marchantiophyta) and mosses (Bryopsida), followed by the divergence of Tracheophytes, Lycophytes and ferns (Monilophytes), 472–419 Mya (Morris et al., 2018). Bryophytes evolved further land plant specific innovations like the cuticula and in some species already stomata, but only Tracheophytes evolved differentiated vascular tissue, leaves, axillary branching and true root systems (Harrison, 2017; Donoghue et al., 2021). Around 450–390 Mya Spermatophytes diverged from ferns and split into gymnosperms and angiosperms (Clarke, Warnock and Donoghue, 2011; Magallón, Hilu and Quandt, 2013).

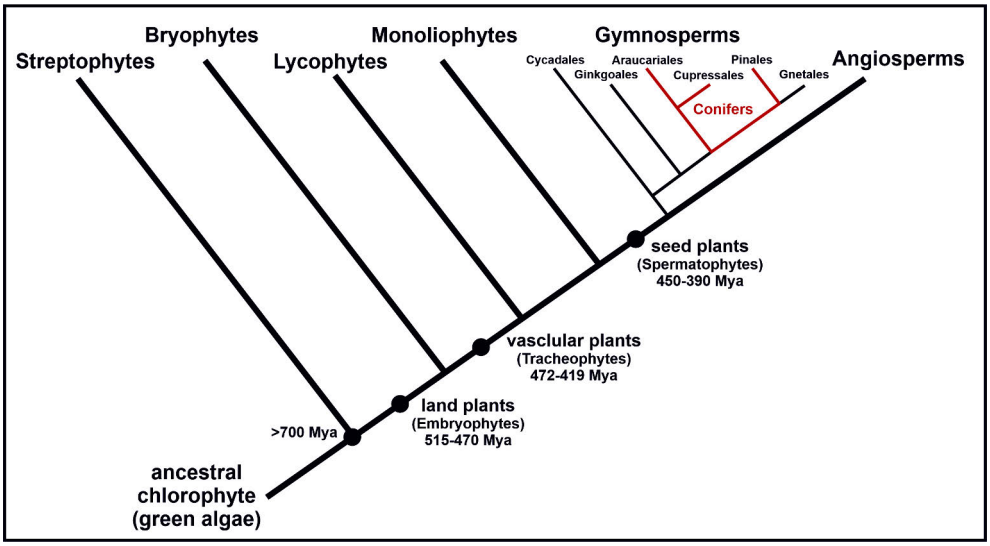

Figure 1: Simplified phylogenetic tree of the evolution of land plants with different orders of gymnosperms (Christenhusz et al., 2011). The gymnosperm orders Araucariales, Cupressales and Pinales are often referred to as conifers (red).

Today, angiosperms comprise the most diverse group of land plants with over 400 families, which can be subdivided into five main clades: ANA-grade, Chloranthales, Magnoliids, monocots and eudicots (The Angiosperm Phylogeny Group et al., 2016). These angiosperm clades diverged between 210–138 Mya, while the most recent clades of mono- and eudicots split between 162–138 Mya (Magallón, Hilu and Quandt, 2013). Likely linked to the explosive radiation of angiosperms 125–80 Mya (Condamine et al., 2020), extant gymnosperms are much less species rich and subdivided into the six main orders: Cycadales, Ginkgoales, Araucariales, Cupressales, Pinales and Gnetales (Christenhusz et al., 2011). These orders diverged between 307–83 Mya, while the Pinaceae family (Pinales), which also includes prominent boreal evergreen conifer genera of fir (*Abies*), pine (*Pinus*) and spruce (*Picea)*, diverged already 251–159 Mya (Lu et al., 2014).

1.1.3 Chloroplasts in photosynthetic eukaryotes

In photosynthetic eukaryotes, photosynthesis takes place in specialized organelles, the chloroplasts. In these, the thylakoid membrane is an extensive internal lipid-bilayer system, which forms two separate compartments inside the chloroplast, the stroma and the lumen.

The lipid composition of the thylakoids is well conserved from cyanobacteria to seed plants (Boudière et al., 2014) and is characterized by a low abundance of phosphoglycerolipids, like phosphatidylglycerol (PG), and high contents of

glycoglycerolipids, like monogalactosyldiacylglycerol (MGDG), digalactosyldiacylglycerol (DGDG) and sulfoquinovosyldiacylglycerol (SQDG) (Kobayashi and Wada, 2016). However, these lipids make up only 30% of the membrane area, the other 70% are occupied by transmembrane proteins (Kirchhoff, Mukherjee and Galla, 2002) including the main photosynthetic multisubunit protein complexes photosystem I (PSI), photosystem II (PSII), cytochrome-b_6f complex (Cytbf) and the ATP synthase (ATPase). Since these protein complexes consist of multiple chloroplast- and nuclear-encoded proteins, the origins of the individual protein subunits are distinguished by their protein name in either lower (plastid) or upper case (nuclear) throughout the text.

In seed plants, the thylakoid network is organized into structurally distinct morphological domains, consisting of appressed grana stacks and interconnecting non-appressed stroma thylakoids, which adjoin the grana by helically winding around them forming junctional slits (Daum and Kuhlbrandt, 2011; Bussi et al., 2019). These domains are not static and undergo reversible reorganization depending on irradiance (Anderson et al., 2012). Additionally they harbor different photosynthetic complexes, which are unevenly distributed between different thylakoid domains (lateral heterogeneity), with PSII complexes present predominantly in the grana, while PSI and ATPase complexes are confined in the unappressed thylakoid membrane, because of their large membrane perturbing structures (Andersson and Anderson, 1980; Albertsson, 2001; Nevo et al., 2012). The Cytbf complex, on the other hand, is more evenly distributed in the thylakoid membrane but also varies depending on light conditions (Vallon et al., 1991; Kirchhoff, Li and Puthiyaveetil, 2017).

The interphase between the grana and stroma thylakoids forms its own distinct domain, called the margins (Anderson, 1989; Albertsson et al., 1991; Wollenberger et al., 1994), which should not be confused with curvature domains at the edge of grana thylakoids (Trotta et al., 2019). Rather, the margins are suggested to be biochemical fusions domains (Rantala, Rantala and Aro, 2020) of grana and stroma lamellae harboring both photosystems (Danielsson and Albertsson, 2009; Järvi et al., 2011; Suorsa et al., 2014; Rantala and Tikkanen, 2018; Rantala, Rantala and Aro, 2020). This is in contrast to green algae, which lack a clear morphological differentiation between grana and stroma thylakoids and do not form margin domains (Engel et al., 2015; Wietrzynski et al., 2020).

1.2 Linear electron flow (LEF) – Production of NADPH and ATP for CO_2 assimilation

In all oxygenic photosynthetic autotrophs, the light driven electron transfer from water to CO_2 is referred to as linear electron flow (LEF, Figure 2). It is facilitated by PSII, Cytbf and PSI, which form the main units of the photosynthetic electron transport chain (ETC), and coupled to proton translocation into the thylakoid lumen (Rochaix, 2011). PSII and PSI, together with their respective antenna proteins, are responsible for light absorption and catalyze the primary light-dependent reactions. The two photosystems work in series, whereby electrons from water-splitting in PSII are transported via Cytbf towards PSI, ultimately leading to reduction of $NADP^+$. These electron transfer reactions are coupled to proton pumping into the thylakoid lumen and generation of a proton gradient over the thylakoid membrane, which in turn is used by the ATPase to produce ATP. NADPH and ATP are utilized in the CBB cycle to assimilate CO_2 or for other metabolic reactions.

1.2.1 Photosystem II

LEF begins at PSII, a water:plastoquinone oxidoreductase, which catalyzes a series of light-driven electron transfer reactions from water to plastoquinone (PQ). PSII is a is a large transmembrane spanning, multisubunit protein complex which acts as a dimer *in vivo*. Each monomer, which itself is a hetero-dimeric complex, consists of over 20 different protein subunits, binding 35 chlorophylls and 10 β-carotenes and other cofactors (Shen, 2015; Wei et al., 2016). Functionally, each monomer is divided into the reaction center core (RC), formed by the subunits PsbA (D1), PsbD (D2), PsbE and PsbF, the internal antenna complex, formed by the subunits PsbB (CP47) and PsbC (CP43), and the luminal extrinsic subunits shielding the oxygen evolving complex (OEC), which in plants consists of PSBO, PSBP and PSBQ proteins. In plants and algae, PSII is mostly found in the grana, where it binds additional light-harvesting antenna complexes (LHC), consisting of the LHCII trimers, formed by trimeric LHCII subunits LHCB1, LHCB2, LHCB3, which are linked to PSII via monomeric LHCII subunits consisting of LHCB4/8 (CP29), LHCB5 (CP26) and LHCB6 (CP24) (Caffarri et al., 2009).

These LHCII proteins increase the overall light absorption of PSII and funnel the light energy towards the internal antenna, which transmits the light energy to the RC, where the excitation of a cluster of four chlorophylls (P_{680}, according to their absorption maximum) initiates the primary charge separation. This leads to electron transfer from P_{680} to the primary acceptor pheophytin (Pheo). From pheophytin the electron is further transferred to the secondary acceptor plastoquinone A (Q_A) and subsequently to plastoquinone B (Q_B). After a second charge separation event and subsequent electron transfer to Q_B, the fully reduced Q_B is released from PSII

(plastoquinol, PQH_2) and diffuses into the mobile PQ-pool inside the thylakoid membrane.

Each charge separation leaves P680 oxidized, which has a very low redox potential that ultimately drives the splitting of water. Oxidized P680 is re-reduced by an electron donation of a nearby tyrosine residue, Tyr_Z, which in turn oxidizes the Mn_4CaO_5 cluster, the catalytic center for water splitting inside the OEC. After the extraction of four electrons from the Mn_4CaO_5 cluster (proceeding through the S-states of the Kok-Cycle), two water molecules are split into four protons (H^+) and O_2 (Kok, Forbush and McGloin, 1970; Joliot, 2003).

1.2.2 Cytochrome-b_6f complex

From the mobile PQ-pool inside the thylakoid membrane electrons are transferred towards the Cytbf complex, a plastoquinol:plastocyanin oxidoreductase, which mediates the electron transfer from the mobile electron carriers PQH_2 to plastocyanin (PC). The Cytbf complex functions as dimeric multisubunit protein complex *in vivo*, in which each monomer is made up of eight subunits (Kurisu et al., 2003; Stroebel et al., 2003; Malone et al., 2019), similar to the mitochondrial cytochrome bc_1 complex (Xia et al., 1997; Crofts, 2004). The four larger subunits PetA (cyt f), PetB (cyt b_6), PETC (iron-sulfur protein, Rieske) and PetD (subunit IV) make up the "core" of Cytbf, harboring the Rieske 2Fe-2S cluster, two cytochrome b_6 (b_H and b_L) and cytochrome f cofactors involved in electron transfer, while the four smaller subunits PetG, PETL, PETM and PetN are arranged in the periphery. In contrast to the mitochondrial cytochrome bc_1 complex, the chloroplastic Cytbf complex additionally incorporates an atypical heme (c_i), two β-carotenes and one chlorophyll-*a*. The Cytbf has two binding sites for PQ/PQH_2, the lumenal Q_o-site near the 2Fe-2S cluster for PQH_2 and the stromal Q_i-site located near heme c_i and the large inter-protein quinone exchange cavity formed between the two monomers for PQ (Kurisu et al., 2003; Yamashita, Zhang and Cramer, 2007).

Electron transport through Cytbf is bifurcated, after binding of PQH_2 to the Q_o-site, two H^+ are released into the lumen and one electron is transferred via 2Fe-S2 cluster towards cytochrome f in the high potential chain, from where it is transferred to the mobile electron carrier PC in the lumen. The second electron is cycled to an oxidized PQ at the Q_i-site via the hemes b_L and b_H in the low potential chain. After an additional electron transfer from the Q_o-site through the low potential chain to the Q_i-site, known as the modified Q-cycle, the now double reduced PQ at Q_i takes up two H^+ from the stroma and is released as PQH_2 into the PQ-pool (Crofts, 2005; Baniulis et al., 2008; Cramer, Hasan and Yamashita, 2011; Tikhonov, 2018). This operation increases the ratio of protons pumped into the lumen compared to forward electron transfer in the high potential chain and greatly contributes to formation of

the proton motive force (PMF), composed of a proton (ΔpH) and electric potential (ΔΨ) over the thylakoid membrane (Cruz et al., 2005; Tikhonov, 2014).

It is important to highlight that the Cytbf complex catalyzes the slowest electron transport reaction of the ETC, the PQH_2 re-oxidation at the Q_o-site (Stiehl and Witt, 1969; Rochaix, 2011). This reaction is further decelerated by acidification of the lumen, creating a negative feedback loop, called photosynthetic control, that limits the overall ETC (Tikhonov, 2014). Under certain conditions, however, electron transfer can also be limited by PC diffusion inside the lumen (Kirchhoff, Horstmann and Weis, 2000; Kirchhoff et al., 2004; Schöttler, Kirchhoff and Weis, 2004; Höhner et al., 2020).

1.2.3 Photosystem I

PC shuttles electrons from Cytbf to PSI, a plastocyanin-ferredoxin oxidoreductase, which catalyzes a series of light driven electron transport reactions from PC in the lumen to ferredoxin (Fd) in the stroma. PSI is a large transmembrane spanning, multisubunit protein complex typically found in stroma exposed, unstacked thylakoid membranes. In photosynthetic eukaryotes, it is active as a monomer *in vivo*, forming PSI-LHCI complexes with a belt of tightly bound LHCI proteins. It consists of more than 19 protein subunits and binds around 175 chlorophylls, 32 carotenoids and other cofactors (Amunts et al., 2010; Mazor, Borovikova and Nelson, 2015). Functionally, PSI can be subdivided into the heterodimeric reaction center formed by PsaA and PsaB subunits, the stromal ridge formed by PsaC, PSAD and PSAE forming the Fd binding site, and the luminal PC binding site composed of PSAF and PsaJ, while the contact surface for the LHCI belt, in angiosperms consisting of LHCA1-4 subunits, is provided by the smaller subunits PSAG and PSAK on opposite sides of the PSI complex (Hippler, Ratajczak and Haehnel, 1989; Jensen et al., 2007; Caspy and Nelson, 2018; Caspy, Fadeeva, et al., 2021). Opposite of the LHCI belt, PSAH, PSAL, PSAO and PsaI subunits form a specific docking site for phosphorylated LHCII proteins (Lunde et al., 2000; Galka et al., 2012; Mazor, Borovikova and Nelson, 2015; Pan et al., 2018; Huang et al., 2021).

After the electron donation from PC to the reaction center chlorophyll pair (P_{700}, according to their absorption maximum) and excitation transfer from the LHCI antenna to P700, the primary charge separation in PSI takes place. PSI has two electron transfer branches A and B, and after charge separation at P700 an electron is transferred to the primary acceptor chlorophyll (A_{0A} or A_{0B}) and further to the secondary acceptor phylloquinone (A_{1A} or A_{1B}) in either branch. It is argued that the slight asymmetry in the redox potentials of A_{1A} and A_{1B} favors forward electron transfer via the B-branch, while the A-branch allows for save back-reactions including charge recombinations (Rutherford, Osyczka and Rappaport, 2012), which

do not lead to oxidative damage of PSI (Warren, Golbeck and Warden, 1993). Regardless from which branch, forward electron transfer of PSI continues from $A_{1A/B}$ via a single chain of three 4Fe-4S clusters (F_X, F_A and F_B) to the stromal site of PSI and ultimately reducing Fd (Brettel and Leibl, 2001). Electrons from two Fds are then transferred in the final step of LEF to the leaf-type ferredoxin NAD(P)H oxidoreductase (FNR) to catalyze the reduction of $NADP^+$ to NADPH (Mulo, 2011).

1.2.4 ATP synthase

The electron transport through the ETC is coupled to the generation of a proton gradient over the thylakoid membrane. Three H^+ are translocated into the lumen per one electron transferred in LEF ($1H^+/e^-$ from PSII and $2H^+/e^-$ from Cytbf, (Allen, 2003)), which generates the PMF. This in turn is used by the chloroplast ATP synthase (ATPase) to catalyze production of ATP from ADP and orthophosphate in the stroma.

The ATPase is a cF_1F_0 type, homologous to bacteria and mitochondria, and a multisubunit protein complex consisting of 26 subunits of which 17 are fully or partially embedded in the thylakoid membrane (Hahn et al., 2018). The cF_1 head domain ($\alpha_3\beta_3\gamma\varepsilon\delta$), sticking out into the stroma, consists of the catalytic $\alpha_3\beta_3$-hexamers (AtpA/cF_1-α and AtpB/cF_1-β), which is powered by the membrane embedded cF_0 rotary domain (abb′c_{14}) consisting of multipe *c*-subunits (AtpH/cF_0-III/cF_0-c) and the *a*-subunit (AtpI/cF_0-IV/cF_0-a) providing the proton entry point. The central stalk domain of the γ- and ε-subunits (ATPC1/cF_1-γ and AtpE/cF_1-ε) transfers the torque of rotary to the head domain, while the peripheral stalk domain, consisting of *b*- and *b'*-subunits (AtpF1/cF_O-I/cF_0-b and ATPG/cF_0-II/cF_0-b') together with the δ-subunit (ATPD/cF_1-δ), acts as stator to prevent unproductive rotation of cF_0 with cF_1 (Yoshida, Muneyuki and Hisabori, 2001; Adachi et al., 2012; Watanabe et al., 2012). The activity of ATPase is redox regulated by the thioredoxin network at the γ-subunit (Nalin and McCarty, 1984; Carrillo et al., 2016; Yokochi et al., 2021), which prevents hydrolysis of ATP back to ADP in the dark. In plants, a full rotation of the central stalk domain requires translocation of 14 protons from the lumen to the stroma by the cF_0 rotary domain, which leads to the synthesis of three ATP molecules at the cF_1 head domain (Seelert et al., 2000; Varco-Merth et al., 2008; Vollmar et al., 2009; Hahn et al., 2018).

