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REVIEW

Photostasis and photosynthetic adaptation to polar life

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Abstract

Photostasis is the light-dependent maintenance of energy balance associated with cellular homeostasis in photoautotrophs. We review evidence that illustrates how photosynthetic adaptation in polar photoautrophs such as aquatic green algae, cyanobacteria, boreal conifers as well as terrestrial angiosperms exhibit an astonishing plasticity in structure and function of the photosynthetic apparatus. This plasticity contributes to the maintenance of photostasis, which is essential for the long-term survival in the seemingly inhospitable Antarctic and Arctic habitats. However, evidence indicates that polar photoautrophic species exhibit different functional solutions for the maintenance of photostasis. We suggest that this reflects, in part, the genetic diversity symbolized by inherent genetic redundancy characteristic of polar photoautotrophs which enhances their survival in a thermodynamically challenging environment.

Keywords Photostasis · Adaptation · Polar · Photoautrophs · Genomes · Redundancy

Abbreviations

AOX	Alternative oxidase
CBFs	Cold binding transcription factors
CEF	Cyclic electron flow around PSI
COX	Cytochrome oxidase
DPOR	Light-independent protochlorophyllide oxidoreductase
ETR	Electron transport rate
EEE	Excessive excitation energy
Φ_{PSII}	Effective quantum yield of PSII
Φ_{NPQ}	Quantum yield of regulated non-photochemical energy dissipation of PSII
Φ_{NO}	Quantum yield of non-regulated non-photochemical energy dissipation of PSII
F_v/F_m	Maximum photochemical efficiency of PSII in the dark-adapted state
LEF	Linear electron flow
LHCII	Light-harvesting chlorophyll a/b-protein complex of PSII
LHCI	Light-harvesting chlorophyll a/b-protein complex of PSI
LPOR	Light-dependent protochlorophyllide oxidoreductase
NPQ	Non-photochemical quenching
PAR	Photosynthetically active radiation
PETC	Photosynthetic electron transport chain
P700	Reaction center chlorophyll of PSI
$P700^+$	Oxidized form of PSI reaction center
PQ	Plastoquinone
PSI	Photosystem I
PSII	Photosystem II
PTOX	Plastid terminal oxidase
qP, qL	Photochemical quenching
Q_A, Q_B	Primary and secondary electron-accepting quinone in PSII
ROS	Reactive oxygen species

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Introduction

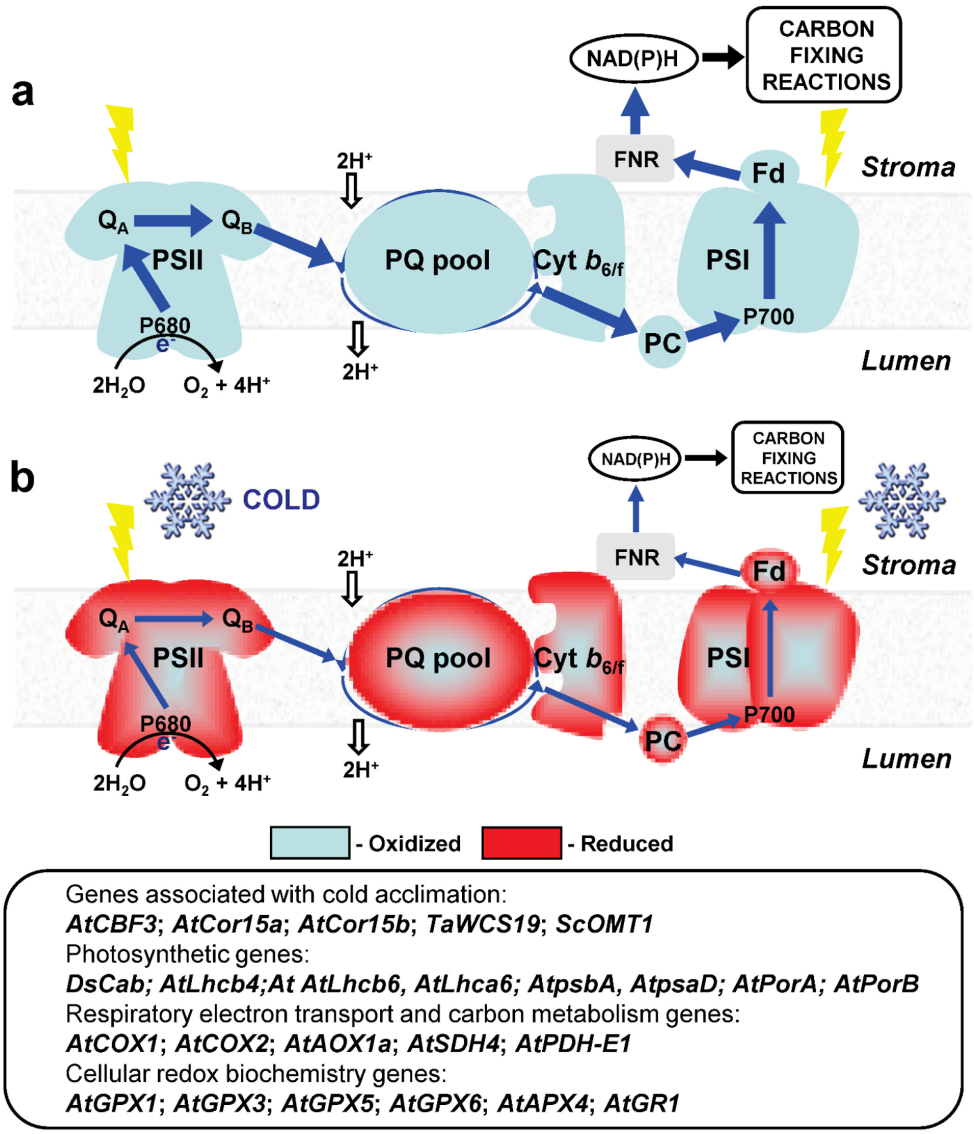
Structural and functional organization is a characteristic of all Life. Maintenance of this complex organization requires a constant throughput of free energy (G) from the environment into and through all living organisms to counteract the relentless tendency of this complex organization to decay into disorder over time according to the second law of thermodynamics resulting in the dissipation of free energy (G) as entropy (S). Life on Earth is an open system with the Sun as the primary external energy source harnessed by all prokaryotic and eukaryotic photoautrophs through the process of photosynthesis and stored as stable, energy-rich compounds that are subsequently transformed by the process of respiration and cellular metabolism to generate the free energy needed for growth, development, and reproduction (Arnon 1982). This constant flow of energy through biological organisms provides the driving force for the biosynthesis of essential metabolites, import and export of nutrients needed for growth, development, and reproduction to maintain structural and functional integrity needed for acclimation and adaptation to environmental change. This continuous flow of energy from the environment ensures that a living biological organism is never at equilibrium, that is, ΔG never equals zero. Living organisms remain far from equilibrium in a meta-stable, steady-state condition called homeostasis. Thus, living organisms can be considered transient, energy-transforming devices with finite, but varying lifetimes governed by the second law of thermodynamics (Nelson 2023).

