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Humboldt Review

Photosynthetic adaptation to polar life: Energy balance, photoprotection and genetic redundancy

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ABSTRACT

The persistent low temperature that characterize polar habitats combined with the requirement for light for all photoautotrophs creates a conundrum. The absorption of too much light at low temperature can cause an energy imbalance that decreases photosynthetic performance that has a negative impact on growth and can affect long-term survival. The goal of this review is to survey the mechanism(s) by which polar photoautotrophs maintain cellular energy balance, that is, photostasis to overcome the potential for cellular energy imbalance in their low temperature environments. Photopsychrophiles are photosynthetic organisms that are obligately adapted to low temperature (0°- 15 °C) but usually die at higher temperatures (≥20 °C). In contrast, photopsychrotolerant species can usually tolerate and survive a broad range of temperatures (5°- 40 °C). First, we summarize the basic concepts of excess excitation energy, energy balance, photoprotection and photostasis and their importance to survival in polar habitats. Second, we compare the photoprotective mechanisms that underlie photostasis and survival in aquatic cyanobacteria and green algae as well as terrestrial Antarctic and Arctic plants. We show that polar photopsychrophilic and photopsychrotolerant organisms attain energy balance at low temperature either through a regulated reduction in the efficiency of light absorption or through enhanced capacity to consume photosynthetic electrons by the induction of O_2 as an alternative electron acceptor. Finally, we compare the published genomes of three photopsychrophilic and one photopsychrotolerant alga with five mesophilic green algae including the model green alga, *Chlamydomonas reinhardtii.* We relate our genomic analyses to photoprotective mechanisms that contribute to the potential attainment of photostasis. Finally, we discuss how the observed genomic redundancy in photopsychrophilic genomes may confer energy balance, photoprotection and resilience to their harsh polar environment. Primary production in aquatic, Antarctic and Arctic environments is dependent on diverse algal and cyanobacterial communities. Although mosses and lichens dominate the Antarctic terrestrial landscape, only two extant angiosperms exist in the Antarctic. The identification of a single 'molecular key' to unravel adaptation of photopsychrophily and photopsychrotolerance remains elusive. Since these photoautotrophs represent excellent biomarkers to assess the impact of global warming on polar ecosystems, increased study of these polar photoautotrophs remains essential.

1. Introduction

A surprise to many people is the fact that Earth can generally be considered a cold place. Oceans cover about 70% of the Earth's surface with temperatures ≤5 °C, the north and south polar regions of the Arctic and Antarctic respectively together constitute approximately 20%, and

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Abbreviations

AFP	anti-freeze proteins
C	carbon
CBB	Calvin-Benson-Bassham cycle
CEF	photosystem I cyclic electron flow
C-169	Antarctic isolate of *Coccomyxa subellipsoidea*
Chl	chlorophyll
chlL, *chlN*, *chlB*	genes involved in Chl biosynthesis
Cytb6f	cytochrome b6/f complex
dN/dS	nonsynonymous to synonymous substitution rates
DPOR	light-independent protochlorophyllide oxidoreductase
EEE	excessive excitation energy
E_k	the light intensity at which the rate of photosynthetic electron transport matches the turnover of the electron sinks
Fd	ferredoxin
HGT	horizontal gene transfer
HSDs	highly similar gene duplicates
IBPs	ice-binding proteins
ICE-L, ICE- MVD, ICE-W,	isolates of the Antarctic psychrophile *Chlamydomonas sp.* ICE
ITS	internal transcribed spacer DNA
LEF	linear electron flow
LHCI	light harvesting complex associated with photosystem I
LHCII	light harvesting complex associated with photosystem II
Lhca	polypeptide of the family of light harvesting proteins associated with LHCI
Lhcb	polypeptide of the family of light harvesting proteins associated with LHCII
LPOR	light-dependent protochlorophyllide oxidoreductase
n	the number metabolic sinks that consume photosynthetic electrons
N	nitrogen
NPQ	nonphotocheimical quenching
petA	gene encoding cytochrome f
PETC	photosynthetic electron transport chain
petF	gene encoding the major form of ferredoxin; pmf; proton motive force
PQ	plasoquinone
PQH_2	plastoquinol
PSI	photosystem I
PSII	photosystem II
PsaN	gene encoding the N-subunit of photosystem I
psbA	gene encoding the D1 photosystem II reaction centre polypeptide;
Psb-P,	subunit of the photosystem I-cytochrome b6f supercomplex
rbcL,	gene encoding the large subunit of Rubisco
RCC2488	isolate of the Arctic psychrophile, *Chlamydomonas sp.*
RCC2488	ROS, reactive oxygen species
S	sulfur
SAG49.72	strain of *Chlamydomonas raudensis*
σ_{PSII}	the absorptive cross section of photosystem II
Stt7, *Stl1*	genes encoding thylakoid protein kinases in *Chlamydomonas reinhardtii*
STN7, *STN8*	genes encoding thylakoid protein kinases in *Arabidopsis thaliana*
SDS-PAGE	sodium dodecylsulfate polyacrylamide gel electrophoresis
τ	the turnover of electron sinks
TE	transposable elements
UWO241	isolate of the Antarctic psychrophile, *Chlamydomonas sp.* UWO241