1.2.5 CO_2 assimilation and the CBB cycle

The CO_2 intake of plant leaves is regulated by small pores in the leaf epidermis, called stomata. The aperture of the stomata determines the stomatal conductance of CO_2 diffusion which is sensitive to environmental factors like light and relative

humidity, involving a plethora of dynamic signaling processes (Shimazaki et al., 2007; Engineer et al., 2016; Zhang et al., 2018). After CO_2 has passed into the leaf, its diffusion is further limited by the mesophyll conductance as it passes from the intracellular air space across the cell wall, plasma membrane, cytosol and chloroplast envelope membranes into the stroma (Gago et al., 2020; Evans, 2021). Inside the stroma, CO_2 together with NADPH and ATP, produced by the light reactions during photosynthesis, are used in the CBB cycle to assimilate CO_2 into carbohydrates. While this general scheme is consistent with C3 plants, other plant species evolved specialized carbon concentration mechanisms to increase the CO_2 concentration in the chloroplasts, which is referred to as C4 and CAM photosynthesis depending on the mechanisms (Sage, Sage and Kocacinar, 2012; Edwards, 2019; Schreier and Hibberd, 2019).

Mechanistically, the CBB cycle comprises of 11 different enzymes catalyzing 13 reactions which can be divided into three functional phases: carboxylation, reduction and regeneration (Bassham et al., 1954; Sharkey, 2019), which are under strong control of the thioredoxin system (Michelet et al., 2013; Yokochi et al., 2021).

During the carboxylation phase, Rubisco (ribulose-1,5-bisphospate carboxylase/oxygenase) catalyzes the carboxylation of RuBP (ribulose-1,5-bisphospate, 5C backbone) with CO_2, producing two molecules of 3-PGA (3-phophoglycerate, 3C backbone).

In the reduction phase, ATP and NADPH, generated by the light reactions, are sequentially used to first phosphorylate (phosphoglycerate kinase, PGK) and then reduce (glyceraldehyde-3-phosphate dehydrogenase, GAPDH) 3-PGA to GAP (glyceraldehyde-3-phosphate, 3C backbone), respectively, while GAP can additionally be converted into DHAP (dihydroxyacetone-3-phosphate, 3C backbone) by the TPI (triose phosphate isomerase). GAP and DHAP are commonly referred to as triose phosphates, which are used in the regeneration phase to recover RuBP.

The regeneration phase involves several sequential enzymatic reactions of aldolase, bisphosphatase and transketolase to rearrange triose phosphates into pentose phosphates. Combinations of triose phosphates with aldolase and either FBPase (fructose-1,6-bisphosphatase) or SBPase (seduheptulose-1,7-bisphosphatase) produces F6P (fructose-6-phosphate, 6C backbone) and S7P (seduheptulose-7-bisphosphate, 7C backbone), respectively. F6P and S7P are then converted by transketolase into Xu5P (xylulose 5-phosphate, 5C backbone) and R5P (ribose 5-phosphate, 5C backbone) followed by production of Ru5P (ribulose-5-phosphate, 5C backbone) from RPE (ribulose-5-phosphate-3-epimerase) and RPI (ribose-5-phosphate isomerase), respectively. In the last step, PRK (phosphoribulokinase) catalyzes the regeneration of RuBP from Ru5P with ATP, so

that in a complete cycle nine ATP and six NADPH are used to fix three molecules of CO_2 (3 ATP and 2 NADPH per CO_2).

Although consumption of ATP and NADPH through LEF is mainly connected to CO_2 assimilation, the CBB cycle in its central position in the carbon metabolism is additionally linked to many other metabolic pathways including sucrose and starch synthesis, as well as the shikimate pathway, isoprenoid biosynthesis, nucleotide metabolism and cell wall synthesis (Raines, 2003; Tcherkez and Limami, 2019).

1.3 Non-linear electron pathways – Balancing the products of LEF

Efficient operation of the CBB cycle requires 2 NADPH and 3 ATP per assimilation of 1 CO_2 molecule. However, electron transport via LEF accounts only for production of 2 NADPH and 2.57 ATP, based on the proton requirement of 4.67 H^+/ATP of the chloroplastic ATPase in plants, resulting in an ATP deficit (Allen, 2003). It is important to note, that this theoretical suboptimal ATP/NADPH ratio is singularly based on structural studies of spinach (*Spinacia oleracea*) chloroplastic ATPase containing 14 *c*-subunits (Seelert et al., 2000; Varco-Merth et al., 2008; Vollmar et al., 2009; Hahn et al., 2018), while biochemical determinations of ATP synthesis from the Gibbs free energy suggest a H^+/ATP ratio close to 4.0 (Turina, Samoray and Gräber, 2003; Steigmiller, Turina and Graber, 2008; Petersen et al., 2012), which would precisely match the 3 ATP demand of the CBB cycle, as simulated during steady-state photosynthesis (Morales et al., 2018).

Nevertheless, since plants are exposed to constantly changing environment under natural conditions with differing stress mitigations and metabolic requirements, the ATP/NADPH ratio of the chloroplast is unlikely to remain optimal for the metabolic demand without strict regulation, especially since plants are unable to efficiently import ATP into chloroplasts (Voon et al., 2018). Such regulatory mechanisms are largely controlled by the thioredoxin network (Buchanan, 2016; Cejudo et al., 2019; Nikkanen and Rintamäki, 2019; Yoshida, Yokochi and Hisabori, 2019), to balance the photosynthetic reactions and avoid oxidative damage. These balancing reactions include non-linear electron pathways (Figure 2), which lead to additional ATP or lower NADPH net production relative to LEF, and include the engagement of cyclic electron flow (CEF) and rerouting of electrons into alternative electron flow (AEF).

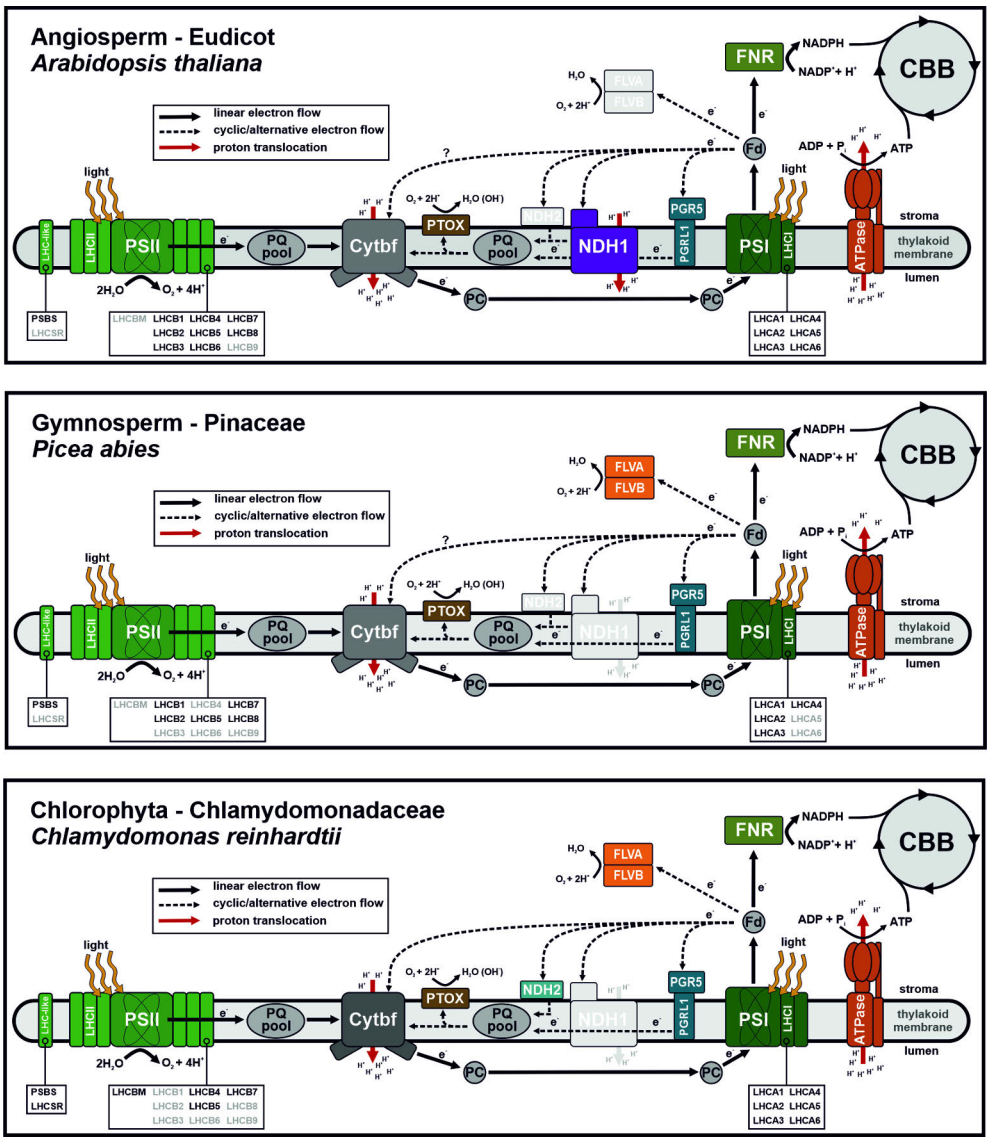

Figure 2: Overview of the linear and non-linear electron transport pathways in the thylakoid membrane of the angiosperm *Arabidopsis thaliana*, gymnosperm *Picea abies* and green-algae *Chlamoydomonas reinhardtii*. Boxes indicate presence of different LHC and LHC-like proteins in each species. Greyed out complexes are not present in respective species. For more details, see text.

1.3.1 Cyclic electron flow (CEF)

CEF is generally understood as shuttling electrons around PSI back to the PQ-pool which generates extra PMF for the production of ATP (Arnon, Allen and Whatley, 1954; Arnon, Whatley and Allen, 1958; Tagawa, Tsujimoto and Arnon, 1963), but

should not be confused with cyclic electron transport around PSII (Prasil et al., 1996; Shinopoulos and Brudvig, 2012), which physiological role still remains largely unknown.

Since the first proposal of a CEF mediating enzyme FQR, ferredoxin:plastoquinone oxidoreductase (Moss and Bendall, 1984; Cleland and Bendall, 1992; Bendall and Manasse, 1995), multiple CEF pathways around PSI have been identified, which all share the same common electron carries from PQ towards Fd with LEF, but differ mechanistically in how they recycle electrons back to the PQ-pool, by either NDH1, PGR5/PGRL1 or the Cytbf complex.

In the NDH1-dependent pathway, CEF is mediated by the chloroplastic NAD(P)H:PQ oxidoreductase type I (NDH1, NAD(P)H dehydrogenase), which is a large multi subunit complex consisting of at least 27 subunits and homologue to the mitochondrial complex I (Ifuku et al., 2011; Shikanai, 2016; Laughlin et al., 2019; Zhang et al., 2020). Despite its name, the electron donor to NDH1 is Fd and not NADPH (Yamamoto et al., 2011; Yamamoto and Shikanai, 2013; He et al., 2015) and an efficient proton pump, which facilitates an extra $2H^+/e^-$ via CEF (Strand, Fisher and Kramer, 2017; Walker et al., 2020). In plants, it forms PSI-NDH1 supercomplexes with multiple copies of PSI and specific LHCA proteins, LHCA5 and LHCA6 (Peng, Shimizu and Shikanai, 2008; Peng et al., 2009; Kouřil et al., 2014; Yadav et al., 2017; Shen et al., 2022; Su et al., 2022).

In the PGR5/PGRL1-depedent pathway, CEF is mediated by PROTON GRADIENT REGULATION 5 (PGR5), which is a small soluble protein (aprox. 10 kDa) without any known motives (Shikanai et al., 1999; Munekage et al., 2002, 2004), and PGR5-LIKE PHOTOSYNTHETIC PHENOTYPE 1 (PGRL1), which is a thylakoid membrane protein (approx. 30. kDa) with two transmembrane domains (DalCorso et al., 2008; Dann and Leister, 2019). PGRL1 together with PGR5 could be shown to facilitate CEF *in vitro* (Hertle et al., 2013) and contribute an extra $1H^+/e^-$ via CEF (Walker et al., 2020). Studies in the green algae *Chlamydomonas reinhardtii* suggest that the PGR5/PGRL1-mediated pathway facilitates CEF by forming large supercomplexes consisting of PSI-LHCI-LHCII-FNR-Cytbf-PGRL1, thought to minimize diffusion distances between electron carriers (Iwai et al., 2010; Steinbeck et al., 2018).

In plants, it is generally accepted that the PGR5/PGRL1 dependent pathway is the main route for CEF (Yamori and Shikanai, 2016), because of its severe phenotype (Munekage et al., 2002, 2004; Tikkanen et al., 2010). However, it has been frequently pointed out that PGR5/PGRL1 might not be only defective in CEF (Johnson, 2004; Suorsa et al., 2012; Yamamoto and Shikanai, 2019). This view is supported by the recent identification of a second mutation enhancing PSI photoinhibition in the pgr5-background in *Arabidopsis thaliana*, which suggests an overestimation of the physiological role of PGR5/PGRL1 (Wada, Amako and Miyake, 2021).

Additionally, a Cytbf-dependent pathway has been (re)suggested in the green algae *Chlamydomonas reinhardtii*, in which CEF would operate via a Fd-assisted Q-cycle within the Cytbf complex by accepting electrons at the Q_i-site from Fd (W. J. Nawrocki et al., 2019; Buchert et al., 2020; Buchert, Scholz and Hippler, 2022) and contribute an extra $1H^+/e^-$ via CEF (Walker et al., 2020). These works built up on the previously proposed CEF pathway, involving Cytbf complex interacting with FNR (Joliot and Joliot, 2006; Joliot and Johnson, 2011). The Cytbf-dependent CEF does not directly involve PGR5 or PGRL1, which instead are suggested to be important for redox tuning of the Q_i-site to maintain efficient CEF (Buchert et al., 2020) in addition to STT7, the state transition kinase orthologue of STN7 in *Chlamydomonas reinhardtii* (Buchert, Scholz and Hippler, 2022). Additionally, it is suggested that a PQ molecule inside the quinone exchange cavity is shuttled back and forth between both monomers, which would make Cytbf-mediated CEF independent from the redox state of the PQ-pool (Nawrocki et al., 2019).

Regardless of the involved pathway, CEF around PSI is widely considered to be of physiological relevance. It is suggested to be important not only for generating extra PMF to balance the ATP/NADPH ratio, but also supporting thermal energy dissipation mechanisms under excess light conditions (Clarke and Johnson, 2001; Miyake et al., 2004, 2005; Joliot and Joliot, 2006; Kou et al., 2013; Walker et al., 2014; Huang et al., 2015) and during the induction of photosynthesis (Joliot, Béal and Joliot, 2004; Fan et al., 2007; Nawrocki et al., 2019), when light energy exceeds the metabolic demand. Additionally, CEF was also shown to be important under fluctuating light conditions (Tikkanen et al., 2010; Suorsa et al., 2012).

Upregulation of NDH1- and PGR5/PGRL1-dependent CEF pathways have been associated with various environmental stress conditions, where both CEF pathways show very large functional overlap (reviewed in (Yamori and Shikanai, 2016)), suggesting a functional redundancy between the two pathways. This could at least partially explain, why NDH1 is not conserved in all plant species and has been lost in gymnosperm families of Pinaceae, Gnetaceae and Welwitschiaceae and various angiosperm families (Braukmann, Kuzmina and Stefanović, 2009; Ruhlman et al., 2015; Strand, D'Andrea and Bock, 2019). In general, the loss of NDH1 in many different genera suggest that NDH1-dependent CEF is not essential for photosynthesis, however, this does not exclude the possibility of NDH1-dependent CEF playing an important role in different species under specific conditions (Johnson, 2011; Yamori and Shikanai, 2016; Strand, D'Andrea and Bock, 2019), especially in C4 plants (Munekage and Taniguchi, 2016).

Simultaneously, CEF remains difficult to measure as it generates no net product. Various techniques are used to estimate CEF, which make qualitative and quantitative comparisons between different studies challenging, in addition to the varying assumptions and technical drawbacks associated with each technique (Fan et al., 2016).

1.3.2 Alternative electron flow (AEF)

Summarized under the term AEF, are different forms of electron transports to acceptors other than CO_2, which are mediated by different pathways, including the Mehler-reaction, plastid terminal oxidase (PTOX, IMMUTANS), flavodiiron proteins (C-class FDP or FLV) and photorespiration coupled to the malate-valve (Alric and Johnson, 2017; Alboresi, Storti and Morosinotto, 2019; Walker et al., 2020).

In the Mehler-reaction, electrons from PSI are directly reducing O_2 leading to production of superoxide (Mehler, 1951; Asada and Kiso, 1973). This reactive oxygen species (ROS) is rapidly detoxified by the superoxide dismutase (SOD) to H_2O_2 and by ascorbate-specific peroxidase (APX) to H_2O, hence referred to as the water-water cycle (Asada, 1999). The water-water cycle can contribute to balance of NADPH and ATP ratio, although it is not a safe AEF pathway due to the production of ROS (Ort and Baker, 2002), therefore suggesting a stronger role in stress signaling (Li and Kim, 2022).