Homoeostasis in plants and photosynthetic micro-organisms is light-dependent and hence is called *photostasis* (Melis 1998; Hüner et al. 2003). The tendency to shift the organism's photostasis is ceaseless due to inevitable environmental stresses associated with fluctuations in the surrounding abiotic environment, singly or in combination with respect to light quality and intensity, temperature, nutrient, and water availability. Such environmental stresses can shift the energy flow away from photostasis. Thus, any environmental change that impairs the maintenance of photostasis due to insufficient acclimation may be defined as an environmental stress (Körner et al. 2018; Demmig-Adams et al. 2022; Baker et al. 2022).

Since the environment is perpetually changing on an hourly, daily, weekly, monthly as well as on an annual basis, how do photosynthetic organisms sense abiotic stresses to which they are exposed over such a broad temporal scale? Abiotic stresses which shift photostasis can result in photoinhibition, that is, light-dependent inhibition of photosynthesis (Krause 1988; Baker 1991; Greer et al. 1991; Hüner et al. 1993; Krivosheeva et al. 1996), which has a photoprotective quality in overwintering evergreens that arrest growth for the winter season and dissipate all absorbed light via non-photochemical pathways (Őquist and Hüner 2003; Demmig-Adams and Adams 2006; Adams et al. 2018; Demmig-Adams et al. 2020).

Photostasis (Melis 1998; Hüner et al. 2003), the light-dependent homeostatic state in all photoautrophs, is the establishment of a balance between energy input in the form of sunlight absorbed and trapped through extremely rapid, temperature-insensitive photobiophysical and photochemical processes (Nelson 2023) versus the much slower, biochemical, temperature-sensitive metabolic sinks that either consume this energy for normal growth and development or dissipate any excess energy as heat (entropy) back into the environment through non-photochemical quenching processes (Φ_{NPQ}) that govern the process of photoprotection (Horton et al. 1996; Melis 1998; Hüner et al. 2003; Adams et al. 2004; Falkowski and Chen 2003; Ensminger et al. 2006; Demmig-Adams and Adams 2006; Foyer et al. 2012; Horton 2012). Low temperature-induced imbalances in energy flow between the photochemical source and the biochemical and developmental sinks that consume this energy modulates the redox state of the intersystem photosynthetic electron transport chain (PETC) (Fig. 1) which can be quantified in vivo using room temperature Chl fluorescence spectroscopy (Dietz et al. 1985; Schreiber et al. 1986; Krause and Weis 1991; Hüner et al. 1998; Krause and Jahns 2003; Kramer et al. 2004; Hendrickson et al. 2004; Baker 2008).

Oceans cover about 70% of the Earth's surface and the boreal forests of the northern hemisphere represent the largest terrestrial ecosystem on Earth. Since these extensive marine and terrestrial ecosystems are characterized by temperatures of 5 °C or less, Earth can be considered a rather cold place. The northern Arctic and southern Antarctic Oceans together constitute approximately 20% of the Earth's surface (Casanueva et al. 2010) while the northern boreal forests cover approximately 17% of the Earth's surface. The extreme environments of these aquatic and terrestrial polar regions offer opportunity to further elucidate the evolutionary basis for successful photosynthetic adaptation to polar life (Chown et al. 2015; Priscu et al. 1998; Bielewicz et al. 2011; Morgan-Kiss et al. 2006; Bakermans 2012; Yumoto 2013; Zakhia et al. 2008; Vincent 2000, 2007; Dolhi et al. 2013; Kennicutt II et al. 2014; Kennicutt et al. 2015; Xavier et al. 2016; Yin et al. 2023). In contrast to transient exposures to low temperature to induce cold acclimation of temperate plant species, persistent cold temperatures are a predominant characteristic of Antarctic and Arctic habitats. However, exposure to low temperature is coupled with variation in seasonal light intensities as well as predictable annual photoperiod. In addition, polar marine algae are exposed to variations in salt and nutrient levels



Genes associated with cold acclimation:
AtCBF3*; *AtCor15a*; *AtCor15b*; *TaWCS19*; *ScOMT1
Photosynthetic genes:
DsCab; AtLhcb4;At AtLhcb6, AtLhca6; AtpsbA, AtpsaD; AtPorA; AtPorB
Respiratory electron transport and carbon metabolism genes:
AtCOX1*; *AtCOX2*; *AtAOX1a*; *AtSDH4*; *AtPDH-E1
Cellular redox biochemistry genes:
AtGPX1*; *AtGPX3*; *AtGPX5*; *AtGPX6*; *AtAPX4*; *AtGR1