finally, the mountainous, alpine regions of Asia, Europe, North and South America constitute another 5% of the Earth's surface (Casanueva et al., 2010). The extreme environments of the terrestrial and aquatic habitats in polar regions provide an exceptional opportunity to explore the basis of adaptation to extreme environments (Chown et al., 2015; Priscu et al., 1998; Bielewicz et al., 2011; Morgan-Kiss, 2006; Bakermans, 2012; Yumoto, 2013; Zakhia et al., 2008; Vincent, 2000, 2007; Dolhi et al., 2013; Kennicutt et al. 2014, 2015; Xavier et al., 2016).

Although persistent low temperature is a predominate characteristic of Antarctic and Arctic environments, this may be coupled with predictable variation in light intensities and annual photoperiod as well as altered salt and nutrient levels depending on the specific polar habitat. The combination of extreme low temperature combined with variations in light can result in the absorption of light that exceeds the capacity of photosynthesis to utilize this energy (Ort, 2001). This results in cellular energy imbalances that can limit photosynthetic performance, growth and survival (Hüner et al. 1998, 2003, 2016; Kramer and Evans, 2011). Adaptation of photoautotrophs to a polar environment must compensate for the potential energy imbalances experienced by living in a low temperature environment. Thus, non-model biological species endemic to natural, seemingly inhospitable Antarctic and Arctic ecosystems allows one to preview the evolution of individuals and populations that have survived and adapted to life under these extreme conditions (Kennicutt et al. 2014, 2015; Xavier et al., 2016; Grossman, 2021). Primary production in perpetually cold Antarctic and Arctic environments is largely dependent on aquatic, micro- and macroalgae that inhabit diverse aquatic habitats that include the water column below perennially ice-covered lakes such as Lake Bonney, Antarctica (Bielewicz et al., 2011; Morgan-Kiss et al., 2006; Priscu et al., 1998; Chrismas et al., 2015), meltwater pools of the McMurdo ice shelf (Sutherland et al., 2020), sea ice (Arrigo, 1997; Thomas and Dieckmann, 2002; Liu et al., 2006; Zhang et al., 2019), coastal waters (Wiencke and Hop, 2016) and snowfields (Rogers, 2007; Morgan-Kiss et al., 2006; Zhang et al., 2019). Species diversity of these aquatic photoautotrophs is rich and includes rotifers, ciliates, phytoplankton, bacteria, and viruses (Bielewicz et al., 2011; Morgan-Kiss et al., 2006; Priscu et al., 1998). Despite the diversity of aquatic protists and micro-organisms, they represent some of the least studied organisms in one of the most important ecosystems on Earth (Kennicutt, 2014, 2015; Xavier, 2016; Priscu, 1998; Rogers, 2007; Bielewicz, 2011; Morgan-Kiss et al., 2006; Cvetkovska et al., 2017). In contrast to the biodiversity of aquatic organisms, the diversity of terrestrial polar plant populations is more restricted and dominated by mosses and lichens (Chown et al., 2015). There are only two angiosperms endemic to the Antarctic peninsula, *Colobanthus quitensis* (Kunth) Bartl., a dicot (Supplementary Fig. 1A) and *Deschampsia antarctica* Desv., a monocot (Supplementary Fig. 1B) (Bravo et al., 2001; Bravo and Griffith, 2005).

Psychrophiles are obligately adapted to cold climates and usually have optimal growth temperatures of $\leq$15 °C and typically do not survive temperatures exceeding 18°- 20 °C (Morita, 1975). Heterotrophic psychrophiles include the Bacteria and Archeae as well as eukaryotic species such as yeast and fungi. Photospychrophiles, a term first introduced by Morgan-Kiss et al. (2008), are distinguishable from all heterotrophic psychrophiles by their dependence on the process of photosynthesis and their use sunlight as their external energy source. In contrast to photopsychrophiles, organisms that exhibit maximum growth rates at $\geq$ 20 °C but can also acclimate, grow and survive at low temperatures (0°–5 °C) are considered to be cold tolerant, that is, either psychrotolerant (Morita, 1975) or photopsychrotolerant. However, other terms frequently found in the cold tolerance literature associated

with macroalgae, invertebrates and fish include 'stenotherm' and 'eurytherm' (Bligh and Johnson, 1973). The former represents organisms that can grow and survive only over a narrow temperature range in contrast to eurythermal organisms that exhibit growth and survival over a broad temperature range. Based on these definitions, psychrophiles and photopsychrophiles are stenotherms while psychrotolerant and photopsychrotolerant organisms are eurytherms. A more detailed discussion of this issue can be found in the recent review by Cvetkovska et al. (2017).