PTOX is a diiron containing peripheral membrane protein (40-50 kDa), strongly binding to the stromal side of thylakoid membrane and the functional analogue to the mitochondrial alternative oxidase in chloroplasts (Carol et al., 1999; Wu et al., 1999; Lennon, Prommeenate and Nixon, 2003). PTOX acts as plastoquinol:oxygen oxidoreductase taking up electrons from PQH_2 to reduce O_2 to H_2O (Josse et al., 2003; Yu et al., 2014), but is also known to produce ROS (Heyno et al., 2009; Feilke et al., 2014). PTOX functions in carotenoid biosynthesis during biogenesis (Wu et al., 1999; Carol and Kuntz, 2001) and in chlororespiration together with NDH1 in plants (Peltier and Cournac, 2002; Rumeau, Peltier and Cournac, 2007; Nawrocki et al., 2015), but has also been suggested to work as safety valve for excess electrons (Niyogi, 2000; Ort and Baker, 2002). Although PTOX has no role in AEF under steady-state photosynthesis in *Arabidopsis thaliana* (Rosso et al., 2006), it was found to be upregulated in different species under heat, cold, high light and salt stress conditions (reviewed in (Sun and Wen, 2011)). However, the physiological significance as a major AEF pathway still remains elusive. PTOX is unlikely to be competitive with LEF under saturating light conditions, because of its low electron flux capacity, and its capability to produce ROS is contradicting a sole protective function, rather suggesting a role in ROS signaling (Nawrocki et al., 2015).

C-class FDPs (FLV) are stromal proteins conserved in cyanobacteria, green algae, early land plants, and gymnosperms but not angiosperms (Zhang et al., 2009; Yamamoto et al., 2016; Ilík et al., 2017; Alboresi et al., 2019). FLVs consist of a metallo-β-lactamase, flavodoxin and flavin-reductase domain and in photosynthetic eukaryotes are present in two isoforms, FLVA and FLVB, which are homologues to the cyanobacterial Flv1 and Flv3 isoforms (Peltier et al., 2010; Allahverdiyeva et al., 2015). FLVA and FLVB form heterodimers (120 kDa), which function as a

NAD(P)H:oxygen oxidoreductase, catalyzing a Mehler-like reaction by transferring electrons from NAD(P)H to O_2 producing H_2O, however, without formation of ROS (Helman et al., 2003; Allahverdiyeva et al., 2011). Recently, cyanobacterial Flv1/3 proteins were shown to mainly accept electrons from Fd or potentially FeS-clusters of PSI (Sétif et al., 2020), suggesting a similar electron donor for photosynthetic eukaryotes. Physiologically, FLVA/B heterodimers confer PSI photoprotection in various species, especially during dark-light transitions and fluctuating light conditions by efficiently removing electrons from the PSI acceptor side and acting as an electron safety valve (Allahverdiyeva et al., 2013; Gerotto et al., 2016; Chaux et al., 2017; Ilík et al., 2017; Shimakawa et al., 2017; Jokel et al., 2018). Occasionally, the FLV pathway is referred to as pseudo-cyclic, because of its overlapping functionality with CEF to contribute to PMF formation (Yamamoto et al., 2016; Shikanai and Yamamoto, 2017; Yamamoto and Shikanai, 2019), although both reactions operate on different time scales (Jokel et al., 2018).

The photorespiration pathway relates to the oxygenase activity of Rubisco, in which O_2 instead of CO_2 is used as a substrate, leading to production of 2-PG (2-phosphoglycolate) (Bowes, Ogren and Hageman, 1971). 2-PG inhibits the activity of several enzymes in the CBB cycle and therefore is rapidly metabolized by a series of reactions performed in the chloroplasts, mitochondria, and peroxisomes (Busch, 2020). These reactions are not wasteful (Tcherkez and Limami, 2019; Shi and Bloom, 2021), since they ultimately recover CO_2 and are connected to other metabolic pathways, like the C1 metabolism (glycine and serine) as well as nitrogen and sulfur assimilation (Timm, 2020). Photorespiration is also considered an AEF pathway, since its activity is linked to the malate-valve (Selinski and Scheibe, 2019; Dao et al., 2021). The malate-valve operates via chloroplastic malate dehydrogenase (MDH), which consumes NADPH to reduce oxaloacetate to malate. This malate is then exported from the chloroplast where it can be oxidized to form NADH in the cytosol, peroxisomes and mitochondria. The export of NADPH from the chloroplast to the mitochondria is used to sustain the reactions involved in chlororespiration (Gardeström and Wigge, 1988; Igamberdiev, Romanowska and Gardeström, 2001; Lee, Eubel and Millar, 2010; Lim et al., 2020) and in this way effectively contributes to the balance of NADPH and ATP demands of the chloroplast (Walker et al., 2020).

1.4 Regulation of photosynthetic light reactions – Controlling the source of electrons

Conceptually, the ATP/NAPDH ratio of the chloroplast provides the bridge between efficient metabolisms and light reactions in the thylakoid membrane. Considering that ATP and NADPH pools are relatively small compared to primary fluxes through metabolism (Noctor and Foyer, 2000; Kramer and Evans, 2011), plants not only need

to regulate the end point of photosynthetic electron transport (LEF vs CEF vs AEF), but also the source of the electrons – the light reactions.

In plants, the regulation of light reactions is tightly linked to thylakoid protein phosphorylation and highly interconnected, ranging from adjustments the thylakoid membrane ultrastructure, the functional architecture and excitation balance of photosystems to the engagement of photoprotective mechanisms.

1.4.1 Thylakoid protein phosphorylations

Thylakoid phosphoproteins make up around 15% of the identified 174 chloroplastic phosophoproteins (Reiland et al., 2009; Bayer et al., 2012). From algae to angiosperms (excluding gymnosperms), 38 of 142 phosphosites in thylakoid proteins are conserved, suggesting similar function in the phosphorylation dependent regulation of photosynthesis in different organisms (Grieco et al., 2016). Of all thylakoid phosphoproteins, the phosphorylations of PSII and LHCII are the best studied, however, the functional roles of many phosphorylation in Cyt b_6f complex, PSI and the ATP synthase as well as conserved phospho-sites in luminal domains of multiple photosynthetic proteins are still unknown (Grieco et al., 2016).

LHCII and PSII protein phosphorylations typically show opposite behavior upon change in actinic light intensities with increased LHCII phosphorylation after a shift to low light, while after a shift to high light LHCII is dephosphorylated and PSII core phosphorylations increase (Rintamäki et al., 1997; Tikkanen et al., 2010). These light-dependent phosphorylations are mediated by antagonistic kinases/phosphatases STN7/TAP38 and STN8/PBCP (Pesaresi et al., 2011; Rochaix et al., 2012).

While the STATE TRANSITION 7 (STN7) kinase is mostly responsible for the phosphorylation of N-terminal Thr residues in LHCB1 and LHCB2 subunits of LHCII trimers (Depège, Bellafiore and Rochaix, 2003; Bellafiore et al., 2005), the STATE TRANSITION 8 (STN8) kinase mostly phosphorylates Thr residues of the PSII core subunits (D1, D2, CP43, PsbH) (Bonardi et al., 2005; Vainonen, Hansson and Vener, 2005). These are counteracted by the THYLAKOID-ASSOCIATED PHOSPHATASE OF 38KDa / PROTEIN PHOSPHATASE 1 (TAP38/PPH1) dephosphorylating LHCB1 and LHCB2 (Pribil et al., 2010; Shapiguzov et al., 2010) and PHOTOSYSTEM II CORE PHOSPHATASE (PBCP) dephosphorylating PSII core proteins (Samol et al., 2012).

The regulation of STN7 kinase is redox dependent, activated by binding of PQH_2 at the Q_O-side of the Cytbf complex and inactivated by the thioredoxin system (Rintamäki et al., 2000) but its activity is also modulated by phosphorylation of STN7 itself (Trotta et al., 2016). TAP38 phosphatase is constitutively active and dephosphorylates LHCII subunits when STN7 kinase is inactivated, e.g. during high light (Pribil et al., 2010; Shapiguzov et al., 2010). On the other hand, regulation of

STN8 and PBCP still remains elusive, but a concentration dependent regulation mechanism for STN8 has been suggested (Wunder et al., 2013).

Overall, the phosphorylation of LHCII and PSII proteins is an important regulatory mechanism of photosynthetic acclimation to different light environments and plays a role in different aspects of the regulation of photosynthesis, including ultrastructural changes of the thylakoid membrane, excitation balance of photosystems as well as affinity and stability of protein complexes (Rantala, Rantala and Aro, 2020; Hepworth et al., 2021). For overwintering conifers a specific role of thylakoid protein phosphorylations, connected to a form of sustained energy-energy dissipation, has also been suggested (Ebbert et al., 2005; Merry et al., 2017; Grebe et al., 2020).

1.4.2 Light dependent changes of the thylakoid membrane ultrastructure

The ultrastructure of the thylakoid membrane is dynamic and changes within minutes in response to the light environment. These alterations include changes in the amount of grana per chloroplast, width of lumen and stromal gap alongside changes of grana diameter and vertical stacking of grana membranes (Anderson et al., 2012). In particular, changes in thylakoid stacking are suggested to be functionally connected to different photosynthetic regulatory processes, including partitioning of electron flow, redistribution of light energy between photosystems, photoprotection via excess energy dissipation and efficient PSII repair (Chow and Aro, 2005; Chow et al., 2005; Tikkanen et al., 2012; Pribil, Labs and Leister, 2014; Ruban and Johnson, 2015; Johnson, 2018; Koochak et al., 2019; Johnson and Wientjes, 2020).

Factors determining membrane stacking are still under debate and involve a combination of van der Waals, hydro-structural and electrostatic forces, with the latter being influenced by stromal cation concentrations screening electrostatic repulsion (Barber, 1980; Chow et al., 2005). Other factors contributing to grana stacking include vertical “velcro-like” interactions of the stromal N-termini of PSII core and LHCII subunits between PSII-LHCII complexes over the stromal gap (Standfuss et al., 2005; Daum et al., 2010; Albanese et al., 2017, 2020), and other proteins specifically involved in regulation of grana stacking, like CURVATURE THYLAKOID (CURT) proteins (Armbruster et al., 2013; Pribil et al., 2018; Trotta et al., 2019) and REDUCED INDUCTION OF NON-PHOTOCHEMICAL QUENCHING (RIQ) proteins (Yokoyama et al., 2016).

Additionally, grana stacking is also affected by different carotenoid (Bykowski et al., 2020) and lipid contents (Mazur et al., 2019) in the thylakoids, which functions are highly interconnected (Goss and Latowski, 2020).

Importantly, ultrastructural changes of the thylakoid membrane are also influenced by thylakoid protein phosphorylations, in particular of PSII-LHCII sc. While modeling suggests that phosphorylations of PSII-LHCII sc only have a small direct contribution to forces directly involved in grana stacking (Puthiyaveetil, van Oort and Kirchhoff, 2017), they are suggested to increase mobility of PSII-LHCII sc complexes between different domains (Goral et al., 2010; Herbstová et al., 2012; Pietrzykowska et al., 2014; Crepin and Caffarri, 2015; Grieco et al., 2015; Rantala and Tikkanen, 2018). This is conceived to lead to a decrease in grana size (Wood et al., 2019) and in turn, to a change of the lateral organization and functional architecture of photosynthetic complexes in the margin domains, effecting the balance of excitation energy in low light and PSII repair in high light conditions (Rantala, Rantala and Aro, 2020).

Ultrastructural changes of the thylakoid membrane are particularly prominent in evergreen conifers during winter and early spring, where a strong decrease up to a complete loss of thylakoid stacking has been associated with a sustained form of light energy dissipation in members of Pinaceae (Martin and Öquist, 1979; Demmig-Adams et al., 2015; Bag et al., 2020; Yang et al., 2020) and Taxaceae (Verhoeven et al., 2005; Yokono, Akimoto and Tanaka, 2008).

1.4.3 Dynamic functional architecture of photosystems

Since around 70% of the thylakoid membrane is occupied by transmembrane proteins (Kirchhoff, Mukherjee and Galla, 2002), changes in the ultrastructure ultimately lead to a rearrangement of the photosynthetic complexes embedded in membrane. These rearrangements are closely associated with the different organizations of the photosystem themselves, which is referred to as their functional architecture. Due to the large variability in the functional organization of photosystems with their diverse light harvesting antenna in oxygenic photosynthesis (Büchel, 2015; Kirilovsky and Büchel, 2019), the diverse structures in cyanobacteria, red algae and diatoms cannot be covered here, instead only major aspects of the green lineage (Viridiplantae) from green algae to angiosperms are presented (Caffarri et al., 2014; Croce and van Amerongen, 2020; Pan et al., 2020; Bai et al., 2021; Sheng et al., 2021).

Conserved from green algae to angiosperms, PSII binds additional LHCII proteins and forms PSII-LHCII sc to increase the light absorption (Cao et al., 2020). In angiosperms, these PSII-LHCII sc typically form functional units of C2S2M2 complexes, in which two PSII monomers (C) are associated with two strongly (S) and moderately (M) bound LHCII trimers at specific binding sites (Kouřil, Dekker and Boekema, 2012; Su et al., 2017; van Bezouwen et al., 2017; Cao et al., 2018). Additionally, loosely (L) bound LHCII trimers can associate with the C2S2M2

complex, which are considered part of the free LHCII-trimer pool and suggested to energetically connect both photosystems in unappressed thylakoid domains, particularly in the margins (Wientjes, van Amerongen and Croce, 2013a; Grieco et al., 2015; Suorsa et al., 2015; Rantala, Tikkanen and Aro, 2017). In angiosperms, the LHCII trimers are build up from different combinations of trimeric LHCII subunits LHCB1, LHCB2 and LHCB3, and are linked to PSII via the monomeric LHCII subunits LHCB4/8 (CP29), LHCB5 (CP26) and LHCB6 (CP24) (Caffarri et al., 2009), with slight variations in chlorophyll and carotenoid cofactors (Cao et al., 2018). In the angiosperm *Arabidopsis thaliana*, the S-LHCII trimer consists mostly of LHCB1 and LHCB2, the M-LHCII mostly of LHCB1 and LHCB3, while the L-LHCII is enriched in LHCB1 and LHCB2 subunits with small amounts of LHCB3 (Caffarri et al., 2004, 2009; Rantala, Tikkanen and Aro, 2017).

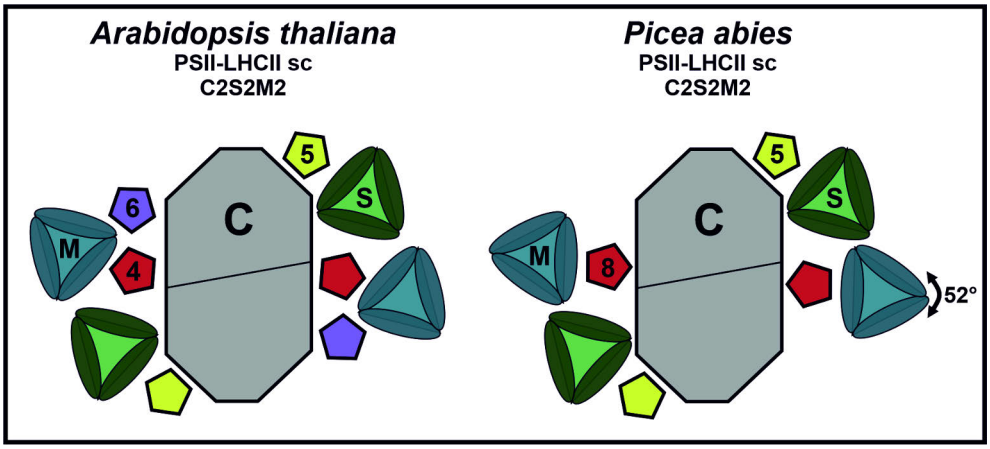

Figure 3: Topview of the functional architecture of PSII-LHCII sc from *Arabidopsis thaliana* (left) and *Picea abies* (right) with PSII core (C), minor antenna complexes LHCB4 (4), LHCB5 (5), LHCB6 (6) and LHCB8 (8) as well as strongly bound (S) LHCII trimer and moderately bound (M) LHCII trimer. LHCB4 in Picea abies is replaced by LHCB8, likely influencing the M-LHCII binding site and angle. Drawn after (Kouřil et al., 2016).