Fig. 1 Simplified overview of possible effects of cold stress on the redox state of the photosynthetic electron transport chain (PETC) components. (**a**) During growth and development of plants under optimal temperature conditions, the plastoquinone (PQ) pool and all components of the photosynthetic electron transport chain remain preferentially oxidized (light blue) because the rate of consumption of photosynthetic electrons through metabolic sinks (carbon fixing reactions) keeps pace with the rate at which PSII undergoes charge separation to reduce the PQ pool. Under these conditions, the linear photosynthetic electron flow (dark blue arrows) from PSII (water splitting) to PSI ($NADP^+$ generation) dominates and is fully operational; (**b**) Exposure of plants to cold stress results in lower demand for electrons required for carbon fixing reactions. Cold stress imposes thermodynamic limitations in the rates of consumption of photosynthetically-generated electrons by the carbon fixation reactions on the acceptor side of PSI which increases the reduction state of PQ pool and all components of the photosynthetic electron transport chain. Such a reduction state is quantified in vivo as excitation pressure using chlorophyll fluorescence induction. Excitation pressure reflects the relative redox state of Q_A, the first stable quinone electron acceptor in the PSII reaction centre. Under cold stress conditions (Fig. 1b), the linear photosynthetic electron flow between PSII and PSI is partially restricted relative to controls (Fig. 1a)

dependent on the specific aquatic habitat. Thus, the study of extant life forms ostensibly present in these Antarctic and Arctic ecosystems provides important insights into the evolution of populations of myriad photosynthetic species that have adapted to life at the edge (Kennicutt et al. 2014, 2015; Xavier et al. 2016; Yin et al. 2023).

The conversion of sunlight into biomass energy is the "magic of photosynthesis" on which all carbon-based life on Earth's surface is dependent (Arnon 1982). Photosynthetic adaptation in *Chlamydomonas priscuii* (Morgan-Kiss et al. 2006; Cvetkovska et al. 2022a; Hüner et al. 2022, 2023), provides important insights into the physiological, biochemical, and molecular mechanisms that underlie photosynthetic adaptation, photostasis and energy balance in polar photosychrophiles and psychrotolerant species. Organisms capable of cold acclimation are usually labelled as either eurythermic or stenothermic. The former can acclimate to and survive a wide range of temperatures whereas the latter are restricted to much narrower temperature range. In addition, psychrophilic micro-organisms are those adapted specifically to low temperature and die when exposed to warm temperatures. Below we focus on the role of photostasis in photosynthetic adaptation to polar life and discuss its general applicability to a polar photoautotrophic lifestyle in aquatic green algae, cyanobacteria as well as boreal conifers and extant terrestrial Antarctic angiosperms.

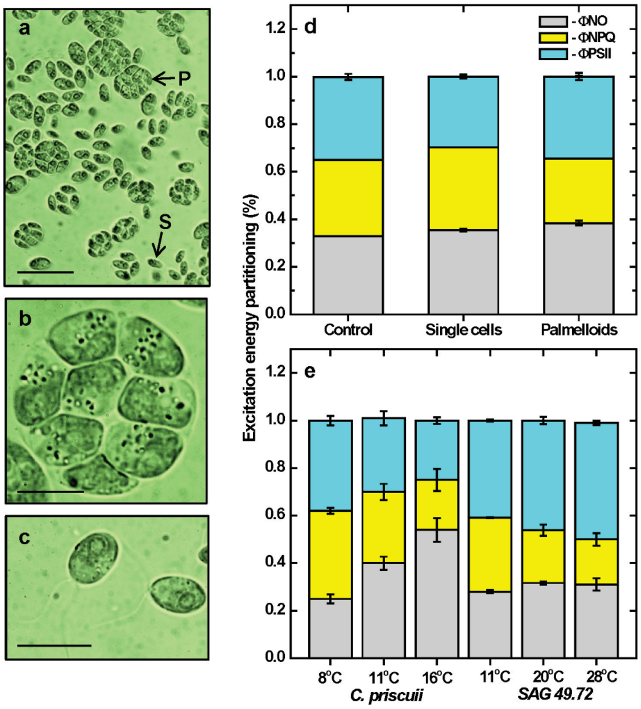


Fig. 2 **a.** Light microscope images of *Chlamydomonas priscuii* cultures grown at steady-state temperatures of 8 °C consisting of motile, flagellated single cells (S) and muticellular palmelloids (P) (100x). Isolated palmelloids (**b**) and single cells (**c**) fractions (1000x). **d** - Excitation energy partitioning in *C. priscuii* culture (Control) and isolated single cells and palmelloids fractions. Bars represent the relative yields of Φ_{NO} (non-regulated energy dissipation, gray), Φ_{NPQ} (ΔpH- and Zeaxanthin- dependent non-photochemical quenching, yellow) and Φ_{PSII} (efficiency of PSII, blue). **e** - Temperature dependence of excitation energy partitioning at PSII of both mesophilic (*C. priscuii*) and psychrophilic (*C. raudensis* SAG 49.79) strains. Cultures were grown at an irradiance of 150 µmol photons m^{-2} s^{-1} and the corresponding growth temperatures.
Modified from Szyszka et al. (2007)

Photostasis and adaptation to polar environments

Polar algae

Continental Antarctica represents one of the most unique and extreme environments on Earth. Although continental Antarctica is considered a polar desert essentially devoid of terrestrial life, surprisingly, life does exist here but localized in the perennially ice-covered, meromictic lakes of the McMurdo Dry Valleys such as Lake Bonney (Angino et al. 1964; Priscu et al. 1999). Minimal snowfall in the McMurdo Dry Valleys contribute to the desert conditions (Fountain et al. 2010). The combination of year-round liquid water in these meromictic lakes and sunlight as the energy source supports microbially dominated food webs within these lakes (Bowman et al. 2016). Sodium and magnesium chloride represent two principal salts that account for up to 96% of the dissolved salts in Lake Bonney (Angino et al. 1964; Spigell and Priscu 1996). Given the cold, dry desert conditions of the McMurdo Dry Valleys, the primary source of water and nutrients to these lakes is glacial meltwater (Dore and Priscu 2001). Although heterotrophic microbial eukaryotes represent the primary predators in ice-covered Lake Bonney, photosynthetic microbes such as *Chlamydomonas priscuii* are the primary producers that sustain this aqueous ecosystem (Priscu et al. 1999; Roberts et al. 2004).