The study of organisms from extreme polar environments gives us a glimpse of the phenotypic plasticity, and hence the resilience, that is possible due to long-term evolution under extreme environments. A goal of this review is to illustrate how the study of non-model, polar, aquatic and terrestrial photosynthetic species, in contrast to model photoautotrophs such as *Chlamydomonas reinhardtii* and *Arabidopsis thaliana,* provide evidence of what is not only biologically feasible but also biologically possible through the slow but inexorable process of evolution in polar environments. For example, using a video camera that provided access to the surface of a boulder located more than 1 km below the surface of the Antarctic Filchner Ice Shelf, Griffiths et al. (2021), discovered a benthic community of apparently filter-feeding organisms including sponges. Incredibly, this sessile community was estimated to be between 624 and 1500 km from the nearest photosynthetic region! (Griffiths et al., 2021). Furthermore, *Planococcus halocryophilus* strain Or1, a bacterium isolated from the Arctic permafrost, has been reported to grow and survive at the lowest temperature (−15 °C) of any biological organism to date and remains metabolically active at temperatures as low as −25 °C while frozen in permafrost (Mykytczuk et al., 2013). Clearly, the polar regions continue to provide surprising examples of what is evolutionarily possible for life at the edge (Jackson et al., 2021; Sommers et al., 2017). Thus, research on cold adapted polar species can provide unprecedented insights into the evolution and adaptation over the past 100M years to harsh, extreme environments (Rogers, 2007). More important, these polar habitats exhibit the greatest global warming due to climate change. Thus, the status and biodiversity of these polar species are excellent biological markers for the assessment of the impacts of global warming associated with climate change (Gooseff et al., 2017; Obryk et al., 2016; Neukermans et al., 2018; Terrado et al., 2013).

The second law of thermodynamics dictates that a constant flux of energy from the environment is an absolute requirement to sustain life on Earth by maximizing available free energy while minimizing entropy (Schroedinger, 1947; Atkins, 2010; England, 2020). Thus, Schroedinger (1947) concluded that life in general may be defined as 'negative entropy'. Photosynthesis is the process that provides access to a relatively constant and reliable external energy source in the form of sunlight, either directly, in the case of photoautotrophs, or indirectly for all other forms of heterotrophic life on our planet through their diet of photosynthetic organisms (Nelson, 2011). The goals of this review are to, first, summarize the basic concepts of energy balance and photostasis; second, to compare the photoprotective mechanisms that underlie the attainment of energy balance (Hüner et al. 1998, 2003; Petrou et al. 2010, 2011; Kramer and Evans, 2011) and survival in aquatic cyanobacteria and green algae as well as terrestrial Antarctic (mosses, lichens and angiosperms) and Arctic plants (angiosperms and conifers); third, to compare the published genomes of 3 photosychrophilic and one photopsychrotolerant species with 5 mesophilic species including the model green alga, *Chlamydomonas reinhardtii*, to gain insights into evidence for adaptation at the genomic level. We suggest that the attainment of photostasis through photoprotective mechanisms combined with genomic redundancy may confer resilience to the harsh polar environment.

2. Photostasis and energy balance

The oxygenic, photoautotrophic lifestyle of cyanobacteria and chloroplasts of green algae and terrestrial plants absorb light by the photosynthetic pigments bound to light harvesting pigment-protein complexes. Subsequently, energy is transferred to photosystem I (PSI) and photosystem II (PSII) reaction centres where photochemical oxidation of P700 and P680 respectively convert the absorbed energy into electrons (see legend to Fig. 1 for details). The light harvesting complexes present in the thylakoid membranes of cyanobacteria are rod-like structures called phycobilisomes and are localized on the surfaces of the thylakoid membranes (Fig. 1A). Chloroplasts of green algae and terrestrial plants originated through successive rounds of endosymbiosis resulting in the fusion of a cyanobacterium and a eukaryotic heterotrophic host to produce the first photoautotrophic eukaryotic cell (Sagan, 1967; Gray, 2017). In contrast to cyanobacteria, the light harvesting complexes (LHCII and LHCI) of chloroplasts are integral thylakoid membrane pigment-protein complexes (Fig. 1B).

The very rapid, temperature-insensitive photobiophysical processes of light absorption and energy transfer associated with the light harvesting complexes coupled to the photochemistry associated with PSI and PSII reaction centres are integrated with the much slower and highly temperature-sensitive, redox reactions associated with the intersystem photosynthetic electron transport chain (PETC) and the soluble enzymes of the Calvin-Benson-Bassham Cycle (CBB) which utilize the photosynthetic reductant, NADPH, and ATP to reduce C, N and S required either for energy storage or for growth, development and reproduction (see legend Fig. 1 for details). Thus, a major challenge for all photoautotrophs endemic to the polar regions is to balance the energy flux of absorbed photons from the Sun with the energy consumed (NADPH and ATP) through enzyme-catalyzed metabolism for growth, development and reproduction in an extremely inhospitable, and thermodynamically challenging environment (Hüner et al. 1998, 2003; Petrou et al. 2010, 2011; Kramer and Evans, 2011). The maintenance of such cellular energy balance in photoautotrophs is called photostasis (Melis, 1998; Hüner et al., 2003; Hollis and Hüner, 2014). Falkowski and co-workers (Durnford and Falkowski, 1997; Falkowski and Chen, 2003) have shown that the following relationship (equation (1)) reflects the balance between energy acquired through the rapid photobiophysical and photochemical processes versus energy consumed through slower, photosynthetic and respiratory carbon metabolism:

$$(\sigma_{PSII})\ (E_k) = n\ (\tau^{-1}) \quad (1)$$

where σ_{PSII} is the absorptive cross section of PSII, n is the number metabolic sinks that consume photosynthetic electrons, τ^{-1} is the turnover of these electron sinks and E_k is the light intensity at which the rate of photosynthetic electron transport matches the turnover of the metabolic electron sinks (see legend to Fig. 2 for details). Consequently, exposure to low temperature can mimic the effects of high light exposure such that either condition can lead to absorbed excitation energy that exceeds the requirement for photosynthetic CO_2 assimilation (Hüner et al. 1998, 2003) Exposure to excessive excitation energy (EEE) (Karpinski et al., 1999) will result in an imbalance in energy flux such that

$$(\sigma_{PSII})\ (E_k) > n\ (\tau^{-1}) \quad (2)$$

Such an imbalance can be detected as an increase in excitation pressure measured as the relative reduction state of the PETC (Ensminger et al., 2006; Hüner et al., 2003). As discussed in detail below, the maintenance of photostasis may involve the regulation of energy transfer from light harvesting complexes to reaction centers, the regulation of electron flow through linear (LEF) versus cyclic electron pathways (CEF) or the use of alternative electron acceptors such as O_2 rather than CO_2 (Fig. 1A and B). In addition to the regulation of photochemistry itself, mechanisms have evolved that govern the partitioning of energy between photochemical versus nonphotochemical pathways (Fig. 2). Nonphotochemical pathways dissipate EEE safely as heat either via the PSII light harvesting antenna or via PSII reaction centers (Fig. 2). This affects σ_{PSII} either through adjustments in the