However, the composition of PSII-LHCII sc with different LHCII trimers cannot be easily generalized for all organisms and environmental conditions (Galka et al., 2012; Crepin and Caffarri, 2018), in particular not for green algae and bryophytes, which express evolutionary older LHCBM proteins, considered to be ancestors to LHCB1 and LHCB2 subunits (Alboresi et al., 2008; Iwai and Yokono, 2017). The difficulty to generalize the composition of PSII-LHCII sc is further emphasized by the lack of LHCB3 and LHCB6 subunit as well as replacement of LHCB4 with LHCB8 in gymnosperm families of Pinacea, Gnetaceae and Welwitschiaceae (Grebe et al., 2019), which leads to a change of binding sites of LHCII trimers to PSII

(Kouřil et al., 2016) (Figure 3). Aside from differences between species, the lateral organization of multiple PSII-LHCII sc inside the thylakoid membrane is also quite diverse (Nosek et al., 2017; Kouřil et al., 2020), ranging from apparent random organizations (Kouřil, Dekker and Boekema, 2012; Ruban and Johnson, 2015) to the formation of highly ordered semi-crystalline arrays in the grana (Kirchhoff et al., 2007; Daum et al., 2010; Kouřil, Dekker and Boekema, 2012).Similar to PSII, also PSI forms supercomplexes with its light-harvesting antenna, which typically bind to a PSI monomer forming a LHCI-belt consisting of LHCA heterodimers. However, the PSI-LHCI sc differ between species by the amounts and types of LHCI proteins present per PSI monomer. In green algae, PSI-LHCI sc binds two LHCI-belts, while in land plants generally only a single LHCI-belt of LHCI heterodimers is associated with PSI (Pan et al., 2020). In angiosperms, the LHCI-belt consists of two LHCI heterodimers LHCA1-LHCA4 and LHCA2-LHCA3 and in the bryophyte *Physcomitrella patens* of LHCA1-LHCA2a and LHCA3-LHCA2b, as LHCA4 is not conserved (Yan et al., 2021; Gorski et al., 2022). Additionally, recent studies suggest that even more LHCI heterodimers can bind to PSI-LHCI sc in green algae (Suga et al., 2019; Caspy, Neumann, et al., 2021), bryophytes (Iwai et al., 2018; Pinnola et al., 2018) and angiosperms (Crepin et al., 2020). Furthermore, PSI-LHCI sc additionally harbor low-energy (red-form) chlorophylls, which differ in amounts and energy levels between cyanobacteria, green algae and land plants (Gobets and van Grondelle, 2001). In angiosperms, these red-form chlorophylls are located in LHCI heterodimers LHCA1-LHCA4 and LHCA2-LHCA3, with the LHCA3 and LHCA4 harboring the lowest-energy chlorophylls of the LHCA proteins (Croce et al., 2007; Wientjes and Croce, 2011). However, between angiosperms these also vary in content leading to different energy trapping kinetics of PSI-LHCI sc per species (Chukhutsina et al., 2020).

From evolutionary perspective it seems clear that the functional architecture of PSI and PSII is not fixed between different photosynthetic organisms. This further complicates the general understanding of how the dynamic changes in the photosynthetic supercomplexes influence the regulation of excitation balance between both photosystems.

1.4.4 Regulation of excitation balance between photosystems

Photosynthetic organism under natural conditions are frequently exposed to changes in irradiance and spectral quality. These require dynamic readjustments of the antenna size of both photosystems to maintain the redox balance of the ETC. This is necessary to facilitate efficient electron flow and prevent overexcitation of one photosystem over the other, which would otherwise lead to oxidative damage to the

photosynthetic apparatus. While long-term acclimation to an imbalance in excitation leads to adjustment of overall photosystem stoichiometries (Chow, Melis and Anderson, 1990; Schöttler and Tóth, 2014), short-term responses include dynamic changes of the functional architecture to adjust the antenna size of both photosystems (Rochaix, 2014; Croce, 2020; Rantala, Rantala and Aro, 2020).

For PSII, these adjustments include a decrease in antenna size from C2S2M2-type to C2S2-type supercomplexes after acclimation to high irradiances (Ballottari et al., 2007; Kouřil et al., 2013; Wientjes, van Amerongen and Croce, 2013b; Bielczynski, Schansker and Croce, 2016). This antenna disassembly is suggested to be dependent on PSII core phosphorylations mediated by STN8 (Tikkanen et al., 2008; Fristedt et al., 2010). Additionally, this PSII antenna decrease is distinct from the LHCII phosophorylation dependent increase of the PSI antenna, classically referred to as state transitions (Lemeille and Rochaix, 2010; Minagawa, 2011). In the state transition model, a LHCII trimer associated with PSII in the grana (State 1) migrates, upon phosphorylation by STN7, towards PSI in stroma thylakoids (state 2) and back to state 1 upon dephosphorylation by TAP38, thereby balancing excitation between the two photosystems.

However, extensive studies in *Arabidopsis thaliana* showed that this does not adequately reflect the *in vivo* situation in the thylakoid membranes. First, L-LHCII trimers of the "free LHCII pool" are the antenna of both photosystems in grana margins (Wientjes, van Amerongen and Croce, 2013a; Grieco et al., 2015; Suorsa et al., 2015; Rantala, Tikkanen and Aro, 2017) arguing against a strict movement of LHCII from PSII towards PSI. Second, LHCII can attach independently of LHCII phosphorylation to the LHCI belt of PSI-LHCI sc and efficiently transfer energy to PSI (Benson et al., 2015; Akhtar et al., 2016; Bressan, Bassi and Dall'Osto, 2018; Bos et al., 2019; Chukhutsina et al., 2020; Schiphorst et al., 2022) arguing against a strict requirement of LHCII phosphorylation for changes in PSI antenna size. Additionally, recent studies also demonstrated that phosphorylations are not the only post-translational modification affecting state transitions, also Lys acetylations, mediated by the chloroplast acetyltransferase NSI, are critical for formation of PSI-LHCI-LHCII "state transition" complexes (Koskela et al., 2018, 2020).

Taken together, these studies emphasize a more nuanced view on the regulation of excitation balance between photosystems. This also includes differentiation between low light induced phosphorylation of bulk LHCII in contrast to the specific LHCB1 and LHCB2 subunits and their location in different photosynthetic supercomplexes. Phosphorylation of LHCB2 in the L-LHCII trimer is essential for the formation of a PSI-LHCI-LHCII "state transition" complex (Pietrzykowska et al., 2014; Crepin and Caffarri, 2015; Longoni et al., 2015) as the phosphorylated Thr residue of LHCB2 binds to a specific docking side of PSI (Pan et al., 2018; Huang et al., 2021). On the other hand, the role of LHCB1 phosphorylation is much less

clear. It is suggested to increase overall mobility of PSII-LHCII sc complexes in the grana and thereby facilitate the intermixing of PSII and PSI complexes in the margin domains (Crepin and Caffarri, 2015; Grieco et al., 2015; Rantala and Tikkanen, 2018). Even though, the functional role of intermixed clusters of PSI and PSII complexes in the grana margins still remains elusive (Croce, 2020; Rantala, Rantala and Aro, 2020).

1.4.5 Thermal dissipation of excess energy

Many of the above described regulation processes facilitate photoprotection to avoid oxidative damage of the photosynthetic apparatus (Niyogi, 2000; Pinnola et al., 2018), either by rerouting electrons to prevent accumulation of reduced acceptors (AEF and CEF) or by redirecting light energy between photosystems (state transitions). However, photosynthetic organisms can also engage photoprotection mechanisms that directly dissipates excess light energy.

During illumination, absorption of photons by chlorophyll molecules leads to the formation of excited singlet chlorophyll states, which drive photochemistry in RCs. However, under excess light conditions, when not all light can be utilized for charge separations, the singlet states have a high probability to convert to long-lived triplet chlorophyll states (Gruber et al., 2015). These triplet states can readily react with O_2 to form singlet oxygen, this ROS can lead to oxidative damage of the photosynthetic apparatus.

Therefore, photosynthetic organisms have evolved excess-energy dissipative mechanisms, which efficiently regulate the light harvesting of PSII and safely dissipate excess excitation as heat. The thermal energy dissipation directly competes with charge separations in the RCs both leading to quenching of singlet chlorophyll-*a* excited states, measured as a reduction in chlorophyll fluorescence of PSII (Kitajima and Butler, 1975). This PSII fluorescence quenching by charge separation is typically referred to as photochemical quenching, while regulated thermal energy dissipation also leading to quenching of fluorescence is referred to as non-photochemical quenching (NPQ, (Demmig-Adams and Adams, 1996; Horton, Ruban and Walters, 1996; de Bianchi et al., 2010; Ruban, Johnson and Duffy, 2012; Demmig-Adams et al., 2014)).

The naming convention of NPQ unfortunately resulted in simultaneously referring to a decrease in chlorophyll fluorescence as well as to the thermal energy dissipation process itself (Murchie and Ruban, 2020). This can lead to misunderstandings in the discussion of different components contributing to quenching of PSII fluorescence like chloroplast movement, state transitions and damage of photosystems – which are not dissipative pathways (Papageorgiou and Govindjee, 2014; Stirbet et al., 2020). Therefore, I will only refer to NPQ in the

context of fluorescence decrease/quenching and otherwise refer to energy dissipation. Additionally, only the thermal energy dissipation in seed plants will be described, while the specific aspects of cyanobacteria, algae and bryophytes (Niyogi and Truong, 2013; Goss and Lepetit, 2015; Giovagnetti and Ruban, 2018; Magdaong and Blankenship, 2018) are put aside.

Many aspects of the thermal energy dissipation in plants are still unknown, because it is a complex process with multiple components, traditionally differentiated by induction and relaxation kinetics of NPQ at the onset or after illumination, respectively. The components refer to fast ΔpH (energy)-dependent quenching as qE (seconds to minutes), intermediate zeaxanthin-dependent quenching as qZ (minutes to tens of minutes), and nearly irreversible or very slowly relaxing photoinhibitory quenching as qI (Nilkens et al., 2010). These kinetic components are however difficult to assign to single molecular players as qZ contributes to both qE and qI depending on the prevailing light conditions (Jahns and Holzwarth, 2012; Kress and Jahns, 2017). This also concerns the qI component, which is kinetically and conceptually very loosely defined, referring to multiple and functionally opposing processes ranging from downregulation, photoinactivation and damage of PSII (Krause, 1988) to sustained thermal energy dissipation (Demmig-Adams and Adams, 2006; García-Plazaola et al., 2012; Verhoeven, 2014; Malnoë, 2018).

1.4.5.1 Short-term thermal energy dissipation

Research on the molecular basis of the thermal energy dissipation pathways in plants has been focusing mostly on the short-term qE component of NPQ, gaining new insights into potential dissipation sites, de-excitation pathways, trigger and allosteric factors of thermal energy dissipation.

Multiple potential sites of thermal energy dissipation have been suggested, including LHCII trimers (Horton et al., 1991; Horton, Wentworth and Ruban, 2005), monomeric LHCII antenna proteins (Avenson et al., 2008; Guardini et al., 2020) and PSII reaction centers (Finazzi et al., 2004; Farooq et al., 2018). Although the sites are not necessarily mutually exclusive (Holzwarth et al., 2009; Dall'Osto et al., 2017; Nicol, Nawrocki and Croce, 2019), there seems to be general consensus that the major site of thermal energy dissipation in plants resides within aggregated LHCII trimers (Horton, Wentworth and Ruban, 2005; Ruban, 2016; Ruban and Wilson, 2021).

The physical mechanism of thermal energy dissipation, on the other hand, is still actively discussed and revolves around quenching of singlet chlorophyll excited states either by charge transfer (CT) or excitation energy transfer (EET) between central chlorophylls and carotenoids within LHCII proteins (Bennett et al., 2019;

Cignoni et al., 2021; Gray et al., 2022; Ruban and Saccon, 2022). The de-excitation pathway in turn is suggested to be regulated by small structural changes of the bound carotenoids (Balevičius et al., 2017; Liguori et al., 2017; Li et al., 2021). Interestingly, EET has also been recently observed in LHC-like proteins, ancestral to the whole LHC protein family, which suggests that the EET de-excitation pathway could be conserved in all LHC proteins (Staleva et al., 2015; Skotnicová et al., 2021).

The trigger for thermal energy dissipation in qE is a decrease in lumen pH, generated by the light-driven electron transport reactions (Briantais et al., 1979). The increased proton concentration leads to aggregation LHCII trimers and causes conformational changes within LHCII proteins, switching them from light harvesting to dissipation mode (Ruban, Johnson and Duffy, 2012). The decreased lumen pH also leads to protonation of PSBS protein (Li et al., 2000, 2004) and accumulation of the xanthophyll zeaxanthin in the thylakoid membrane (Demmig-Adams, 1990), but both their functional roles remain still to be resolved.

PSBS has been suggested to play an indirect role in thermal energy dissipation, as it does not bind chlorophylls and therefore is not the site of dissipation itself (Fan et al., 2015). Protonation of PSBS is suggested to induce conformational changes within the protein (Liguori et al., 2019), leading to its monomerization and activation (Bergantino et al., 2003; Correa-Galvis et al., 2016), which in turn allows it to promote thermal energy dissipation by facilitating aggregation of LHCII trimers (Goral et al., 2012; Ware et al., 2015; Nicol and Croce, 2021).

Zeaxanthin has a prominent role as an antioxidant in the thylakoid membranes (Havaux, Dall'Osto and Bassi, 2007; Johnson et al., 2007; Dall'Osto et al., 2010), but its additional function in thermal energy dissipation is less clear (Kress and Jahns, 2017). Zeaxanthin is formed from violaxanthin in the xanthophyll cycle (Demmig et al., 1987; Demmig-Adams and Adams, 1996), in which ΔpH-regulated lumenal violaxanthin de-epoxidase (VDE) and stromal zeaxanthin epoxidase (ZE) catalyze the interconversion of violaxanthin to zeaxanthin (Jahns, Latowski and Strzalka, 2009; Hoang et al., 2020). On the one hand, zeaxanthin has been suggested to take directly part in thermal energy dissipation (Holt et al., 2005; Ahn et al., 2008; Avenson et al., 2008), but on the other hand, xanthophyll cycle mutants suggest an indirect role in the kinetic modulation of thermal energy dissipation (Nilkens et al., 2010; Kress and Jahns, 2017). An indirect role is also supported by *in vitro* studies, in which thermal energy dissipation is zeaxanthin independent (Xu et al., 2015; Son, Pinnola and Schlau-Cohen, 2020).

As zeaxanthin shows functional redundancy with PSBS in increasing LHCII aggregation (Gruszecki and Strzałka, 2005; Johnson et al., 2011), a combined role has been suggested, in which zeaxanthin enhances the functional role of PSBS by allowing a faster reactivation and additionally prolonging thermal energy dissipation in LHCII trimers in the absence of ΔpH (Kress and Jahns, 2017; Sacharz et al., 2017).

1.4.5.2 Sustained thermal energy dissipation

In contrast to the detailed, albeit incomplete, molecular picture of the qE-type thermal energy dissipation, far less is known about sustained forms of thermal energy dissipation. As the name suggests, these recover very slowly (from hours to days) and are typically assigned to the photoinhibitory NPQ parameter qI.

Sustained forms of thermal energy dissipation have been reported for different evergreen (Demmig-Adams and Adams, 2006; Verhoeven, 2014) and desiccation tolerant species (Verhoeven, García-Plazaola and Fernández-Marín, 2018). In all these, sustained energy dissipation is associated with a decrease in maximum quantum efficiency of PSII (F_v/F_m) and retention of zeaxanthin in the dark, however both factors vary substantially depending on species and environmental factors (Adams et al., 2001; García-Plazaola et al., 2012; Verhoeven, 2013; Míguez et al., 2015; Walter-McNeill et al., 2021).

In boreal evergreen conifers the sustained thermal energy dissipation is typically observed during winter and early spring, when low temperatures inhibit CO_2 assimilation but light is still absorbed by evergreen needles. It represents an effective protection mechanism during the combination of freezing temperatures and high irradiance in the wider array of winter acclimation processes of conifers, when the photosynthetic apparatus is prone to oxidative damage (Öquist and Huner, 2003; Adams et al., 2004; Huner et al., 2013; Verhoeven, 2014; Chang et al., 2021).

The molecular mechanism and regulation of sustained thermal energy dissipation during winter acclimation of conifers still remain unclear. However, increased and retained zeaxanthin contents during winter (Adams and Demmig-Adams, 1994; Verhoeven, Adams and Demmig-Adams, 1996; Ensminger et al., 2004; Verhoeven et al., 2009) and reported LHCII aggregates with PSBS (Ottander, Campbell and Oquist, 1995; Ebbert et al., 2005) suggest at least partially shared components (Verhoeven, 2014) and co-regulation (Porcar-Castell, 2011) between sustained and short-term thermal energy dissipation mechanisms. Independent from short-term qE-type dissipation mechanisms, PSI-spillover quenching has been suggested to be the main mechanism of sustained thermal energy dissipation in overwintering boreal evergreen conifers (Bag et al., 2020). During PSI-spillover quenching, light energy from the internal antenna of PSII is directly transferred to PSI, which also in its oxidized state ($P700^+$) acts as an efficient trap, leading to non-radiative decay of excitation energy (Butler and Kitajima, 1975; Van Der Weij-De Wit et al., 2007).

1.4.6 Photoinhibition and repair of photosystems

If thermal energy dissipation and capacity of other photoprotection mechanisms are overwhelmed, excess excitation can lead to the production of ROS and in turn to photooxidative damage and photoinhibition of photosystems. Although various

types of ROS (Khorobrykh et al., 2020) are associated with photoinhibition, it should also be mentioned, that ROS are simultaneously an important signaling component of the chloroplasts under various stress conditions (Dietz, Turkan and Krieger-Liszkay, 2016; Noctor, Reichheld and Foyer, 2018). Additionally, the term photoinhibition in the literature is loosely defined, already since the early days of photosynthesis research (Kok, 1956), referring simultaneously to a decrease in activity and inactivation caused by damage to the photosystems. Since the regulation of photosystem activity overlaps with thermal energy dissipation processes (see above), here photoinhibition is only referred to in the context of inactivation and photooxidative damage caused by ROS.