The photopsychrophile, *Chlamydomonas priscuii*, was isolated 17 m below the ice of perennially ice covered Lake Bonney, Antarctica located in Taylor Dry Valley (Priscu et al. 1998; Morgan-Kiss et al. 2006). This green alga exhibits maximum light- and CO_2-saturated rates of O_2 evolution at its optimum growth temperature (8–12 °C) that are comparable to the optimum rates of photosynthesis in *C. reinhardtii* measured at its optimal growth temperature of 28 °C (Pocock et al. 2007). Furthermore, the light response curves for the relative redox state of the intersystem photosynthetic electron transport chain, measured as either 1-qP (Schreiber 1986) or 1-qL (Kramer et al. 2004), are comparable for *C. priscuii* and the mesophiles *C. reinhardtii* and *C. raudensis* SAG49.72 when measured at their optimal growth temperatures (Szyszka et al. 2007), which would be expected based on the above-described comparable apparent rates of photosynthetic electron flow. Thus, the photopsychrophile maintains a similar energy balance as that observed for the photomesophiles, even though they experience drastically different thermodynamic constraints. This, in part, reflects an upregulation of photosynthetic capacity, including Calvin cycle enzymes (Berry and Björkman 1980) and enzymes involved in sugar metabolism. However, the regulation of energy partitioning to maintain photostasis in the photopsychrophile differs significantly from the mesophiles (Szyszka et al. 2007). In *C. priscuii*, constitutive, non-regulated non-photochemical energy dissipation (Φ_{NO}) predominates whereas the mesophiles exhibit non-photochemical energy dissipation through xanthophyll cycle-dependent processes (Φ_{NPQ}) (Fig. 2d and e) (Szyszka et al. 2007). Furthermore, examination of the primary metabolome and transcriptome of *C. priscuii* grown at permissive, low temperature conditions indicates that this photopsychrophile constitutively accumulates metabolites and proteins normally considered markers of acclimation in *C. reinhardtii*, including soluble sugars, antioxidants, polyamines, and heat shock proteins which ensure proper protein folding at low temperatures (Cvetkovska et al. 2022b). We suggest that these characteristic features of energy partitioning and the metabolome in *C. priscuii* compared to those of the mesophiles can be accounted for, in part, by the significant genetic redundancy reported for *C. priscuii* (Zhang et al. 2021) as well as the other photopsychrophiles such as *Chlamydomonas* ICE-L (Zhang et al. 2020) and the diatom, *Fragilariopsis cylindrus* (Mock et al. 2017). The superior stress tolerance of diatoms typically involves close energetic coupling of chloroplasts and mitochondria with unusual plastid transporters (Liu at al. 2022), allowing facile transfer of reduction equivalents to mitochondria for dissipation in alternative electron flow routes (Bailleul et al. 2015; Prihoda et al. 2012). It has been also reported that the morphological plasticity and the constitutive protection of thylakoid membranes allows the Antarctic alga, *Prasiola antarctica*, to survive and thrive in contrasting harsh environments (Arzac et al. 2024). We suggest that the genetic redundancy translates into significant plasticity in the structure, function and organization of the photosynthetic apparatus of *C. priscuii* relative to the model green alga, *C. reinhardtii* (Szyszka-Mroz et al. 2015, 2019; Cvetkovska et al. 2018, 2019; Kalra et al. 2020, 2023). This can be detected in vivo by low temperature (77 K) fluorescence emission spectroscopy combined with in vitro separation of the major thylakoid pigment-protein complexes (Szyszka-Mroz et al. 2019). *C. priscuii* consistently exhibits an unusual 77 K chlorophyll fluorescence emission spectrum characterized by prominent emission bands between 680 and 685 nm associated with LHCII and PSII core complexes but lacks the prominent PSI emission band at 715 nm even though PSI is present and functional in this psychrophile (Morgan et al. 1998; Morgan-Kiss et al. 2005; Szyszka-Mroz et al. 2007; Szyszka-Mroz et al. 2019; Szyszka-Mroz et al. 2015; Cook et al. 2019; Kalra et al. 2020). Structurally, this novel 77 K fluorescence emission spectrum is associated with the presence of a PSI-Cyt$_{b6/f}$ supercomplex that appears to be important in the regulation of PSI cyclic electron flow (CEF) (Szyszka-Mroz et al. 2015; Kalra et al. 2020). In addition, the distribution of PSI-LHCI and PSII-LHCII pigment-protein complexes within thylakoid membranes of *C. priscuii* is significantly altered based on digitonin fractionation and immunoblot analyses (Szyszka-Mroz et al. 2019). Although the Arctic photopsychrophile, *Chlamydomonas malina*, exhibits comparable 77 K emission spectra to that of the Antarctic psychrophile, *C. priscuii* (Hüner et al. 2020), not all photopsychrophiles exhibit this characteristic 77 K Chl fluorescence emission spectrum (Kalra et al. 2020, 2023).

The capacity to perform state transitions is regarded as essential for successful photoacclimation to a fluctuating light environment for all known green algae and terrestrial plants. This process is regulated by reversible LHCII protein phosphorylation governed by the thylakoid membrane protein kinases, Stt7 and Stl1, in *C. reinhardtii* and by STN7 and STN8, in *A. thaliana* (Rochaix 2014; Wunder et al. 2013) which sense and respond to the reduction state of the intersystem PETC (Allen et al. 1981; Oxborough et al. 1987; Allen 1992; Bennett 1991; Zer and Ohad 2003). Enhanced reduction of the intersystem PETC at low temperature (Fig. 1) should induce phosphorylation of a mobile population of LHCII which subsequently disengages from PSII coupled to its subsequent migration to become physically associated with PSI. Thus, normally state transitions in plants and green algae govern the energy distribution between PSII and PSI in a co-ordinated manner under fluctuating light conditions to maximize rates of photosynthetic electron transport. However, a unique feature of *C. priscuii* is that it lacks the capacity to perform state transitions (Morgan-Kiss et al. 2002; Kalra et al. 2023). Since it has been shown that psychrophilic *Chlorella sp*. strain BI as well as *Chlamydomonas sp.* ICE-MVD do undergo short-term state transitions (Morgan-Kiss et al. 2008; Kalra et al. 2023), it appears that the maintenance of the capacity to perform short-term state transitions is not essential for the survival of photopsychrophiles in Lake Bonney. Furthermore, the capacity to perform short-term state transitions is not a prerequisite for photopsychrophily in eukaryotic algae in general. This may reflect, in part, the very different habitats and ecosystems occupied by *C. priscuii*, *Chlorella sp*. strain BI and *Chlamydomonas sp.* ICE-MVD.