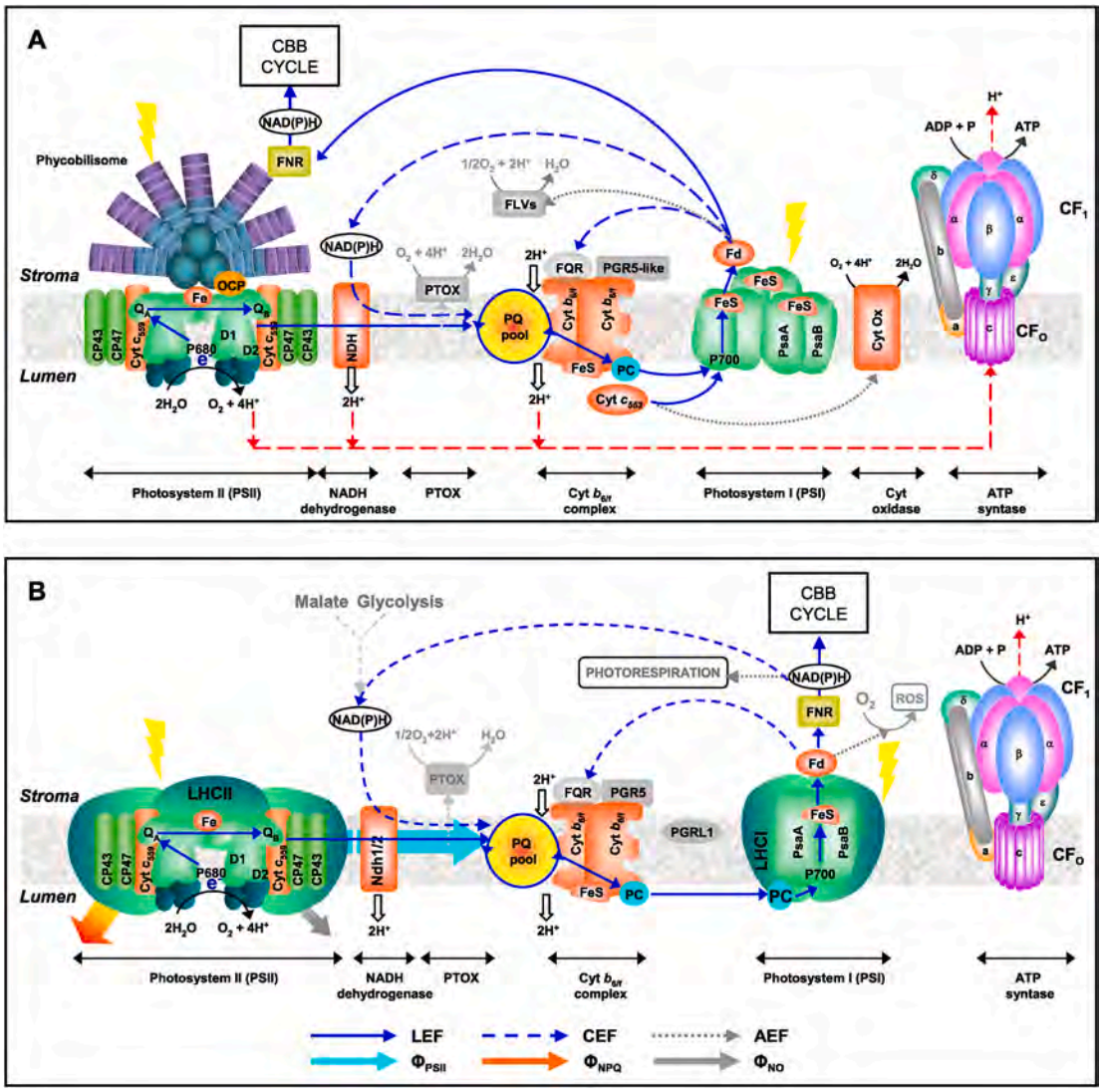


Fig. 1. Schematic representations of linear photosynthetic electron flow (LEF), PSIdriven cyclic electron flow (CEF) and alternative electron flow (AEF) pathways in cyanobacteria (A) and higher plants/green algae (B) thylakoid membranes. During growth and development under optimal conditions the plastoquinone (PQ) pool remains preferentially oxidized because the rate of consumption of photosynthetic electrons through major metabolic sinks such as carbon fixing reactions in the Calvin–Benson–Bassham (CBB) cycle, as well as, N and S reduction keeps pace with the rate at which PSII undergoes charge separation to reduce the PQ pool. In cyanobacteria and chloroplasts, PSI and PSII are linked in series by an intersystem photosynthetic electron transport chain (PETC) consisting of coupled redox carriers, plastoquinone (PQ), the cytochrome b6/f complex and plastocyanin (PC), all localized within the plane of the thylakoid membrane (Fig. 1A and B). Co-ordination of these events results in the production of the strongest oxidizing agent in nature associated with PSII (P680+) with the concomitant production of O2 and the strongest reducing agent in nature (reduced Fd) as a consequence of the photooxidation of P700 to P700+ and the storage of reductant in the form of NADPH coupled to the generation of a proton motive force (pmf) which the chloroplast ATPase converts into ATP (Hopkins and Huner, 2009). The photosynthetic reductant and ATP are consumed in CO2 fixation by the Calvin-Benson-Bassham cycle (Fig. 1). Under normal conditions, linear photosynthetic electron flow (LEF, dark blue solid arrows) from PSII (water splitting) to PSI (NADP + generation) dominates, although additional PSI cyclic electron flow (CEF, blue dashed lines) and alternative electron transport pathways (gray dashed arrows) may also be induced. When under various environmental stress conditions such as low temperature, the rate of electron consumption governed by the metabolic sink capacity of the CBB-cycle may be insufficient to consume all of the photochemically-generated electrons. Consequently, the excess photosynthetic electrons are diverted at ferredoxin (Fd) serving as the major electron distribution hub, and re-circulated by NDH and FQR-dependent PSI-driven CEFs and/or safely utilized through oxygen-dependent electron sinks by PTOX- and/or FLVs-alternative electron pathways. Regulation of the circulation of electron flow contributes to the protection of the photosynthetic apparatus from photodamage due to exposure to excess excitation energy (EEE). PSII, photosystem II; PSI, photosystem I; PQ, plastoquinone pool; Cytb6/f; cytochrome b6/f complex; PTOX, plastid terminal oxidase; PC, plastocyanin; Cyt oxidase; cytochrome oxidase; Fd, ferredoxin; NDH, NADPH dehydrogenase; FNR, ferredoxin-NADP + reductase; FLVs, flavodiuron proteins.

physical size of the light harvesting complexes through photosynthetic redox regulation of the expression and accumulation of light harvesting polypeptides in photosynthetic eukaryotes or the polypeptides of the phycobilisomes of cyanobacteria. Alternatively, the *functional size* of the light harvesting complexes can be adjusted by the induction of the xanthophyll cycle in plants and green algae which enhances the safe dissipation of EEE as heat through nonphotochemical quenching processes (NPQ) (Demmig-Adams and Adams, 1996; Horton and Ruban, 2005) (Fig. 2). The cost of these photoprotective mechanisms is decreased photosynthetic efficiency. The benefits include enhanced probability of survival usually associated with an impressive phenotypic plasticity as a consequence of the changes in pigmentation associated with short-term acclimation and long-term adaptation of photosynthetic organisms to EEE (Hüner et al. 1998, 2003, 2016; Ensminger et al., 2006; Verhoeven, 2014). Thus, regulation of photochemistry through electron flow (Fig. 1A and B) as well as energy partitioning (Fig. 2) help