PSII photoinhibition is caused by oxidative damage of the reaction center proteins, preferentially D1 (Aro, Virgin and Andersson, 1993; Kale et al., 2017). The mechanism is still not completely resolved, likely caused by a combination of increased charge recombinations ($P680^+$ and $Pheo^-$) resulting in ROS formation and direct damage by light absorption of the of Mn_4CaO_2 in the OEC (Vass, 2012; Tyystjärvi, 2013; Zavafer and Mancilla, 2021). PSII is particularly susceptible to photoinhibition due to its strong oxidative potential, so that it is constantly photodamaged in the light (Tyystjärvi and Aro, 1996). *In vivo*, however, PSII photoinhibition only accumulates under excess light conditions and overreduction of the PQ pool, when the rate of D1 damage exceeds the capacity of the efficient repair cycle replacing damaged D1 within PSII complexes (Aro, Virgin and Andersson, 1993; Theis and Schroda, 2016; Liu et al., 2019). The PSII repair cycle is assisted by a plethora of auxiliary proteins regulating PSII maintenance and consists of multiple phases (Chow and Aro, 2005; Järvi, Suorsa and Aro, 2015; Lu, 2016): (I) phosphorylation of damaged PSII core proteins and monomerization of PSII complexes, (II) lateral migration of PSII monomers to non-appressed thylakoid membranes, (III) dephosphorylation, partial disassembly of PSII monomers and proteolytic degradation of D1, (IV) *de-novo* synthesis and replacement of D1, (V) reassembly, dimerization and photoactivation of PSII. Since PSII damage and repair in plants take place in the appressed and unappressed thylakoid domains, respectively, the entire process is tightly linked to changes in the thylakoid ultrastructure of the chloroplasts facilitated by reversible thylakoid protein phosphorylations (Khatoon et al., 2009; Herbstová et al., 2012; Puthiyaveetil et al., 2014; Rantala, Rantala and Aro, 2020).

PSI photoinhibition is triggered by acceptor side limitation and similar to PSII, the photoinhibition mechanism is still under debate, including the site and type of ROS leading to PSI inactivation (Sonoike, 2011; Lima-Melo et al., 2021). ROS is suggested to be produced within PSI either at the iron-sulfur clusters (Sonoike et al., 1997), phylloquinone A_1 (Kozuleva and Ivanov, 2016; Kozuleva et al., 2021) or through charge recombination between $P700^+$ and A_0^- (Rutherford, Osyczka and

Rappaport, 2012; Takagi et al., 2016). Regardless of the site of ROS production, the iron-sulfur clusters (F_X, F_A, F_B) at the PSI acceptor side are thought to be early targets of ROS, leading to inactivation of PSI (Inoue, Sakurai and Hiyama, 1986; Sonoike et al., 1995; Tiwari et al., 2016). This is followed by degradation of PSI centers (Tjus, Lindberg Møller and Vibe Scheller, 1998; Kudoh and Sonoike, 2002; Zhang and Scheller, 2004) and decline of maximal PSI activity, measured as a decrease of the redox active PSI fraction/maximal P700 oxidation (Ivanov et al., 1998; Kim et al., 2001; Zhang and Scheller, 2004; Sejima et al., 2014; Tikkanen and Grebe, 2018). Under severe photoinhibitory conditions this can also lead to decreased CO_2 assimilation (Zivcak et al., 2015; Lima-Melo et al., 2019), especially as PSI lacks an efficient repair cycle compared to PSII, so that recovery of PSI depends exclusively on comparably slow *de-novo* biosynthesis of the PSI complex (Scheller and Haldrup, 2005).

2 Aims of the Study

The goals of this doctoral thesis were to further elucidate the composition and regulation of the photosynthetic apparatus in the, so far not extensively studied, species of the gymnosperm family of Pinaceae. The current understanding of photosynthesis on the thylakoid level is largely shaped by the model angiosperm *Arabidopsis thaliana,* focusing on comparisons of wild type and mutant plants lacking regulatory proteins. However, it is unclear how much of this research is easily transferable to other land plant groups, and how differences in the composition of the photosynthetic apparatus might shape the regulation of photosynthesis in these species.

Therefore, the aims of this doctoral research were:

- to characterize the photosynthetic apparatus of *Picae abies* and establish the species as a photosynthetic model for the gymnosperm family of Pinaceae (paper I).

- to investigate of thylakoid protein phosphorylations connected to the sustained non-photochemical quenching in *Picea abies* (paper II).

- to disentangle PSII and PSI dynamics during the seasonal acclimation of *Picea abies* and *Pinus sylvestris* during the spring recovery of photosynthesis (paper III).

3 Materials and Methods

3.1 Plant material and sampling sites

For all experiments, mature (non-current year) needles from Norway spruce (*Picea abies*) or Scots Pine (*Pinus sylvestris*) were used from trees grown in natural environments (for details see individual papers I, II and III).

In papers I and II, cut shoots were placed in light-proof plastic bags and transported to the laboratory (at freezing temperatures on ice). One part of the harvested needles was immediately used for thylakoid isolations, while the other part was used for *in vivo* chlorophyll-*a* fluorescence and P700 difference absorption measurements. In paper III, shoots were transported to the laboratory and recut under water within 10–15 minutes after harvesting, prior to CO_2 gas exchange, chlorophyll-a fluorescence and P700 difference absorption measurements. Additionally, small batches of mature needles from both species were transferred into cryotubes and frozen in liquid nitrogen for later thylakoid isolations.

In paper I, *Arabidopsis thaliana* (Col-0) was grown in short day conditions (8h day/16h night cycle, 23°C, 50% rel. humidity) at constant light intensity of 125 µmol photons m^{-2} s^{-1}. 4–5-week-old plants were used for fresh thylakoid isolations.

3.2 Thylakoid isolations and chlorophyll determination

Isolation of thylakoids from *Arabidopsis thaliana* (paper I) were carried out as previously described (Suorsa et al., 2015). Thylakoid isolations from fresh or frozen *Picea abies* or *Pinus sylvestris* needles were performed under dim light at 10°C with ice-cold reagents. Needles were homogenized for 90 s at 8000 rpm (2-inch blades with stainless steel chamber, Omni-Inc) in grinding buffer (50 mM Hepes-KOH, pH 7.5; 330 mM sorbitol; 5 mM $MgCl_2$; 10 mM NaF; 10% (w/v) polyethylene glycol, 6000 kDa; 0.075% (w/v) bovine serum albumin; 0.065% (w/v) Na-ascorbate). Homogenate was filtered through two layers of Miracloth and centrifuged at 4600 x *g* for 6 min. The pellet was re-suspended in shock buffer (50 mM Hepes-KOH, pH 7.5; 5 mM $MgCl_2$; 10 mM NaF) and pelleted again at 4600 × *g* for 6 min. Thylakoids were re-suspended in storage buffer (50 mM Hepes-KOH, pH 7.5; 5 mM $MgCl_2$;

100 mM sorbitol; 10 mM NaF), starch and residual PEG were removed by brief centrifugation (2 min, 200 × *g*), after which thylakoids were again pelleted at 4600 × *g* for 6 min. The final thylakoids were carefully re-suspended in storage buffer, aliquoted and immediately frozen in liquid nitrogen for later use.

Chlorophyll concentrations of isolated thylakoids were determined in buffered 80% (v/v) acetone (Porra, Thompson and Kriedemann, 1989).

3.3 Gel electrophoresis, protein staining and immunoblotting

To analyze native thylakoid protein complexes, isolated thylakoids were solubilized with n-dodecyl β-D-maltoside (β-DM) in 1% and 2% (w/v) final concentration for *Arabidopsis thaliana* and *Picea abies*, respectively, and then separated in lpBN-PAGE (Järvi et al., 2011). For SDS-PAGE, thylakoids were solubilized in Laemmli buffer (Laemmli, 1970), and then separated in 12% (w/v) acrylamide gels containing 6 M urea. To analyze subunit compositions of native thylakoid protein complexes, both approaches were combined in two-dimensional (2d) lpBN/SDS-PAGE, as previously described (Järvi et al., 2011).

ProQ Diamond phosphoprotein and SYPRO Ruby total protein staining of gels were performed according to manufacturer instructions (Invitrogen/Molecular Probes). For MS/MS identification gels were silver stained (Blum, Beier and Gross, 1987).

For immunoblotting, proteins were transferred on PVDF membrane (Millipore) and recognized by specific antibodies (for details see papers II and III). For detection, horseradish peroxidase-linked secondary antibody (Agrisera) and Amersham ECL Western blotting detection reagents (GE Healthcare) were used. Blots were subsequently stained with 0.1% (w/v) Coomassie Brilliant Blue diluted in 40% (v/v) methanol and 10% (v/v) acetic acid.

3.4 MS/MS protein and phosphorylation identifications

Protein spots were cut from silver stained gels and subjected to in-gel tryptic digestion, as described previously (Suorsa et al., 2015). Eluted peptides were loaded on a nanoflow HPLC system (EasyNanoLC 1000, Thermo Fisher Scientific) coupled to electrospray ionization-hybrid quadrupole-orbitrap mass spectrometer (MS/MS, Q-Exactive or Q-Exactive-HF, Thermo Scientific). Mass spectrometer was run in data-dependent acquisition (DDA) mode with higher-energy collisional dissociation (HCD) fragmentation (Olsen et al., 2007). N-terminal LHCB1_A phosphorylations (paper II) were additionally subjected to Orbitrap Fusion Lumos mass spectrometer

(Thermo Fisher Scientific) run with electron-transfer/higher-energy collision dissociation (EThcD) fragmentation (Yu et al., 2017).

The acquired spectra were matched against a custom spruce protein database, allowing Cys carbamidomethylation as fixed modification and Met oxidation, protein N-terminal acetylation and Asn/Gln deamination (paper I) or phosphorylation of Ser/Thr/Tyr (paper 2) as dynamic modifications. For details see paper I and II.

3.5 Custom *Picea abies* protein database

To ensure reliable MS/MS protein identifications, a custom spruce protein database was constructed from chloroplast- and nuclear-encoded protein databases (Figure 1, paper I). These were supplemented with manually annotated and curated thylakoid-associated proteins derived from transcripts (Figure 1, Database 3, paper I), as the *Picea abies* draft genome (Nystedt et al., 2013) often contained not full-length polypeptide sequences. In total, the merged custom database yielded 66,874 *Picea abies* polypeptide sequences, which were used for MS/MS thylakoid protein identifications.

3.6 Identification of LHC family proteins

LHC protein sequences in various land plants were identified by homology searches using reference LHCA1-6 and LHCB1-9 protein sequences from *Arabidopsis thaliana* and *Physcomitrella patens* against genome and transcriptome databases from different species (Supplemental table S1, paper I). Individual candidate LHC sequences were referenced against LHC diagnostic regions (Figure 2, paper I) and considered true orthologues of specific LHCA and LHCB proteins, when they shared >75% sequence identity with a particular reference sequence within at least one diagnostic region. For more details see Material and Methods in paper I.

3.7 77K chlorophyll fluorescence measurements

77K fluorescence emission spectra (paper II) of isolated thylakoids were recorded using an Ocean Optics spectrophotometer (S2000). Thylakoid samples were diluted in storage buffer to a concentration of 10 μg Chl mL^{-1}. Fluorescence spectra (excitation 440 nm) were background corrected and normalized to PSII fluorescence peak at 686 nm.

3.8 CO_2 gas exchange measurements and CO_2 flux data

Maximal CO_2 assimilation (A_{max}) rates from needles (paper III) were obtained at 1500 ppm CO_2 and 1500 µmol photons m^{-2} s^{-1} after rapid light curve induction and stabilization for several minutes in custom-made cuvettes with a GFS-3000 (Walz). Maximal CO_2 assimilation rate was calculated by subtracting the dark respiration rate (Kolari et al., 2014).

Net ecosystem CO_2 fluxes (paper III) were estimated with eddy covariance methods (Aubinet et al., 1999) at 24 m height using a Gill Solent 1012R anemometer/thermometer & LI-COR LI-6262 gas analyzer.

3.9 *In* vivo chlorophyll-*a* fluorescence and P700 difference absorption measurements

Simultaneous *in vivo* chlorophyll-*a* fluorescence (>700 nm) and P700 difference absorption measurements (870-830 nm) from needles were performed with a Dual-PAM 100 (Walz). Measurements were performed after dark acclimation and with homemade adapters to ensure parallel alignment and minimal gap size between needles.

Initial F_m and F_0 were recorded directly after dark-acclimation, followed by ΔP_m determination. Needles were then subjected to light curve protocols (for details see papers II and III) with intervals of increasing light intensities (635 nm, applied to ad- and abaxial surfaces), each with a saturating pulse (SP) to determine relative PSI and PSII quantum yields.

Fluorescence measuring light intensity was set to <1.0 µmol photons m^{-2} s^{-1} (620 nm) and SP intensity between 6000-8000 µmol photons m^{-2} s^{-1} (635 nm) with a pulse width of 700 ms. F_0' was determined with a short far-red pulse after each SP (F_0' subroutine in the Dual-PAM 100 software). ΔP_m was determined with a SP after 10 s of far-red pre-illumination (720 nm, 130 µmol photons m^{-2} s^{-1}).

In paper III, additional *in vivo* chlorophyll-*a* fluorescence measurements were performed with a Dual-PAM 2500 (Walz) at ambient temperatures, estimating the sustained non-photochemical quenching parameter, NPQ_S (Porcar-Castell, 2011)). Instrument settings were identical to measurements with Dual-PAM 100 as described above.

3.10 Calculation of PSII and PSI *in vivo* parameters

Complementary quantum yields of PSII (Genty, Briantais and Baker, 1989; Kramer et al., 2004) were calculated as Y_{II}, effective quantum yield of PSII photochemistry ($Y_{II} = (F_m' - F)/F_m'$), Y_{NO}, quantum yield of non-regulatory energy dissipation

(Y_{NO} = 1/(NPQ + 1 + qL (F_m/F_O – 1)) and Y_{NPQ}, quantum yield of regulatory non-photochemical quenching (Y_{NPQ} = 1 – Y_{II} – Y_{NO}).

The NPQ_S parameter was calculated as NPQ_S = (F_{mR} – F_m)/F_m, where F_{mR} corresponded to the highest recorded F_m obtained during the summer and assumed to have a NPQ_S = 0 (Porcar-Castell, 2011).

The classical complementary quantum yields of PSI (Klughammer and Schreiber, 1994, 2008) were calculated as Y_I, effective quantum yield of PSI photochemistry (Y_I = (ΔP_m' – ΔP)/ΔP_m), Y_{ND}, PSI donor-side limitation (Y_I = $\Delta P/\Delta P_m$) and Y_{NA}, PSI acceptor-side limitation (Y_{NA} = (ΔP_m – ΔP_m')/ΔP_m). Additionally, we derived corrected PSI quantum yields (Paper III), which incorporated relative changes of ΔP_m. These are expressed relative to highest ΔP_m observed per biological replicate (ΔP_{mR}) throughout the study period, as cY_I, corrected effective quantum yield of PSI photochemistry (cY_I = (ΔP_m' – ΔP)/ΔP_{mR}), cY_{ND}, corrected PSI donor-side limitation (cY_{ND} = $\Delta P/\Delta P_{mR}$), cY_{NA}, corrected PSI acceptor-side limitation (cY_{NA} = (ΔP_m – ΔP_m')/ΔP_{mR}) and Y_{loss}, non-photochemical "loss" of energy due to PSI photoinhibition (Y_{loss} = (ΔP_{mR} – ΔP_m)/ΔP_{mR}). For more details on the derivation of corrected PSI quantum yields, see paper III.

4 Overview of Results

4.1 The photosynthetic apparatus of *Picea abies* – a model species for Pinaceae

To establish *Picea abies* (hereafter spruce) as a photosynthetic model species, we compared its native thylakoid protein complexes with the model angiosperm *Arabidopsis thaliana* (hereafter Arabidopsis). To this end, isolated thylakoids were solubilized with β-DM, which only leaves stronger protein-protein interactions intact, thereby giving insight into the native building blocks of thylakoid protein complexes.

Separation of native thylakoid protein complexes in lpBN-PAGE revealed expected similarities between Arabidopsis and spruce (Figure 5, Paper I). Both species showed separation of larger PSII-LHCII sc, differentiated by their different functional architectures of C2S2M2, C2S2M1, C2S2, C2S1 complexes. Additionally, similar complexes of PSII dimers (C2) and monomers (C1) as well as ATPase and PSI-LHCI complexes could be identified. Also, lower molecular mass complexes referring to native LHCII trimers and monomers were comparable.

This analysis was complemented by a two-dimensional (2d) approach, in which the subunit composition of each native protein complex was analyzed by 2d lpBN/SDS-PAGE (Figure 6–7, Paper I) followed by tandem mass spectrometry (MS/MS) protein identification using a custom spruce thylakoid protein database (see Material and Methods). The MS/MS identifications confirmed similar subunit compositions of PSII, PSI, Cytbf and ATPase protein complexes between Arabidopsis and spruce, although individual subunits slightly differed in their apparent molecular mass between the two species.

Simultaneously, the comparison of native photosynthetic complexes in Arabidopsis and spruce showed clear differences. In spruce, PSI-NDH1 complexes were absent (Figure 5, Paper I), which was in line with the absence of LHCA5 and LHCB6 sequences (Figure 3, Supplemental table S3, Paper I), representing essential binding partners for the formation of PSI-NDH1 complexes. Additionally, spruce showed accumulation of a smaller PSI subcomplex, PSI*, without LHCI heterodimers, which separately migrated close to LHCII trimer band in the first dimension of lpBN-PAGE (Figure 6–7, Paper I). Strikingly, spruce lacked the angiosperm typical pentameric M-LHCII-LHCB4-LHCB6 complex (Figure 5, Paper

I), which was likely the result of an altered LHCII composition compared to Arabidopsis (detailed below).

4.1.1 Distinct characteristics of the light harvesting antenna of PSII in Pinaceae

The collection of LHC family proteins from a large variety of land plants yielded a total of 1366 LHC protein sequences from 84 species with a special focus on angio- and gymnosperm species, largely due to available genome and transcriptome databases (Supplemental table S1, paper I). This LHC collection included LHCB1-9 and LHCA1-6 protein sequences from 41 angiosperms (including 28 eudicots and 6 monocots), 34 gymnosperms (including 15 species of Pinaceae, representing all genera of the family), 4 Lycophytes and Monilophytes, 3 Bryophytes (one species per Anthocerotophyta, Marchantiophyta and Bryopsida) and 2 Chlorophytes.