Despite its lack of state transitions, *C. priscuii* contains *Stt7* and *Stl1* at the genome (Zhang et al. 2021) as well as at protein level, and therefore, is able to regulate thylakoid protein phosphorylation (Szyszka-Mroz et al. 2019). The level of membrane protein phosphorylation in *C. priscuii* is highest at 5 °C but inhibited at 25 °C consistent with its adaptation to low temperature (Szyszka-Mroz et al. 2019). The low temperature-dependence of this protein kinase is associated with alterations in the kinase domain of Stt7 in *C. priscuii* which is interpreted to reflect the predisposition of this protein kinase to function maximally at low temperature as well as its minimal sensitivity to staurosporine, a known protein kinase inhibitor (Szyszka-Mroz et al. 2019). In addition to phosphorylation of the complement of PSII light harvesting polypeptides, *C. priscuii* exhibits unique phosphorylation sites including specific subunits of the PSI-$Cyt_{b6/f}$ supercomplex. Functionally, the phosphorylation status of the PSI-$Cyt_{b6/f}$ supercomplexes combined with a high salt requirement governs the stability and the rates of CEF in *C. priscuii* (Szyszka-Mroz et al. 2019; Kalra et al. 2020, 2023). We suggest that thylakoid protein phosphorylation in *C. priscuii* may regulate thylakoid membrane reorganization as reflected in the distribution PSII, PSI and $Cyt_{b6/f}$ complexes coupled with a marked energy quenching capacity (Szyszka et al. 2007; Szyszka-Mroz et al. 2019). Rather than state transitions, we hypothesize that thylakoid protein phosphorylation status in the photopsychrophile regulates a proposed PSII-PSI spillover quenching mechanism similar to the spillover-mediated PSI-dependent energy quenching reported in cold acclimated pine (Bag et al. 2020), Arabidopsis (Velitchkova et al. 2020) and other organisms exposed to harsh environmental conditions (Slavov et al. 2013, 2016). Furthermore, Hepworth et al. (2021) suggest that the PSI-supercomplexes observed in *C. reinhardtii* (Takahashi et al. 2013; Iwai et al. 2010)C. *priscuii* (Szyszka-Mroz et al. 2019; Kalra et al. 2020, 2023) may govern the ratio of CEF/LEF in green algae.

General models of plant thylakoid membranes describe lateral heterogeneity with asymmetric distributions of PSII and PSI supercomplexes, with PSII largely localized to the granal stacked regions and PSI associated with granal margins and stromal lamellae (Anderson and Andersson 1982; Anderson et al. 1995; Anderson 1986, 2012). However, PSI and PSII can also be found physically associated with one another in mega-PSI-PSII- pigment protein complexes (Järvi et al. 2011; Yokono et al. 2015; Gao et al. 2019; Kim et al. 2023; Ifuku 2023; Yokono et al. 2024) that increase the propensity for energy spillover from PSII to PSI.

Thus, energy spillover represents a mechanism whereby PSI quenches EEE associated with PSII, thereby presumably protecting PSII (Ifuku 2023; Yokono et al. 2024). Based on digitonin fractionation of thylakoid membranes, we reported that isolated thylakoids from *C. priscuii* exhibit a significant alteration in the distribution of PSI and PSII pigment-protein complexes between grana and stromal lamellae that is associated with altered protein phosphorylation patterns (Szyzska-Mroz et al. 2019) compared to the model photomesophile, *C. reinhardtii*. Since the photopsychrophile exhibits minimal capacity for state transitions, we suggest that these changes in thylakoid organization and distribution of PSI and PSII supercomplexes in *C. priscuii* may regulate photosystem energy partitioning and quenching of EEE via PSII-PSI energy spillover and may, in part, account for the absence of state transitions in *C. priscuii*. This hypothesis requires validation through the isolation of PSI-PSII megacomplexes from *C. priscuii*. Recently, we have indeed detected the presence of PSI-PSII megacomplexes in *C. priscuii* (Szyszka-Mroz, Ivanov, Hüner, unpublished).

In addition to adaptation to low temperature and constant low light levels in Lake Bonney during austral summer, *C. priscuii* is also adapted to 6 months of darkness during austral winter. Although *C. priscuii* exhibits a shade-adapted state, it maintains normal Chl levels even during the extended dark austral winter months (Morgan-Kiss et al. 2006, 2015) despite lacking DPOR, the light-independent protochlorophyllide oxidoreductase important in Chl biosynthesis in the dark (Reinbothe and Reinbothe 1996). However, two other duplicated genes, *GUN4* and *CAO* that govern Chl biosynthesis and retrograde signalling (Chory and Wu 2001; Nott et al. 2006; Tanaka and Tanaka 2007) are present in the genome of *C. priscuii*. Therefore, it appears that *C. priscuii* has a functional Chl biosynthetic pathway that is dependent exclusively on LPOR, the "light-dependent" Chl oxidoreductase and has lost DPOR even though this alga is exposed to prolonged annual seasonal darkness. This may be due to the fact that at 17 m below the bottom of the ice cover, *C. priscuii* in Lake Bonney remains photosynthetically active in a light environment of less than 1% of incident photosynthetically active radiation (PAR) combined with extremely high O_2 concentrations (Morgan-Kiss et al. 2006). Unlike LPOR, DPOR is very sensitive to O_2 concentrations due to an essential Fe-S cluster in its active site. Thus, we propose that the evolutionary elimination of DPOR from *C. priscuii* did not adversely affect this photopsychrophile (Cvetkovska et al. 2019). To validate this hypothesis with respect O_2 concentrations and absence of DPOR, more phototrophs from Lake Bonney must be examined. Furthermore, the mechanism by which *C. priscuii* maintains normal Chl levels during the extended dark period of austral winter has yet to be elucidated.