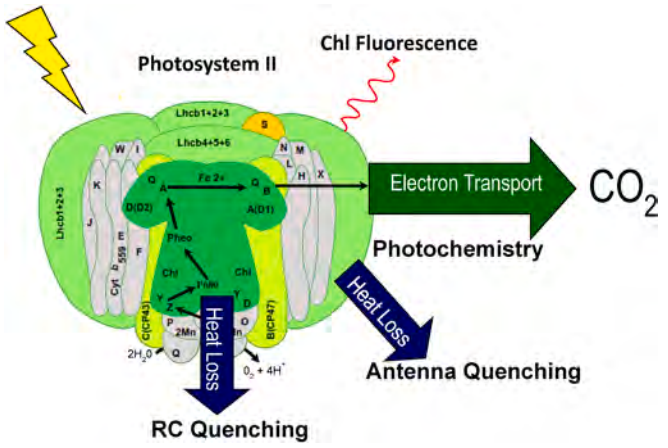


Fig. 2. A model of PSII illustrating the possible fates of absorbed light energy. In vivo Chla fluorescence (red arrow) is a powerful research tool to assess the fates of light energy in the process of photosynthesis (Schreiber et al., 1986; Maxwell and Johnson, 2000; Krause and Weis, 1991; Kramer et al., 2004; Hendrickson et al., 2004; Baker, 2008). At room temperature, the major site from which room temperature Chl fluorescence emanates is PSII as illustrated in Fig. 2. PSII is a multi-subunit pigment-protein complex. PSII Chla-binding reaction center polypeptides include D1 and D2 that bind the P680 Chla reaction centre Chl. The family of light harvesting polypeptides in bright green include Lhcb1, 2, 3,4,5 and 6. The oxygen evolving complex polypeptides (grey) on the lumen side of the thylakoid membrane. Polypeptides B (CP47), C (CP43), BE, F, H, I, J, K, L, M, N, and X represent the PSII core complex. Light is initially absorbed by the light harvest complex and the energy transferred to the PSII reaction centre. This induces PSII reaction center photochemistry resulting in the oxidation of P680 to P680+ + e. The electron (e) is subsequently transferred via Pheo, QA, QB, to the thylakoid plastoquinone pool and the intersystem electron transport chain (see Fig. 1B) and ultimately consumed in the reduction of CO2 by the stromal Calvin-Benson-Bassham Cycle (see Fig. 1B). In turn, P680+ is reduced back to P680 through the oxygen evolving complex situated on the lumen side which oxidizes water and releases O2 plus protons that contribute to the thylakoid proton gradient for the biosynthesis of ATP (see Fig. 1B).