The LHC protein distribution (Figure 3, Supplemental table S3, Paper I) clearly indicated the absence of LHCB3 and LHCB6 from spruce and other members of Pinaceae (as well as Gnetaceae, and Welwitschiaceae), which was supported by the absence of distinct protein spots in the 2d protein map of spruce compared to Arabidopsis (Figure 6, Supplemental table S4, Paper I). Since LHCB3 in Arabidopsis is typically part of M-LHCII trimers facing PSII and LHCB6 is required for anchoring the M-trimer to PSII, the absence of both LHCB3 and LHCB6 in spruce likely explains the loss of M-LHCII-LHCB4-LHCB6 from spruce thylakoids (Figure 5, Paper I).

Additionally, the LHC *in-silico* comparison strongly suggested a complete replacement of LHCB4 with LHCB8 in spruce and other members of Pinaceae (Figure 3, Supplemental table S3, Paper I), which in turn was supported by the identification of LHCB8 in PSII-LHCII sc of spruce (Figure 6, Supplemental table S4, Paper I). A direct amino acid sequences comparison of LHCB4 and LHCB8 across land plants showed distinct differences in their N-terminal extension (diagnostic region 2, Supplemental table S2, Paper I), characteristic for LHCB4 and LHCB8 compared to other LHCII proteins, and their C-terminus, in which a 15 amino acid sequence motive (WxTHLxDPLHTTIxD) was only conserved in LHCB4 (Figure 4, Paper I).

Surprisingly, the LHCB8 sequences showed a very fragmented distribution among a large selection of representative land plant species (Figure 3, Supplemental table S3, Paper I). LHCB8 sequences were found in all investigated gymnosperms species, except early diverging Cycadales, while LHCB8 sequences in angiosperms were present only in late diverging Eurosids (Malvids and Fabids) and Caryophyllales (sister group to Asterids). These results, together with the sequence diversion of the LHCB8 C-termini in the different land plant linages (Figure 4, Paper I), suggest that LHCB8 likely evolved through gene duplication from LHCB4 in various land plant groups independently.

4.2 Specific thylakoid protein phosphorylations connected to the sustained thermal energy dissipation in *Picea abies*

The establishment of the custom spruce thylakoid protein database and identification of thylakoid proteins from 2d lpBN/SDS-PAGE in spruce (see paper I) allowed us to investigate the connections between dynamic thylakoid protein phosphorylations and the mechanism of sustained thermal energy dissipation. To this end, we collected spruce needles from shade and sun exposed natural forest habitats for four consecutive years (2016-2019) in conjunction with *in vivo* fluorescence measurements (Figure 1, paper II). For the sake of brevity, only results from sun exposed needles are highlighted, as overall similar results were obtained from shade-exposed samples.

During the sampling period, coinciding with freezing temperatures and high light intensities (Figure 1A, paper II), sustained thermal energy dissipation was only observed once during March 2018, measured as severe decrease in maximal quantum yield of PSII photochemistry (F_v/F_m) (Figure 1B, paper II). The comparison of thylakoid protein phosphorylations of Mar 2018 (sustained NPQ samples) with Jun/Jul 2018 samples (summer controls) on the basis of 2d lpBN/SDS-PAGE (Figure 2A-B, paper II) clearly revealed expected similar PSII core phosphorylations of CP43, D2 and D1 (co-migrating with LHCII) and bulk LHCII (LHCB1 and LHCB2).

4.2.1 Identification of 3p-LHCII and p-PSBS thylakoid protein phosphorylations

Additionally, two specific phosphorylated proteins could be identified in sustained NPQ samples compared to the summer control (Figure 2A-B, paper II). These phosphoproteins corresponded to previously undescribed thylakoid protein phosphorylations: the triply phosphorylated spruce LHCB1 isoform, LHCB1_A (3p-LHCII) present in PSII-LHCII sc, LHCII trimers and monomers (Figure 2B, Supplemental Figure S4, paper II) and the freely migrating phosphorylated PSBS (p-PBSB) proteins (Figure 2B, paper II), which were verified via MS/MS identification (Figure 2C-D, Dataset S1, paper II).

The MS/MS analysis allowed us also to pinpoint phosphorylation sites within the proteins. 3p-LHCII showed simultaneous phosphorylation of two to three Thr and Ser residues at its N-terminus (Figure 2C, Supplemental Figures S5A, S6, S7, paper II), likely responsible for the observed migration shift to higher apparent molecular mass in SDS-PAGE gels. Similar multiple N-terminal phosphorylations were not observed in the other spruce LHCB1 isoform, LHCB1_B, or LHCB2 proteins, although single Thr and Ser phosphorylations of LHCB1_A, LHCB1_B and LHCB2 were found in both sustained NPQ and summer control samples (Figure 2C, paper II).

Likewise, p-PSBS showed multiple single Thr and Ser phosphorylations in stromal exposed regions of both PSBS isoforms in spruce (PSBS_A and PSBS_B), including the N- and C-terminus as well as in the stromal loop (Figure 2D, Supplemental Figure 5B, paper II). The latter also contained single Ser phosphorylations found in summer control samples, suggesting that these were not specific phosphosites during sustained NPQ conditions.

4.2.2 Functional connection of 3p-LHCII and p-PSBS to sustained thermal energy dissipation

Artificial relaxation experiments in darkness at +7°C showed recovery of F_v/F_m after 24h, indicating relaxation of sustained thermal energy dissipation (Figure 3A, paper II). Simultaneously, Thr phosphorylations of 3p-LHCII and p-PSBS, assayed with phospho-Thr antibody, decreased in parallel, (Figure 3B, paper II), although total phosphorylations of 3p-LHCII, assayed with ProQ stain, showed a slower decline compared to p-PSBS (Supplemental Figure 8F, paper II).

Immunoblotting and total protein stains (Coomassie, Sypro) confirmed, that the genuine decrease of 3p-LHCII and p-PSBS phosphorylations were not due to changes in respective protein abundances during artificial relaxation of sustained thermal energy dissipation (Figure 3E, Supplemental Figure 8E, paper II).

Additional artificial induction experiments in darkness or light (900 µmol photons m^{-2} s^{-1}) at -20°C revealed clear differences between 3p-LHCII and p-PSBS (Figure 5, paper II). While the overall induction of 3p-LHCII and p-PSBS was lower compared to natural sustained NPQ conditions, artificial induction of p-PSBS was clearly light dependent and 3p-LHCII induction was independent of light. Both experiments clearly indicated a functional connection between both 3p-LHCII and p-PSBS to sustained thermal energy dissipation.

4.2.3 Connection of sustained thermal energy dissipation to PSII photoinhibition, regulatory thermal energy dissipation and energy distribution between photosystems

The artificial relaxation experiments in conjunction with *in vivo* chlorophyll-*a* fluorescence measurements and 77K fluorescence measurements on isolated thylakoids allowed us to further explore the connection of sustained thermal energy dissipation to other processes.

Recovery of spruce needles in darkness allowed the differentiation between recovery of sustained thermal energy dissipation and PSII photoinhibition (both contributing to sustained NPQ), with the latter requiring light for several

subreactions of the PSII repair cycle. Based on the only partial recovery of F_v/F_m within 96h in darkness compared to non-sustained NPQ samples, 10-30% of the decrease in F_v/F_m of sustained NPQ samples could be assigned to PSII photoinhibition (Figure 3A, paper II). This result agreed with the accumulation of CP43-less PSII subcomplex (RC-CP47), a typical intermediate during the PSII repair cycle, only in sustained NPQ samples (Figure 2A-B, Supplemental Figure S13-15, paper II).

Additionally, the recovery from sustained NPQ conditions also coincided with the recovery of regulatory thermal energy dissipation capacity (Figure 3C, paper II), expressed as the quantum yield of non-photochemical quenching (Y_{NPQ}), which suggested that part of the sustained thermal energy dissipation is build up on already existing qE type thermal energy dissipation.

At last, 77K fluorescence measurements showed a decline in the PSI/PSII (F734/F686) fluorescence ratio during the recovery (Figure 3D, paper II). This strongly suggested a high PSI energy distribution in thylakoids from sustained NPQ conditions, which gradually diminished during the recovery.

4.2.4 3p-LHCII and p-PSBS are prerequisites for the sustained thermal energy dissipation

To further scrutinize 3p-LHCII and p-PSBS functional connection to sustained NPQ, their accumulation in spruce thylakoids across non-sustained NPQ conditions from 2016-2019 was investigated. Interestingly, accumulation of 3p-LHCII and p-PSBS was also observed under non-sustained NPQ conditions of Jan 2016, Feb 2017, Jan 2018, and Jan/Feb 2019 samples (Figure 4A–D, Supplemental Figure S12, paper II), yet in lower amounts compared to Mar 2018. Cross-referencing of different sampling times with light and temperature conditions (Figure 4F, Supplemental Dataset S2, paper II) showed that p-PSBS and 3p-LHCII were present only when the average daily temperatures were ≤ -4°C. Since F_v/F_m was not severely reduced at these sampling times, it strongly advocates that 3p-LHCII and p-PSBS are important prerequisites for the engagement of sustained thermal energy dissipation in spruce.

4.3 Seasonal acclimation of spruce and pine during spring recovery of photosynthesis

The seasonal acclimation response of boreal evergreen conifers is strongly connected to prevailing temperatures and light availability. While the sustained thermal energy dissipation is particularly prevalent under freezing conditions and excess irradiance, the whole acclimation response encompasses also the light reactions and CO_2 assimilation, particularly during the spring recovery of photosynthesis. In a case

study, we followed the photosynthetic acclimation of pine and spruce trees by *in vivo* measurements from Feb to July 2017, with a particular focus on disentangling the seasonal dynamics of PSI and PSII.

4.3.1 Seasonal PSI and PSII dynamics in response to CO_2 assimilation

The spring recovery in pine and spruce was characterized by a non-linear increase in CO_2 assimilation capacity (A_{max}) (Figure 3B, paper III) and maximal PSII activity (F_v/F_m) (Figure 3C, paper III), which both followed expected gradual increase in temperature and light availability from winter to summer (Figure 3A, paper III). The spring period showed more variable responses, in particular low F_v/F_m values following freezing temperatures. These were indicative of partial induction of sustained thermal energy dissipation in pine and spruce, largely in agreement with the sustained NPQ parameter (NPQ_S) from measurements at ambient temperatures (Figure 3D, paper III). Surprisingly, also maximal PSI activity ($\Delta P_m/\Delta P_{mR}$) strongly declined during spring in both species Figure 3E, paper III).

To gain additional insights into seasonal acclimation of PSI and PSII, the protein abundance of both complexes was checked via immunoblots on equal chlorophyll basis. These revealed lower relative PSII (D1 and CP47) abundance during winter and spring compared to summer (Figure 4A-B, paper III), but interestingly the relative D1 abundance was generally higher compared to CP47. These likely represented accumulation of damaged D1 and pre-D1 proteins from an impaired PSII repair cycle during spring. The PSI (PsaB) abundance, albeit lower in pine compared to spruce during winter (Figure 4A-B, paper III), showed a clear continuous decline during spring in both species, strongly indicative for PSI photoinhibition during spring and in agreement with the observed lower $\Delta P_m/\Delta P_{mR}$.

4.3.2 Uncorrected PSI quantum yields overestimate CEF during spring recovery

Since classical PSI quantum yields do not account for relative changes in ΔP_m, we needed to derive corrected PSI quantum yields (cY_I, cY_{ND}, cY_{NA}, Y_{loss}; see Material and Methods, paper III) to adequately describe seasonal changes in PSI activity.

These included a definition of the new yield parameter Y_{loss}, which accounts for the seasonal non-photochemical energy "loss" due to PSI photoinhibition in both pine and spruce (Figure 5A-B, paper III). Inclusion of this parameter rescaled corrected PSI quantum yields (Supplemental Figure S4, paper III) relative to the highest observed redox active PSI fraction per biological replicate (ΔP_{mR}), instead of

uncorrected PSI quantum yields (Supplemental Figure S5, paper III) scaled to the individual redox active PSI fraction of each sample (ΔP_m).

Direct comparison of uncorrected (Y_I) and corrected (cY_I) effective PSI quantum yields in both species revealed different overall seasonal trends. While Y_I showed a particular increase during spring, cY_I remained remarkably stable throughout the same period, similar to the effective quantum yield of PSII (Y_{II}) in both low light (Figure 6A-B, paper III) and high light conditions (Figure 6C-D, paper III).

This had a profound effect on the estimation of steady-state cyclic electron flow (CEF) inferred from the difference of the relative electron transport rates of PSI and PSII based on uncorrected (ΔETR) or corrected (ΔcETR) PSI quantum yields. In pine, ΔcETR was strongly diminished in comparison to ΔETR in both low light (Figure 6A, paper III) and high light conditions (Figure 6C, paper III), while in spruce the effect was less pronounced (Figure 6B and D, paper III). Overall, ΔcETR in pine and spruce showed similar seasonal responses suggesting that neither species upregulated CEF during winter and spring, unlike previously suggested.

5 Discussion

5.1 *Picea abies* as a photosynthetic model species for Pinaceae

In the last decades, the use of model organisms has greatly advanced the knowledge in the field of biology (Müller and Grossniklaus, 2010). In plant sciences, this model organism is *Arabidopsis thaliana* that since its first full genome sequencing (Arabidopsis Genome Initiative, 2000; Provart et al., 2021) has greatly advanced our understanding. Since then the availability of plant genomes and transcriptomes has massively expanded (Sun et al., 2022) and includes now about 1000 species (Wickett et al., 2014; One Thousand Plant Transcriptomes Initiative, 2019). Nevertheless, in the photosynthesis field, the biochemical and molecular understanding of photosynthesis has been mostly shaped by research in the cyanobacterium *Synecchocistis* (Ikeuchi and Tabata, 2001), the chlorophyte *Chlamydomonas reinhardtii* (Rochaix, 2002) and the angiosperm *Arabidopsis thaliana* (Pesaresi et al., 2001), due to early access of genetic tool kits. Although the list of photosynthetic model species is more and more expanding (Rensing et al., 2020; Rotasperti et al., 2020), gymnosperms will likely remain behind compared to other land plants, because of their large genome sizes and challenging genome assemblies (De La Torre et al., 2014).

In that regard, the custom spruce thylakoid protein database (Figure 1, paper I) together with the 2d thylakoid protein map of spruce (Figure 6, Paper I) represent only a small stepping stone towards the establishment of spruce as a photosynthetic model species. Nevertheless, it allows for high confidence comparisons of thylakoid protein complexes and their subunit composition between different species or different environmental conditions (paper II). It is however important to note that the database, in its current version, remains incomplete and is only reliable for the investigation of thylakoid proteins. For more complex samples, like total chloroplasts or cells, the database should be expanded to include more curated protein sequences for reliable MS/MS identification. Furthermore, the general comparability of the photosystem subunit composition should be verified in other members of Pinaceae, for which genomes and transcriptomes are also available (De La Torre et al., 2014; One Thousand Plant Transcriptomes Initiative, 2019), and

additionally expanded to other conifer orders (Cupressales and Araucariales) and gymnosperms as a whole.

5.1.1 LHC protein distribution in Pinaceae in the evolutionary context

Based on the comparison of the LHC protein distribution in a large selection of land plant species (Figure 3, Supplemental table S3, Paper I), spruce and other members of Pinaceae (as well as Gnetaceae and Welwitschiaceae) have lost the trimeric LHCB3 and monomeric LHCB6 subunits, which is in line with previous observations (Kouřil et al., 2016), challenging the common view that the LHCB3 and LHB6 are essential for land plants (Alboresi et al., 2008). Additionally, the same comparisons revealed that these species have also lost the monomeric LHCB4 subunit, which was replaced with its close homologue LHCB8. The apparent fragmented distribution of LHCB8 in land plants (Figure 3, Supplemental table S3, Paper I) together with the lack of conserved C-termini in LHCB8 orthologues (Figure 4, Paper I) suggested that LHCB8 might have evolved independently in gymno- and angiosperms. In that regard, LHCB8 potentially represents the most recent LHCII isoform among land plants, although this hypothesis needs to be confirmed by more in depth phylogenomic analysis.

Additionally, the apparent replacement of LHCB4 with LHCB8 in Pinaceae supports the notion that LHCB8 is not merely an isoform of LHCB4, which essentially stems from the naming convention of LHCB4.3/CP29.3 in *Arabidopsis thaliana* (Jansson, 1999), but instead represents a distinct minor LHCII antenna protein (Klimmek et al., 2006; Albanese et al., 2019). The functional differences between LHCB8 and LHCB4 remain still unclear, but are generally supported by the distinct transcription and translation profile of LHCB8 in *Arabidopsis thaliana* (Klimmek et al., 2006; Sawchuk et al., 2008; Alboresi et al., 2011; Floris et al., 2013) and the accumulation of LHCB8 on protein level under high irradiance in PSII-LHCII sc in *Pisum sativum* (Albanese et al., 2016, 2018) as well as under field conditions in *Arabidopsis thaliana* (Flannery et al., 2021).