C. priscuii cultured under continuous PAR of 100 µmol photons m^{-2} s^{-1} at low, permissive temperatures (4–10 °C) generally exhibit 20% non-motile palmelloid colonies that appear to be a collection of 2 to 16 single cells enclosed within a membrane (Szyszka-Mroz et al. 2022) (Fig. 2a, b, c). However, 77 K fluorescence emission spectra of isolated *C. priscuii* single cells versus isolated colonial palmelloids (Szyszka-Mroz et al. 2022) indicate significant changes in pigment and polypeptide compositions and the organization of PSII and PSI as well as their functional interactions (Krause and Weis 1991; Baker 2008; Swoczyna et al. 2022). Thus, the transition from single cells to colonial palmelloids appears to reorganize PSI and PSII pigment-protein complexes (Szyszka-Mroz et al. 2022), although maximum PSII photochemical efficiency, measured as F_v/F_m, is comparable for isolated single cells and isolated palmelloids (Szyszka-Mroz et al. 2022). Functionally, palmelloids exhibit a lower reduction state of the intersystem electron transport chain as a function of light intensity compared to single cells, which is associated with an increased capacity to dissipate EEE in palmelloids compared to single cells and with a decreased sensitivity of photosynthetic electron transport to high light (Szyszka-Mroz et al. 2022). The decreased sensitivity to high light was, in part, associated with higher non-regulated dissipation of EEE (Φ_{NO}) (Fig. 2d and e) presumably through PSII reaction centre quenching (Szyszka-Mroz et al. 2007; Ivanov et al. 2008; Zavafer et al. 2019; Rautenberger and Hurd 2024) and/or PSII-PSI spillover-mediated PSI(P700$^+$) excess energy quenching (Szyszka-Mroz et al. 2019; Bag et al. 2020) rather than normal antenna quenching (Φ_{NPQ}) via the xanthophyll cycle (Adams and Demmig-Adams 1993; Hüner et al. 2003; Verhoeven 2014; Demmig-Adams et al. 2020). Surprisingly, free, single cells are morphologically and functionally distinct from the single cells enclosed within a colonial palmelloid. The molecular mechanism underlying the observed alterations in the organization of the photosynthetic apparatus in response to the transition of free single cells to colonial palmelloids remains to be elucidated.

Polar terrestrial plants

Bryophytes

The Antarctic is a cold, inhospitable desert (Robinson et al. 2003). Mosses, liverworts (Bryophytes) and lichens dominate the landscape of this polar desert. Visible PAR radiation provides the energy necessary for photosynthesis in these bryophytes but, just as important, infrared radiation provides heat for the compact moss beds as well as lichens located beneath these moss beds (Yin et al. 2023). The morphological characteristic of Antarctic mosses allows them to dramatically alter the microclimate within their dense beds such that the canopy temperature can exceed the ambient air temperatures by an astonishing 10 °C when exposed to the high light of the austral summer season. Their remarkable morphology adapted to the Antarctic habitat counters the limitations imposed by the extreme low temperatures and allows these mosses to optimize growth and photosynthetic rates and maximize biomass productivity during the short austral summer season to ensure their continued, long-term survival under the harsh Antarctic conditions (Pannewitz et al. 2005).

Like other terrestrial plants and aquatic green algae, Antarctic bryophytes and lichens accumulate carotenoids to protect their photosynthetic apparatus under a combination of low temperatures and high light by dissipating the excess light energy not utilized by photosynthesis during the austral summer (Yin et al. 2023). Consequently, reversible photoinhibition occurs during the inevitable freeze-thaw cycles under high light and either low or warm temperatures characteristic of the moss beds (Lovelock et al. 1995). During the long austral winter, bryophytes and liverworts are covered in snow and ice and adopt a shade phenotype characterized by decreased photosynthetic rates combined with high chlorophyll levels (Post and Vesk 1992) like that observed for the aquatic Antarctic algal psychrophile, *C. priscuii* (Hüner et al. 2022, 2023).

Arctic boreal conifers

The developmental strategy of deciduous trees is to normally drop their leaves annually during the fall and winter seasons and to enter a dormant, overwintering state. A benefit of this strategy is that it circumvents any need to protect the photosynthetic apparatus from freezing stress and photoinhibition during the late fall and winter months. However, the cost, is that deciduous trees must allocate substantial energy reserves in the warmer spring to resume growth with the production of new leaves. In contrast, conifers evolved an evergreen developmental strategy to generate long-lived needles which allows them to retain their needles year-round. A benefit of this strategy is that it allows these species to circumvent the annual requirement to allocate substantial energy reserves to the development of new needles in the spring and that the overwintering needles are quickly reactivated to resume photosynthetic carbon gain when soils thaw. This allows evergreen confers in subalpine forests to take in 90% of their annual carbon gain during the first month after soil water thaws and snowmelt water is available, while deciduous trees growing nearby are still regrowing their leaves (Monson et al. 2002). This evergreen strategy of photosynthetic shut-down when growth is arrested in the winter requires replacement of the PSII reaction center protein, D1, and the oxygen-evolving complex in the spring for rapid resumption of full photosynthetic activity (Zarter et al. 2006; Demmig-Adams et al. 2006). This developmental strategy protects the photosynthetic apparatus from photodamage during the freezing and low temperatures of the winter and early spring seasons (Őquist and Hüner 2003).

Common coniferous species within the Arctic and subarctic boreal forest of the northern hemisphere include black and white spruce, balsam fir, Jackpine and tamarack. Although photosynthesis is down regulated during the winter in conifers, their needles remain green, and thus, absorb light even though the capacity to utilize this absorbed energy is minimal. This results in a drastic imbalance in energy flow prior to sufficient acclimation. However, to survive, boreal species have evolved various mechanisms to circumvent this drastic imbalance in energy flow to maintain photostasis (Őquist and Hüner 2003; Bag et al. 2023).