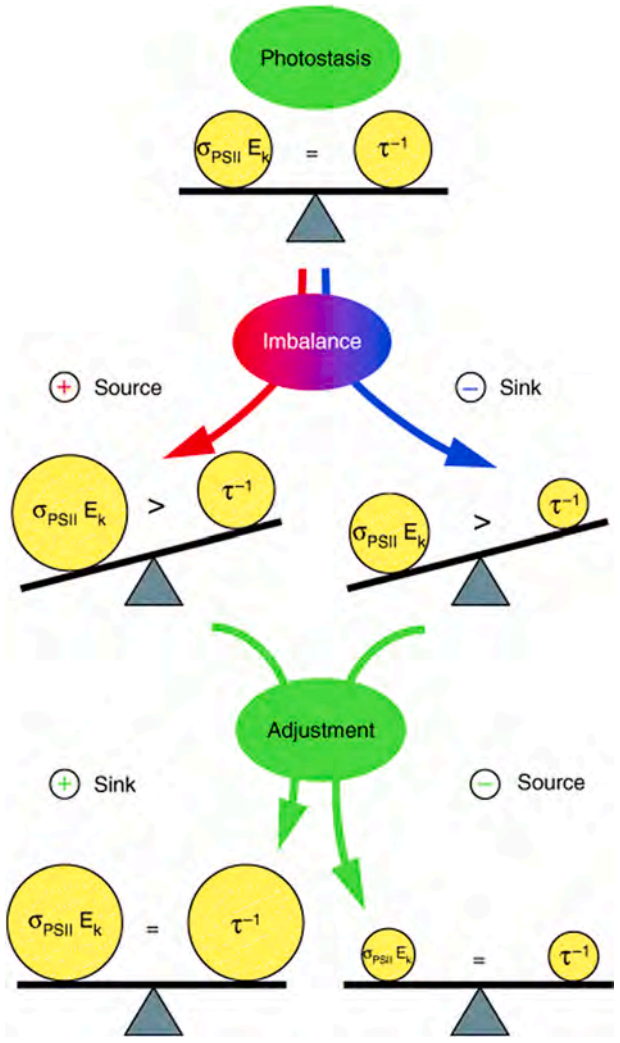


Fig. 3. Schematic illustration of the concept of photostasis and energy balance. Photostasis is achieved through the balance of energy flow from sources to sinks where σPSII is the effective absorption cross-section of PSII, Ek is the irradiance (I) at which the maximum photosynthetic quantum yield balances photosynthetic capacity (estimated from a photosynthetic light response curve) and τ-1 is the rate at which photosynthetic electrons are consumed by a terminal electron acceptor such as CO2 under light-saturated conditions. An imbalance between energy absorbed versus energy utilized will occur whenever the rate at which the energy absorbed through PSII and the rate at which electrons are injected into photosynthetic electron transport exceeds the rate of temperature-dependent metabolism (that is, whenever σPSII x Ek > n τ-1). Such an imbalance can be generated either by exposure to high growth irradiance that exceeds Ek at a given σPSII (red arrow) or by exposure to low growth temperature at a constant irradiance whereby σPSII x Ek > τ-1 because of the temperature-dependent decrease in τ-1 (blue arrow). Adjustments of photosynthesis to balance the flow of energy and to obtain photostasis can either occur via an increase in the rate of enzymatic metabolic reactions or by increasing the concentration of enzymes controlling the metabolic sinks (n). Alternatively, energy balance can be attained by decreasing the efficiency of light harvesting of energy and its conversion to electrons in the PETC (green arrows). The size of the yellow circles are intended to illustrate the relative rates at the level of photosynthetic electron transport source (σPSII x Ek) versus the rates of metabolism (n τ-1). Reproduced from Ensminger et al. (2006).

to attain photostasis and protect of the photosynthetic apparatus from potential photodamage due to exposure to EEE in extreme environments (Fig. 3).

A major challenge for all terrestrial plants and aquatic microorganisms endemic to the polar regions is the maintenance of photostasis (Fig. 3) which includes restructuring and reorganization of photosynthetic apparatus governed by redox retrograde signalling to regulate the expression of photosynthetic nuclear genes in plants and algae (Pfannschmidt, 2003; Pfannschmidt and Yang, 2012; Nott et al., 2006; Jung and Chory, 2010; Woodson and Chory, 2008; Hollis and Hüner, 2014). Similarly, the redox status of the PETC of cyanobacteria (Fig. 1A) governs the remodelling of their photosynthetic apparatus in response to changes in light, temperature and nutrient status (Fujita et al., 1994; Bhaya et al., 2000; Grossman et al., 2010; Vincent, 2007; Zakhia et al., 2008). Exposure to EEE may result in photoinhibition of photosynthesis. Chronic photoinhibition normally leads to damage to PSII reaction centres and is only slowly reversible due to the requirement for resynthesis of damaged PSII reaction centre polypeptide, D1 (*psbA*). In contrast, dynamic photoinhibition is considered photoprotective, is rapidly reversible involving nonphotochemical quenching processes (Fig. 2) associated either with light harvesting antenna complexes or PSII reaction centres (Aro et al., 1993; Hüner et al., 1993; Osmond, 1994; Long et al., 1994; Adams III and Demmig-Adams, 1993; Demmig-Adams and Adams III, 1996; Ivanov et al., 2003; Verhoeven, 2014; Melis, 1999; Oquist et al., 1992; Ö;quist and Hüner, 2003; Murata et al., 2007). Interestingly, exposure to EEE under extreme environments does not appear to be restricted photoautotrophs. Coleine et al. (2020) recently reported that the heterotrophic microbial diversity and abundance localized to the endolithic surfaces of rocks on the ice-free land surfaces of the Antarctic are also extremely sensitive to light exposure (Coleine et al., 2020).

Psychrophiles and photopsychrophiles are excellent biological systems to elucidate the physiological, biochemical and molecular bases for

adaptation to extreme low temperature environments (Siddiqui and Cavicchioli, 2006; Siddiqui et al., 2013; Morgan-Kiss et al. 2006, 2008; Cvetkovska et al., 2017). Furthermore, it has been suggested that psychrophiles from extreme environments such as the McMurdo Dry Valleys (Morgan-Kiss, 2006; Wynn-Williams, 2000) may extend our insights into exobiology, that is, the possibilities for life on other planets (Priscu et al., 1998; Wynn-Williams, 2000). More important, photoautotrophs that flourish in the Earth's cold environments fix a significant proportion of the total CO_2 in our biosphere, and consequently, contribute substantially to the mitigation of global climate change (Lyon and Mock, 2014).

3. Photostasis and photosynthetic adaptation to polar life

Cold adaptation to polar terrestrial and aquatic environments is typically focussed on heterotrophic prokaryotes and animals. Hence, much of the scientific literature on molecular adaptation to extreme environments is biased towards animals and heterotrophic microorganisms (Hochachka and Somero, 2002; Feller and Gerday, 1997; Feller and Gerday, 2003; D'Amico et al., 2006; Collins et al., 2008; Somero, 2004; Hochachka and Somero, 1973; Kashefi and Lovley, 2003; Rainer, 2000; Pinney et al., 2021). Since terrestrial plants, green algae and cyanobacteria are photoautotrophic, adaptation to life in cold, polar environments is unique and necessarily more complex than that of animals and other heterotrophic organisms because of their photosynthetic nature and their requirement to maintain photostasis (Hüner et al. 1998, 2011, 2016; Ensminger et al., 2006).