5.1.2 Functional consequences of the altered PSII light harvesting antenna in Pinaceae

In angiosperms, the M-trimer of PSII-LHCII sc (C2S2M2) is bound by LHCB4 and LHCB6 to the PSII core, while LHCB3 within the M-trimer functions as contact point for both monomeric antenna proteins (Caffarri et al., 2009; Su et al., 2017). Therefore, the lack of these proteins in spruce is likely the cause for the absence of the angiosperm typical M-LHCII-LHCB4-LHCB6 band (Bassi and Dainese, 1992)

from the native thylakoid protein complexes (Figure 5, paper I). However, the absence of both these proteins did not prohibit the formation of the C2S2M2 complex in spruce, likely stabilized by the presence of LHCB8 but in turn affecting the binding of the M-LHCII trimer to the PSII core. Compared to angiosperms, the M-LHCII trimer in the C2S2M2 complex of spruce has a slightly different orientation and closely resembles the functional architecture of PSII-LHCII sc found in the chlorophyte *Chlamydomonas reinhardtii* (Kouřil et al., 2016). Algae PSII-LHCII sc can more stably bind additional L-trimers (or N-trimer for "naked"), thereby forming C2S2M2L2 complexes (Shen et al., 2019; Sheng et al., 2019). These have been recently identified also in spruce and other members of Pinaceae, albeit spruce showing a larger variety of different PSII-LHCII sc with (theoretically) up to 12 L-LHCII trimers bound to one PSII dimer (Kouřil et al., 2020). This suggests that the functional architecture of PSII-LHCII sc in members of Pinaceae is much more flexible compared to other land plants.

Different functional architectures of the PSII-LHCII sc between species, with different compositions or orientations of LHCII trimers and monomers, consequently results in alterations of the energy transfer routes from the LHCII antenna to the PSII core, which define the light harvesting and energy dissipation capacities in these species (Sheng et al., 2021). Thereby, LHCB4 and LHCB8 might play an integral role as they represent the conduit for the energy transfer from M-LHCII to CP47 in the PSII-LHCII sc (Mascoli et al., 2020). This energy transfer pathway could potentially be affected by the absence of the conserved amino acid sequence motive (WxTHLxDPLHTTIxD) in LHCB8 (Figure 4, Paper I), containing the binding site for chlorophyll b614 in LHCB4 (Bassi et al., 1999; Pan et al., 2011). Although, a recent study of an LHCB4 mutant lacking chlorophyll b614 in *Arabidopsis thaliana* suggests that it is not involved in direct energy transfer from M-LHCII to the PSII core, it instead confers an important structural role within the PSII-LHCII sc by mediating the binding of LHCB6 and strongly affecting the lateral organization PSII-LHCII sc in the thylakoid membrane (Guardini et al., 2022).

Such a potential interplay between LHCB4 or LHCB8 and the structural organizations of PSII-LHCII sc, could also be mediated by differences in the N-termini of LHCB4 and LHCB8 (Figure 4). The N-terminus of LHCB4 has been suggested to take part in the "velcro-like" interactions of paired PSII-LHCII sc across the stromal gap involved in grana stacking (Albanese et al., 2017, 2020). In addition to differences in the C-terminus, also the N-termini of LHCB4 and LHCB8 showed considerable sequence variability within the motif conferring this interaction (diagnostic region 2, Supplementary Table S2). Therefore, it might be hypothesized that the presence of LHCB8 in Pinaceae could not only change the lateral organization of PSII-LHCII sc complexes, but also influence the dynamics of grana stacking by changing the interactions of complexes across the stromal gap. Since the

sustained thermal energy dissipation in Pinaceae has been closely associated with a severe decrease in grana stacking (Demmig-Adams et al., 2015; Bag et al., 2020), the replacement of LHCB4 with LHCB8 in Pinaceae might additionally represent an evolutionary adaptation specific for this type of thermal energy dissipation.

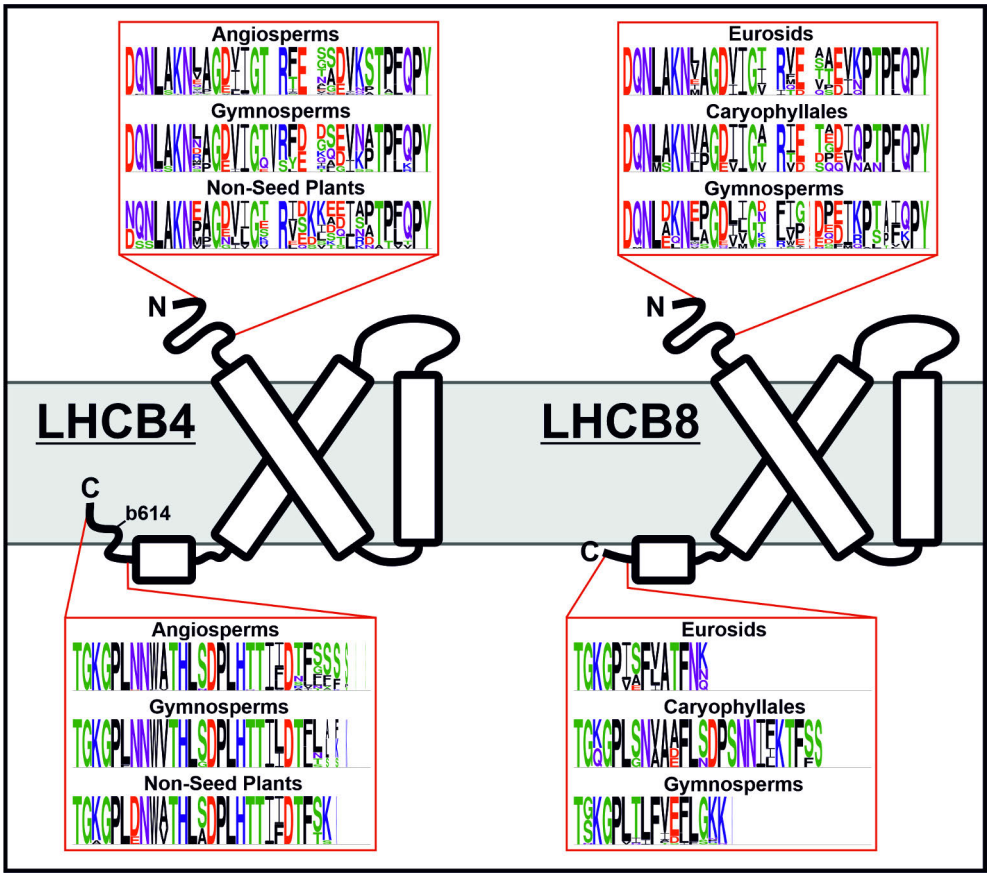

Figure 4: Amino acid sequence differences in N- and C-termini between LHCB4 and LHCB8 as well as various land plant groups. Size of letters in sequences logos is proportional to their occurrence in the respective land plant group. b614 refers to chlorophyll binding site only present in LHCB4 sequences.

5.2 New insights into the sustained thermal energy dissipation in *Picea abies*

During winter and early spring, Pinaceae and other boreal evergreen conifers engage a sustained form of thermal energy dissipation, a specialized photoprotection mechanisms that prevents oxidative damage of the photosynthetic apparatus (Demmig-Adams and Adams, 2006; Verhoeven, 2014). The sustained thermal

energy dissipation in members of Pinaceae occurs during the specific combination of low temperatures and high irradiance (sustained NPQ conditions). Under these conditions, plants show a severe decrease in F_v/F_m together with dark retention of zeaxanthin (Adams and Demmig-Adams, 1994; Verhoeven, Adams and Demmig-Adams, 1996; Ensminger et al., 2004; Verhoeven et al., 2009), but also aggregation of LHCII and PSBS proteins (Ottander, Campbell and Oquist, 1995; Ebbert et al., 2005) as well as a loss of grana stacking have been observed (Martin and Öquist, 1979; Demmig-Adams et al., 2015; Bag et al., 2020; Yang et al., 2020).

The molecular mechanism, however, still remains elusive and has been suggested to involve partially shared components with the short-term qE response and potentially co-regulation (Porcar-Castell, 2011; Verhoeven, 2014), albeit also a distinct dissipation mechanism involving PSI-spillover quenching has been suggested (Bag et al., 2020). Considering the wide array of proposed factors and the engagement under very specific environmental conditions, it seems likely that the sustained thermal energy dissipation takes place in multiple sites and depends on different levels of regulation and interconnected molecular mechanisms. Some of which have been proposed to also include thylakoid protein phosphorylations (Ebbert et al., 2005; Merry et al., 2017).

The comparative analysis of thylakoid protein phosphorylations of spruce needles from sustained NPQ and summer conditions (Figure 2, paper II) together with artificial recovery (Figure 3A-B, paper II) and induction experiments (Figure 5, paper II) revealed that the newly identified 3p-LHCII and p-PSBS are functionally connected to the sustained thermal energy dissipation, even though they likely serve different roles.

5.2.1 The role of 3p-LHCII

3p-LHCII consisted of the triply phosphorylated isoform of LHCB1_A (Figure 2C, paper II), which had a different N-terminus with varying numbers of Ser and Thr residues compared to the LHCB1_B isoform. Both isoforms have been previously identified in *Pinus sylvestris* (Jansson 1990), suggesting that they are potentially conserved in members of Pinaceae. They are, however, difficult to compare to other land plant groups, as the N-terminus of LHCB1 is generally not conserved in length and sequence composition, especially compared to LHCB2 (Crepin and Caffarri, 2018).

While the conserved N-terminal Thr phosphorylation of LHCB2 is responsible for the formation of the PSI-LHCI-LHCII state transition complex (Pietrzykowska et al., 2014; Crepin and Caffarri, 2015; Pan et al., 2018), the role of LHCB1 phosphorylations is much less clear. Few studies differentiate between LHCB1 and LHCB2 phosphorylations, but LHCB1 is suggested to increase the mobility of PSII-

LHCII sc in the thylakoid membrane (Crepin and Caffarri, 2015; Grieco et al., 2015; Rantala and Tikkanen, 2018). This phosphorylation induced mobility is also proposed to be linked to changes in the thylakoid membrane reorganizations, including grana size and stacking (Wood et al., 2019).

Although modeling of repulsive forces in phosphorylated PSII-LHCII sc showed only a small direct contribution to grana stacking (Puthiyaveetil, van Oort and Kirchhoff, 2017), a more mobile PSII-LHCII sc fraction of phosphorylated PSII-LHCII sc might exert a stronger effect. Consequently, triple phosphorylation of LHCB1_A (3p-LHCII) would increase the negative charge between opposite grana thylakoids and could conceivably contribute to destacking or even complete loss of grana in spruce. Such loss of grana stacking would, in turn, lead to a loss of lateral heterogeneity in the thylakoid membrane, bringing PSII and PSI complexes in closer contact and increase the chance for PSI-spillover quenching. This effect could explain the observed increase in relative distribution of excitation energy to PSI under sustained NPQ conditions, which subsequently decreased with dephosphorylation of 3p-LHCII during the relaxation of sustained thermal energy dissipation (Figure 3D, paper II). Functionally, 3p-LHCII might promote favorable conditions for PSI-spillover quenching by decreasing grana stacking.

5.2.2 The role of p-PSBS

p-PSBS consisted of two PSBS isoforms in spruce, PSBS_A and PSBS_B, both with phosphorylations on several Ser and Thr residues at the stromal exposed regions of the proteins (Figure 2D, paper II). PSBS has so far not been recognized as a thylakoid phosphoprotein, but it plays an essential role in the fast qE response mediated by the protonation two conserved lumenal Glu residues of PSBS (Li et al., 2000, 2004). The protonation of PSBS is suggested to induce a conformational change leading to its monomerization and activation (Bergantino et al., 2003; Correa-Galvis et al., 2016; Liguori et al., 2019). Interaction of active PSBS with the LHCII trimers is suggested to facilitate their aggregation, which in turn leads to efficient thermal energy dissipation within the LHCII trimer (Goral et al., 2012; Ruban, Johnson and Duffy, 2012; Ware et al., 2015; Nicol and Croce, 2021). The phosphorylation of PSBS (p-PSBS) in spruce might stabilize its active form and prolong its interaction with LHCII trimers.

This might explain the regaining of regulatory NPQ capacity measured as an increase in Y_{NPQ}, as p-PSBS decreased during the relaxation experiments (Figure 3C, paper II). Functionally, p-PSBS might lock LHCII trimers in their thermal dissipative state, converting the short term qE-type into sustained thermal energy dissipation, whereby the activity of PSBS would effectively become uncoupled from the lumen pH.

5.2.3 Potential kinase/phosphatase system regulating 3p-LHCII and p-PSBS

Hypothesized functions of 3p-LHCII and p-PSBS, as discussed above, would need to be regulated by a kinase/phosphatase system capable of operating at freezing temperatures, which still needs to be determined. At least for 3p-LHCII, it is conceivable that the N-terminal phosphorylated Thr residues would be the targets of STN7. Although the target specificity of the STN7 and STN8 kinases partially overlaps (Bonardi et al., 2005; Vainonen, Hansson and Vener, 2005; Leoni et al., 2013; Longoni, Samol and Goldschmidt-Clermont, 2019), STN7 activity would be in line with the observed light independence of 3p-LHCII (Figure 5, paper II) as both the activation and inhibition of STN7 is strongly redox regulated (Rintamäki et al., 2000). However, activity of STN7 in the dark would require stromal electron donation to the PQ-pool via chlororespiration (Peltier and Cournac, 2002; Nawrocki et al., 2015), since NDH1 is absent from spruce and other Pinaceae (Braukmann, Kuzmina and Stefanović, 2009; Ruhlman et al., 2015; Strand, D'Andrea and Bock, 2019), other enzymes would need to substitute its function, which so far have not been identified in land plants (Peltier, Aro and Shikanai, 2016).

It should also be noted, that 3p-LHCII, as well as LHCB1 and LHCB2 in other photosynthetic eukaryotes, contain not only N-terminal Thr phosphorylations, but also several additional phosphosites that do not seem to be phosphorylated by either STN7 or STN8 (Ingelsson and Vener, 2012), so that it seems plausible that 3p-LHCII and p-PSBS might be phosphorylated by other kinases. It could be speculated that these might be targeted by the TAK1 kinase, which has been shown to also phosphorylate LHCII and PSII proteins (Snyders and Kohorn, 1999, 2001), although more studies on TAK1 need to be conducted.

5.2.4 A theoretical model for the sustained thermal energy dissipation mechanism

Seasonal comparisons, including sustained and non-sustained NPQ conditions (Figure 4, paper II), showed that 3p-LHCII and p-PSBS in spruce thylakoids started to accumulate already when freezing temperatures had been reached (≤ -4°C), strongly suggesting that both 3p-LHCII and p-PSBS are important prerequisites for the engagement of sustained thermal energy dissipation.

It could be hypothesized, that early accumulation of 3p-LHCII and p-PSBS upon freezing temperatures represents an intermediate state, in which sustained thermal energy dissipation is not yet fully engaged (Figure 6B, paper II). In this state, 3p-LHCII would already initiate the repulsion of tightly packed grana thylakoids and eventually lead to destacking of appressed membranes, while p-PSBS only accumulates to small amounts. This easily reversible state is strongly dependent on

temperature but requires additional factors to trigger the sustained thermal energy dissipation.

These additional factors could include high light induced accumulation of zeaxanthin and damage of PSII by photoinhibition. A connection between zeaxanthin and PSII photoinhibition was recently found in multiple angiosperm species (Bethmann et al., 2019), where a concomitant inactivation/degradation of zeaxanthin epoxidase (ZE) and D1 after PSII photoinhibition prevented the reconversion of zeaxanthin to violaxanthin. Zeaxanthin content strongly correlates with sustained NPQ conditions in Pinaceae (Adams and Demmig-Adams, 1994; Verhoeven, Adams and Demmig-Adams, 1996; Ensminger et al., 2004; Verhoeven et al., 2009), while PSII photoinhibition and damaged PSII were clearly present during sustained NPQ conditions, as revealed by only partial recovery of F_v/F_m (Figure 3A, paper II) and the presence of RC-CP47 PSII repair cycle intermediate (Figure 2A-B, paper II). Assuming that a similar co-regulation between ZE and PSII photodamage exists also in spruce, this could likely explain the dependency of the sustained thermal energy dissipation on higher light intensities.

In this scenario, the intermediate state, triggered by freezing temperatures, would represent only a transition to the sustained state under high irradiances. These would induce the conversion of violaxanthin to zeaxanthin via VDE but also lead to PSII photoinhibition, which in turn leads to ZE inhibition and prevention zeaxanthin epoxidation. Zeaxanthin together with p-PSBS would enhance LHCII aggregation and convert the qE-type into sustained thermal energy dissipation, which would simultaneously become independent from lumen acidification, due to inhibited reconversion of zeaxanthin and proposed phosphorylation dependent stabilization of PSBS. Additionally, 3p-LHCII would further enhance the destacking of appressed membranes, which consequently would lead to a loss of lateral heterogeneity and increase the chance for PSI-spillover quenching. In this final state, sustained thermal energy dissipation would be fully engaged, in which quenched LHCII aggregates and PSII-PSI clusters, involved in PSI-spillover quenching, form two independent quenching sites (Figure 5).

Naturally, this hypothetical model would need to be thoroughly validated and the specific thylakoid protein phosphorylations, 3p-LHCII and p-PSBS, ultimately identified also in other species. Additionally, it should be kept in mind that this model might not be transferable to all boreal evergreen conifers, as the extend and recovery of sustained thermal energy dissipation is highly species dependent (Verhoeven, 2013; Míguez et al., 2015; Walter-McNeill et al., 2021).