The mechanisms employed by overwintering evergreen conifers to protect the photosynthetic apparatus from EEE either singly and/or in combination include two forms of sustained regulated non-photochemical energy dissipation associated with either lasting ΔpH-dependent or ΔpH-independent mechanisms both associated with overnight zeaxanthin retention (Verhoeven et al. 1998; Ebbert et al. 2005; Demmig-Adams and Adams 2006; Malnoë 2018; Liu et al. 2024) (Fig. 3a). Non-regulated non-photochemical quenching (Φ_{NO}) through PSII reaction centre quenching has been also suggested as an effective, and in some cases, a predominant mechanism for excess energy dissipation in overwintering and cold-acclimated conifer species (Ivanov et al. 2002, 2003, 2008; Sveshnikov et al. 2006; Savitch et al. 2010) (Fig. 3A). In addition, photosystem I (PSI) non-photochemical quenching (PSI-NPQ) via oxidized P700 ($P700^+$) (Schlodder et al. 2005), occurring when PSII is excitonically coupled with PSI (spillover) and associated with a major structural reorganization of the photosynthetic apparatus has been recently identified as a major energy-dissipating mechanism in overwintering conifers (Bag et al. 2020). The well established much-reduced or even disappearance of grana in overwintering conifers (Martin and Öquist 1979; Demmig-Adams et al. 2015; Bag et al. 2020) allowing homogenous distibution and intermixing of PSII and PSI chlorophyll-protein complexes is a prerequisite for the efficient “spillover”-assisted PSI-dependent EEE quenching in conifers (Bag et al. 2020). These energy-dissipation processes are integrated with up-regulation of the PSI-driven cyclic electron flow (CEF) (Ivanov et al. 2001; Bag et al. 2020; Yang et al. 2020) and re-routing excess electrons to oxygen-reducing, alternative pathways involving the plastid terminal oxidase (PTOX) (Savitch et al. 2010; Busch et al. 2008) and/or flavodiiron proteins (Bag et al. 2023) (Fig. 3b). However, the activation of needle photosynthesis in the spring is preceded by the activation of photosynthesis in specific cortical bark chlorenchyma cells, which leads to the activation of needle mesophyll photosynthesis (Ivanov et al. 2006).

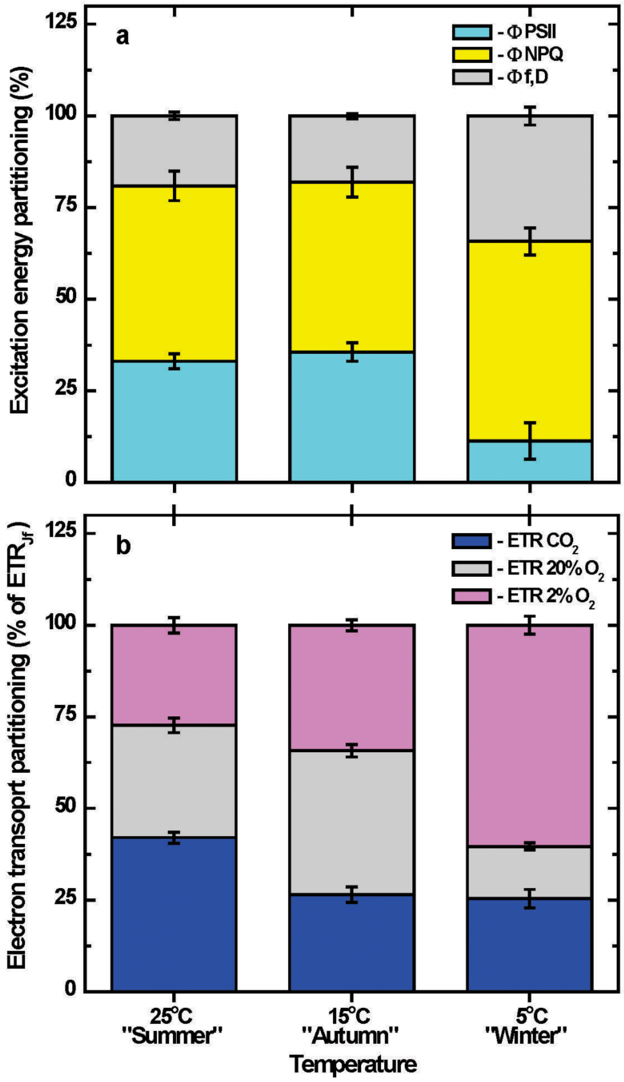


Fig. 3 Schematic representation of the effects of growth temperatures on energy and electron transport partitioning in second year needles of Lodgepole pine (*Pinus contorta* L.). **a** - Relative excitation energy partitioning to PSII, estimated as yield of PSII (Φ_{PSII}), versus regulated non-photochemical quenching (NPQ), estimated as yield of NPQ (Φ_{NPQ}) as well as non-regulated, non-photochemical quenching, estimated as $\Phi_{f,\,D}$ (Hendrickson et al. 2004). **b** - Partitioning of photosynthetic linear electron transport into carbon assimilation (ETR CO_2) in the presence of either 21 kPa or 2 kPa O_2 (**b**) in needles of Lodgepole pine from experimentally induced “Summer” (25 °C), “Autumn” (15 °C) and “Winter” (5 °C) growth conditions under a saturated PFD and ambient $p(CO_2)$ and $p(O_2)$ conditions. Partitioning of photosynthetic linear electron transport is expressed as a percentage of ETR_{Jf}. Original data were presented in Savitch et al. (2010). All measurements were performed at 1,000 PFD, 35 Pa CO_2, either at 21 kPa or at 2 kPa O_2 and a temperature of either 25 °C for ‘“Summer”, 15 °C for ‘“Autumn” or 5°C for “Winter”, pine needles, respectively

Angiosperms

Deschampsia antarctica and *Colobanthus quitensis* are the only known extant flowering plants adapted to the Antarctic terrestrial environment (Bravo et al. 2001, 2007; Pérez-Torres et al. 2004; Ramírez et al. 2024; Yin et al. 2023). The mechanisms that underlie plant cold acclimation and freezing tolerance have been studied and discussed extensively in crop plants and *Arabidopsis thaliana* (Steponkus 1984; Guy 1999; Thomashow 1999, 2010; Wang et al. 2024; Baker et al. 2022; Demmig-Adams et al. 2022). Unlike terrestrial angiosperms adapted to warmer, temperate climates capable of acclimation to transient and time-limited exposures to cold temperatures, Antarctic flowering plants must grow and reproduce under continuous cold and freezing temperatures characteristic for their extreme environment. The accumulation of cryoprotective proteins, such as antifreeze proteins and dehydrins combined with the accumulation of soluble sugars such as sucrose, raffinose and fructans that are osmoprotective, prevent damage due to intracellular freeze dehydration and prevent intracellular ice crystal formation (Ramírez et al. 2024). In addition, cold binding transcription factors (CBFs) have been established as important integrators of chloroplast redox, phytochrome and plant hormone signaling during cold acclimation (Kurepin et al. 2013; Baker et al. 2022) and a network of CBFs appears also to be critical in governing the extent of freezing resistance in these terrestrial Antarctic plants (Ramírez et al. 2024).

Photosynthetically, both Antarctic species (*D. antarctica* and *C. quitensis*) exhibit an active and resilient CO_2 assimilation process allowing them to maintain about 30% of their maximum photosynthetic rates at 0°C relative to that measured in plants grown at their optimum growth temperature between 10°C and 19°C (Ramírez et al. 2024). For *C. quitensis*, net photosynthesis appears to be complemented by a process called "alarm photosynthesis", whereby the CO_2 that is assimilated intracellularly originates from the decomposition of calcium oxalate crystals due to oxalate oxidase activity in the leaves rather than from external CO_2 (Ramírez et al. 2024). It has been suggested that this alternative mechanism may represent a complementary mechanism to enhance carbon supply in response to internal CO_2 limitations due to leaf anatomical constraints (Ramírez et al. 2024).

Enhanced respiration rates have been reported in plants in response to cold acclimation (Guy 1990; Thomashow 1999, 2010; Atkin and Tjoelker 2003; Armstrong et al. 2008). It is well-characterized that cold stress commonly suppresses plant growth through alterations in the levels of growth hormones and stress hormones (Kurepin et al. 2015; Eremina et al. 2016). The plant mitochondrial electron transport chain has two terminal electron acceptors: the normal cytochrome oxidase (COX) and an alternative oxidase (AOX) (Vanlerberghe and MacIntosh 1997; Chadee et al. 2021). The AOX pathway is considered a dissipation pathway that prevents over-reduction of the mitochondrial respiratory electron transport chain due to accumulation of excess electrons. The plastid terminal oxidase (PTOX) has a similar role in modulating the reduction state of PETC of the chloroplast through the process of chlororespiration (McDonald et al. 2011). Thus, AOX and PTOX activity regulate the level of reactive oxidative species (ROS) and may, consequently, protect Antarctic plants from oxidative stress. This is coupled with the activation of Φ_{NPQ} in the chloroplast to dissipate the absorption of EEE through regulated non-photochemical quenching as well as the induction of photorespiration and chlororespiration to consume excess energy to protect the photosynthetic apparatus (Ramirez et al. 2024). Thus, polar terrestrial plants and marine algae possess mechanisms to maintain photostasis and cellular energy balance to allow these photoautotrophs to develop, grow and persist in their cold polar environments.

Conclusions

Access to energy is essential for life regardless of the habitat. We suggest that long-term survival and adaptation to cold, extreme polar environments is due to functional processes that mediate photostasis to maintain energy flow and a thermodynamic energy balance in aquatic polar algae and cyanobacteria as well as terrestrial boreal conifers, Antarctic lichens, bryophytes and angiosperms. However, the mechanisms described to maintain photostasis are not unique to polar photoautrophs but reflect acclimation and adaptation in photoautotrophs exposed to extreme environments in general. Those photosynthetic features novel in *Chlamydomonas priscuii* adapted to its unique Antarctic environment include: (1) the absence of functional state transitions which is supplemented by PSII-PSI energy spillover; (2) a "stay green phenotype" in the absence of DPOR despite exposure to the prolonged Antarctic darkness; (3) the predisposal to favour non-regulated dissipation of EEE (Φ_{NO}) through reaction center quenching and energy spillover between PSII and PSI rather than regulated non-photochemical quenching (Φ_{NPQ}) and (4) the role colony formation of palmelloids in photoprotection from EEE. Consequently, it is the most functionally and structurally stable photosynthetic apparatus that is selected for by evolution within changing environments. We suggest that such "dynamic persistence" is a consequence of the significant evolutionary "possibility space" (Wong et al. 2023) available within the redundant genome of organisms adapted to polar environments. However, one must be careful not to bestow foresight onto evolutionary processes (Doolittle and Brunet 2017). Indeed, it is now widely accepted that most of the processes influencing genome size, particularly the amount of noncoding DNA within a genome - i.e., its "possibility space" - are the product of nonadaptive processes (Lynch 2007), namely mutation and random genetic drift. Moreover, there is no reason to assume that the diversity of genomic architectures, molecular/cellular make-ups, and associated physiologies observed across plants and algae in polar environments are not at least in part the consequence of neutral, nonadaptive mechanisms (Lynch 2007). In fact, one may argue that psychrophilic species are not "adapted" to the cold, but rather, are "un-adapted" to warmer climates. Nevertheless, polar phototrophs have a lot to teach us about evolution.

The astonishing plasticity exhibited by cold tolerant algae and terrestrial plants reflects the different solutions, that is, the diverse functions encompassed within the possibility space provided by the genome. Although different environments will require different functional solutions to ensure survival, the maintenance of photostasis to ensure dynamic energy flow is central to survival of all organisms irrespective of the environment they inhabit. Thus, thermodynamic energy balance encompassed in photostasis is essential in adaptation and acclimation to extreme polar environments. It is processes, such as photostasis, that encapsulate complex gene networks that are selected for by evolution. Therefore, it is the dynamic persistence of these essential processes that is the driving force for evolution! This is why genomics by itself rarely provides the answer to adaptation to extreme environments. The possibility space (the total information encapsulated in the genome) is a consequence of the fact that life remains far from equilibrium (Wong et al. 2023). Governance of the dissipation of free energy as entropy over time during the ultimate path to equilibrium as dictated by the 2nd law of thermodynamics is the driving force for acclimation and adaptation not only to polar life but all life on this planet.

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