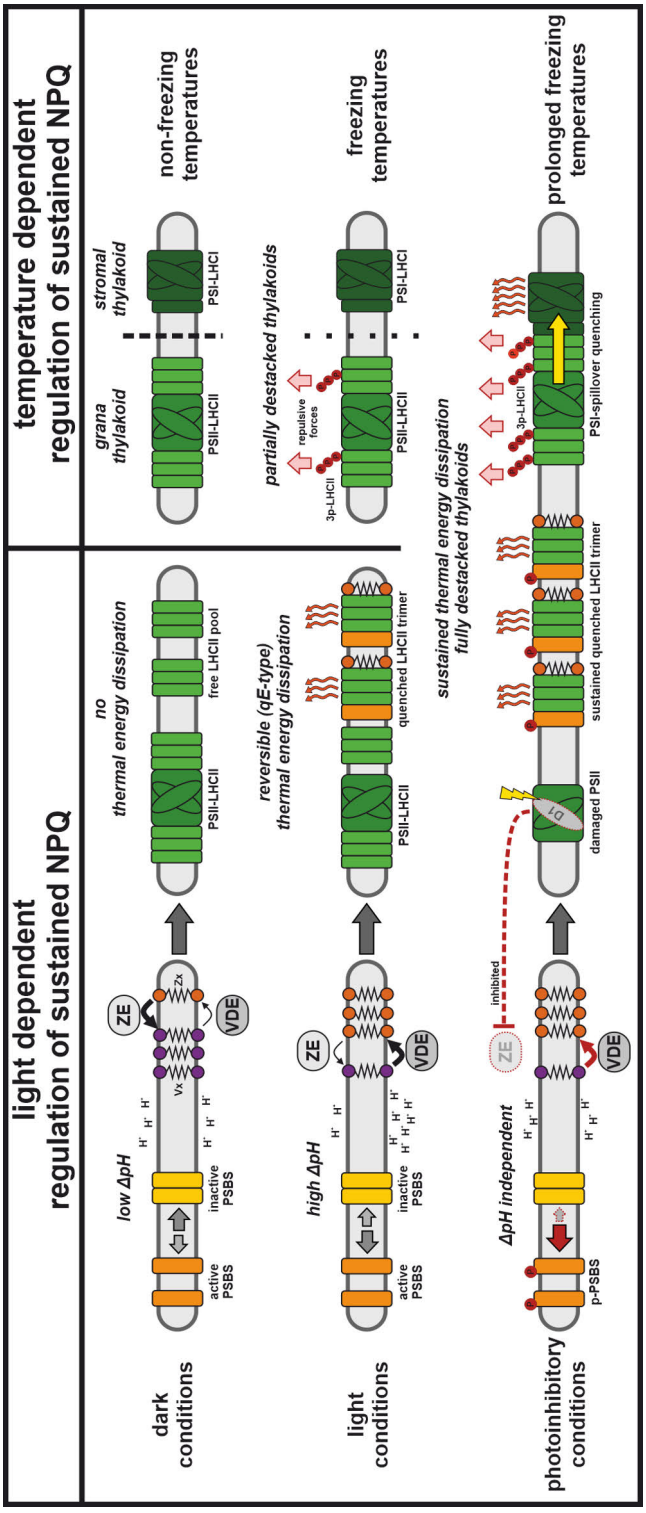
light dependent regulation of sustained NPQ
temperature dependent regulation of sustained NPQ
dark conditions
low ΔpH
active PSBS
inactive PSBS
Vx
Zx
ZE
VDE
no thermal energy dissipation
PSII-LHCII
free LHCII pool
grana thylakoid
stromal thylakoid
PSII-LHCII
PSI-LHCI
non-freezing temperatures
light conditions
high ΔpH
reversible (qE-type) thermal energy dissipation
quenched LHCII trimer
partially destacked thylakoids
repulsive forces
3p-LHCII
freezing temperatures
photoinhibitory conditions
ΔpH independent
p-PSBS
inhibited
D1
damaged PSII
sustained thermal energy dissipation fully destacked thylakoids
sustained quenched LHCII trimer
PSI-spillover quenching
prolonged freezing temperatures

Figure 5: Hypothetical model for the light (left) and temperature dependent regulation (right) of sustained thermal energy dissipation in Picea abies. Sustained thermal energy dissipation in Picea abies occurs only under combined light and temperature stress, leading to the formation of two quenching sites, aggregated LHCII trimers and PSI involved in spillover quenching, respectively.

The sustained thermal energy dissipation in aggregated LHCII trimers is light dependent, as it is built up from the qE-type mechanism. This requires light, leading to acidification of the lumen (high ΔpH) and triggering activation of PSBS and conversion of violaxanthin (Vx) to zeaxanthin (Zx) via the violaxanthin deepoxidase (VDE). According to the qE-type mechanism (Ruban, 2016; Kress and Jahns, 2017; Sacharz et al., 2017), PSBS and Zx facilitate aggregation of LHCII trimers followed by reversible thermal energy dissipation within LHCII. Under highlight conditions, which also lead to PSII damage (photoinhibitory conditions) this reversible qE-mechanism in Picea abies is suggested to become sustained. This is facilitated by inhibition of zeaxanthin epoxidase (ZE) during PSII photoinhibition (Bethmann et al., 2019), preventing the back reaction of Zx to Vx, and accumulation of p-PSBS, suggested to stabilize active PSBS. Under these conditions, both accumulation of Zx and p-PSBS would become ΔpH independent, thereby converting the reversible qE into sustained thermal energy dissipation.

The temperature dependent regulation leads to PSI-spillover quenching, facilitated by the light-independent triply phosphorylation of LHCII (3p-LHCII). Accumulation of 3p-LHCII at freezing temperatures likely leads already to partial destacking of thylakoids, inducing an intermediate state in Picea abies. However, only in combination with high light intensities, 3p-LHCII leads to complete destacking of thylakoids and loss of lateral heterogeneity of PSII and PSI, increasing the chance of PSI-spillover quenching. This enhances the sustained thermal energy dissipation in addition to the LHCII aggregates.

Possibly, low temperatures in combination to high irradiances also increase PSII photoinhibition and impair the PSII repair cycle, thereby further augmenting the accumulation of Zx. These proposed interconnected regulations of sustained thermal energy dissipation need to be further evaluated, but provide a novel framework for investigating the winter acclimation response in boreal evergreen conifers.

5.3 Spring recovery of photosynthesis in Pinaceae

Aside from sustained thermal energy dissipation, boreal evergreen conifers like pine and spruce show also much wider winter acclimation responses (Öquist and Huner, 2003; Chang et al., 2021), including the light reactions as well as CO_2 assimilation. Particularly during the photosynthetic recovery period in spring, these reactions show a complex interplay between short- and long-term responses (Kolari et al., 2014), and have been suggested to include upregulation of CEF (Ivanov et al., 2001; Fréchette et al., 2015; Yang et al., 2020).

Following the spring recovery of photosynthesis in pine and spruce trees from Feb to July 2017, both species showed expected overall recovery of CO_2 assimilation (Figure 3B, paper III) and maximal PSII activity (Figure 3C, paper III), in response to the gradual increase in prevailing temperatures (Kolari et al., 2014). However, maximal PSI activity clearly declined during late spring (Figure 3E, paper III) when PSII activity was already recovering, suggesting that PSI and PSII activities followed apparently contrasting seasonal patterns, indicating varying degrees of photodamage associated with photoinhibition during the seasonal course from late winter to the

summer. PSII activity decreased during partial induction of sustained thermal energy dissipation (Figure 3C-D, paper III) in response to the cold spells during winter and spring (Ensminger, Schmidt and Lloyd, 2008; Wallin et al., 2013). On the protein level, this was accompanied in both pine and spruce by a higher relative abundance of D1 compared CP47 PSII protein (Fig. 4A-B, paper III). This likely represented an accumulation of damaged D1 and pre-D1 proteins from an impaired PSII repair cycle during winter and spring, similar to observations in cold and light stressed cyanobacteria (Allakhverdiev and Murata, 2004; Mohanty, Allakhverdiev and Murata, 2007). This inhibition of the PSII repair cycle might avoid otherwise wasteful recovery of PSII with high ATP demands (Murata and Nishiyama, 2018; Yi et al., 2022) under continuous photoinhibitory conditions in both pine and spruce.

The decline in maximal PSI activity in late spring was accompanied by a continuous decrease of the PsaB protein levels in both species (Fig. 4A-B, paper III). Although *in vivo* P700 absorption measurements only access the maximal redox active fraction of PSI (ΔP_m) and not the total PSI content (Baker, Harbinson and Kramer, 2007), a decline in the total content, as observed on protein level, would naturally limit the maximal redox active fraction and therefore explains the decreased maximal PSI activity. This loss of active PSI was likely the result of PSI photoinhibition in pine and spruce, which was caused by acceptor side limitation leading to damage of the iron-sulfur clusters in PSI (Inoue, Sakurai and Hiyama, 1986; Sonoike et al., 1995; Tiwari et al., 2016).

5.3.1 Corrected PSI quantum yields account for temporal changes in ΔP_m

Since both pine and spruce showed clear signs of PSI photoinhibition at protein level (Fig. 4A-B, paper III) and *in vivo* (Figure 3E, paper III), corrected PSI quantum yields were derived. This was necessary, because the classical PSI quantum yields are based on the implicit assumption of constant ΔP_m (Klughammer and Schreiber, 1994, 2008), which can lead to a funnel effect (Fan et al., 2008), artificially overestimating the PSI yield parameters during PSI photoinhibition (Figure 2B, paper III, Zivcak et al., 2015).

This overestimation is rooted in the definition of the PSI quantum yields as relative subdivisions of the maximal redox active PSI fraction, ΔP_m, assuming to always approach unity (Klughammer and Schreiber, 2008). However, ΔP_m is simultaneously a relative measure of the maximal PSI activity and indicator for PSI photoinhibition (e.g. Havaux and Davaud, 1994; Ivanov et al., 1998; Sonoike, 1999; Kim et al., 2001; Zhang and Scheller, 2004; Sejima et al., 2014; Zivcak et al., 2015; Tikkanen and Grebe, 2018). This duality leads to a distortion of classical PSI

quantum yields, because the forced unity of the yields ignores differences of ΔP_m between samples.

To account for seasonally varying ΔP_m in pine and spruce, corrected PSI quantum yields (cY_I, cY_{ND}, cY_{NA}, Y_{loss}) were expressed relative to highest observed redox active PSI fraction per biological replicate (ΔP_{mR}). Here, the corrected PSI yields are an extension of the classical yields, in which the individual yields (cY_I, cY_{ND}, cY_{NA}) retain their original definitions (Klughammer and Schreiber, 2008) but are expressed relative to the same reference ΔP_{mR}. The newly defined Y_{loss} parameter quantifies the relative difference between ΔP_m and ΔP_{mR} (Figure 5A-B, paper III), but unlike other PSI quantum yields, cannot be associated with any redox state of PSI. Rather, it reflects a relative "loss" of the maximal redox active PSI fraction, which can be viewed as a non-photochemical "loss" of energy due to PSI photoinhibition in terms of PSI energy conversion.

Since corrected PSI quantum yields rely on quantitative comparisons of ΔP_m on the seasonal scale, also other factors affecting absorption measurements *in vivo* need to be considered. These include changes in the structural absorption properties of leaves, like changes in leaf thickness, which have been minimized by restricting measurements on mature needles, which have only limited capacity to reacclimate their photosynthetic tissue (Niinemets, 2007). Furthermore the P700 difference absorption signal also contains contributions of PC and Fd (Schansker et al., 2003; Klughammer and Schreiber, 2016), which might affect the comparisons of ΔP_m. However, since measurements were based on the difference absorption signal (870-830 nm), the plastocyanin contribution was greatly reduced and the remaining Fd contribution was neglectable (Klughammer and Schreiber, 1998). At last, ΔP_m comparisons depend on equal absorption measuring areas between samples, which are difficult to achieve with needle leaves, as each individual leaf is too small to cover the whole measuring area. Therefore, custom made needle adapters were used, which allowed measurements of tightly packed needle matts with minimal gaps size. Although this greatly increased comparability between samples, small errors based on different needle amounts cannot be fully be excluded.

5.3.2 Corrected PSI quantum yields do not support upregulation of CEF

Direct comparison of Y_I and cY_I in low (Figure 6A-B, paper III) and high light conditions (Figure 6C-D, paper III) exemplified the overestimation by uncorrected quantum yields, but also showed that cY_I had remarkable similarity to Y_{II} throughout the spring recovery.

Consequently, steady-state CEF estimations based on differences in relative electron transport rates between PSI and PSII (Harbinson, Genty and Baker, 1989;

Harbinson and Foyer, 1991) with cY_I (ΔcETR) showed no upregulation of CEF during spring in either species (Figure 6, paper III). Although, estimations with Y_I (ΔETR) are in line with previous reports of increased rates of CEF during spring, in particular in pine (Fréchette et al., 2015; Yang et al., 2020), the results strongly suggest that these are results of an calculation artifact caused by not correcting for the temporal dynamics in ΔP_m.

In addition to this calculation artifact, steady-state CEF estimations have several other technical caveats (Fan et al., 2016) that could explain the residual CEF observed in both pine and spruce. Since steady-state CEF is based on Y_{II} and Y_I measured by different *in vivo* spectroscopic techniques, residual CEF could be caused by probing different tissue depths of the leaf with fluorescence and difference absorption measurements (Oguchi et al., 2011). While absorption measurements probe the whole leaf depth, the fluorescence signal originates only from the top tissue layers (Vogelmann and Han, 2000; Vogelmann and Evans, 2002). Consequently, this causes Y_{II} based on fluorescence to be always underestimated compared to Y_I based on difference absorption (Kou et al., 2013), as the light gradient across the leaf will result in the top tissue always receiving more light compared to deeper layers (Terashima and Saeki, 1983; Vogelmann and Bjorn, 1984). This effect is more prominent in thicker needle leaves of boreal conifers (Johnson et al., 2005), but was counteracted by simultaneous actinic illumination from both ad- and abaxial surfaces during measurements. Furthermore, residual CEF could originate from PSI fluorescence, which causes Y_{II} to be underestimated compared to Y_I (Pfündel, 1998; Lazár, 2013; Pfündel et al., 2013). At last, it might be a result of the assumption of equal light distribution between both photosystems, so that small differences in the relative absorption cross-sections between PSII and PSI could readily explain the residual CEF in pine and spruce.

Although residual CEF might still be an overestimate, the overall similar cY_I and Y_{II} for both pine and spruce suggested that both species were capable to overall balance the light reactions of PSI and PSII throughout the seasons, which can be generally viewed as successful photosynthetic acclimation.

It still remains elusive, which processes directly contribute to this acclimation response, but high capacities for oxygen dependent AEF in boreal evergreen conifers (Savitch et al., 2010; Shirao et al., 2013), including FLV proteins (Ilík et al., 2017) might play an important role. Additionally, damage associated with photoinhibition of both photosystems might be equally relevant to restrict overall electron flow, especially when CO_2 assimilation capacities are restricted during spring. Although such regulatory function of photodamage might be wasteful, it could be necessary for the acclimation on the seasonal scale, especially for boreal evergreen conifers facing extreme environmental conditions.

In general, the proposed corrected PSI quantum yields might help to better investigate seasonal PSI dynamics, especially under PSI photoinhibitory conditions. In that regard it should be pointed out that there seems to be a large overlap in the literature between the environmental conditions in which PSI photoinhibition is likely to occur and CEF proposed to be upregulated. These include low temperatures (Ivanov et al., 1998; Sonoike, 1999; Huang, Zhang and Cao, 2011), low CO_2 (Harbinson and Foyer, 1991; Makino, Miyake and Yokota, 2002; Miyake et al., 2004, 2005), drought (Golding and Johnson, 2003) and high irradiances (Clarke and Johnson, 2001; Kou et al., 2013; Huang et al., 2015), which could potentially be affected by changes in ΔP_m causing artificial inflations of CEF.

6 Conclusion and Future Perspectives

The work in this thesis has provided new insights into the composition and regulation of the photosynthetic apparatus of the so far not yet in-detail characterized members of the gymnosperm family Pinaceae.

In paper I, the comparison of LHC protein distribution across a large selection of land plant species revealed the replacement of LHCB4 with LHCB8 in members of Pinaceae. Additionally, the buildup of a custom thylakoid protein database for MS/MS identifications allowed the comparison of the subunit composition of native thylakoid protein complexes in *Picea abies* at the same level as for the angiosperm model species *Arabidopsis thaliana*.

In paper II, the database was used to identify 3p-LHCII and p-PSBS as specific prerequisites for the engagement of the sustained thermal energy dissipation in *Picea abies*. This allowed the proposal of a comprehensive model of sustained thermal energy dissipation, highlighting different temperature and light requirements as well as the connection to ultrastructural changes of the thylakoid membrane and other short thermal energy dissipation mechanisms.

In paper III, it could be shown that the spring recovery of photosynthesis in *Picea abies* and *Pinus sylvestris* coincided with variable amounts of PSII and PSI photoinhibition. The latter required the formulation of new PSI quantum yields to accurately reflect the seasonal acclimation of PSI, which strongly suggested that previous reports of upregulation CEF in these species might be the result of an artifact caused by neglecting seasonal changes in ΔP_m.

Taken together, this work helps to expand the field of modern photosynthesis research beyond the currently dominant angiosperm Arabidopsis model and the most common agricultural crops like rice and maize. There is a desperate need for updating the thylakoid and leaf level photosynthesis models of various plant species, but especially of boreal evergreen conifers like Pinaceae. This would help in monitoring the wellbeing of boreal forests, evaluating their efficiency as carbon sinks and determining the proportion of forest trees available for sustainable bioeconomy. New advances in remote-sensing technologies (Porcar-Castell et al., 2021), generating with datasets beyond the leaf level ranging from canopies and

whole ecosystems, will now and in the future rely on new insights from the thylakoid and leaf level to better connect the different scales involved and describe photosynthesis across space and time.

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