Antarctic photoautrophic biodiversity is more diverse than one may expect (Chown et al., 2015). Microbes represent the largest proportion of the Earth's biomass and they also dominate the cold, polar, aquatic environments of the Antarctic and Arctic regions (Mock et al., 2014). It has been estimated that the North Atlantic, above 30°N, and the Southern Ocean, below 50°S, account for 32% of the global anthropogenic CO_2 inventory which makes these polar aquatic basins major sinks for the sequestration of atmospheric CO_2 (Sabine et al., 2004) and consequently are important components that govern global carbon balance and moderate the impact of climate change on the biosphere. We have restricted this review to cold adaptation of micro- and

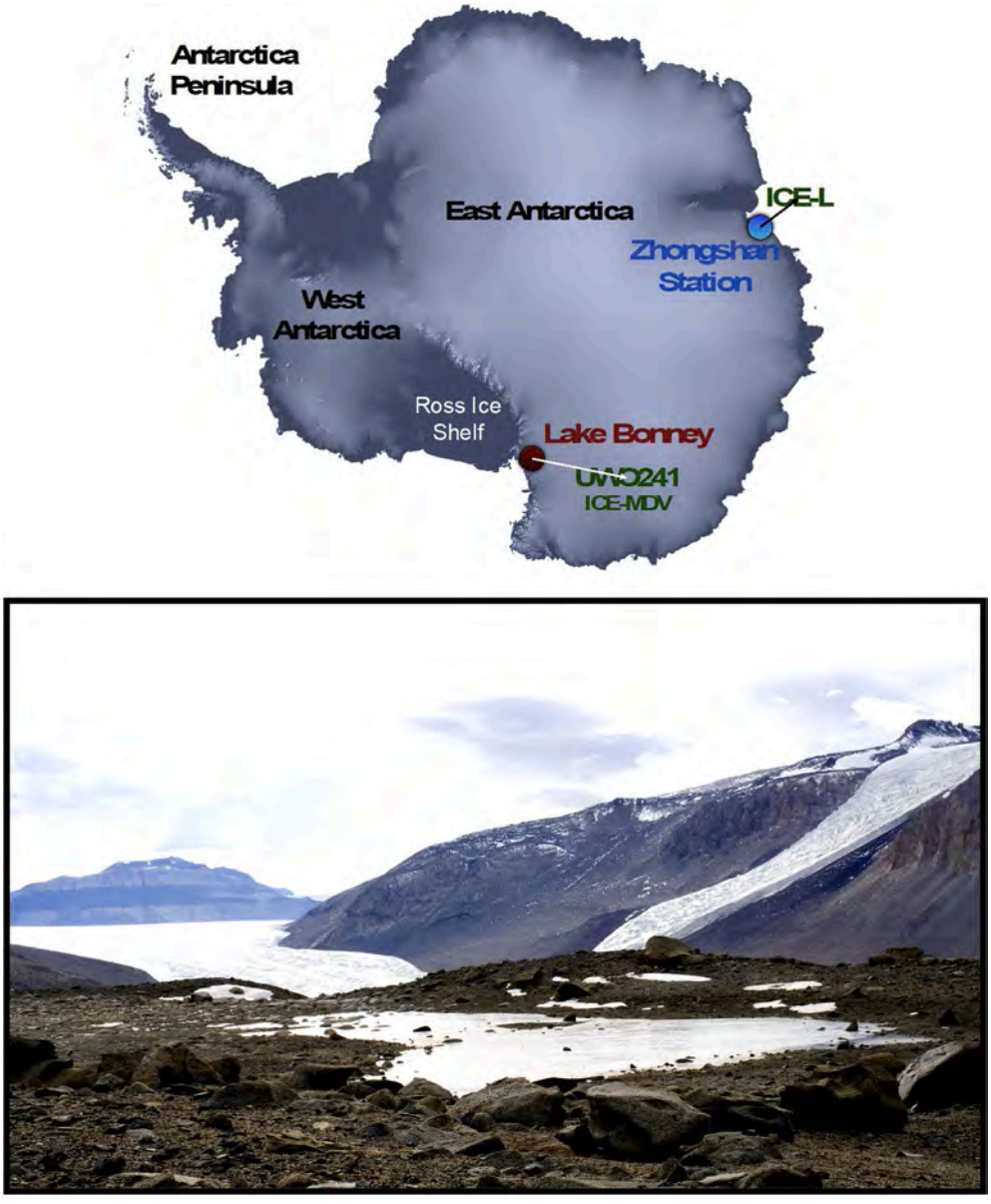


Fig. 4. Image of a snow and ice-covered lake located in the Taylor Dry Valleys. (Top) Map illustrating Antarctica and the positions of Lake Bonney where *Chlamydomonas sp* UWO241 and *Chlamydomonas* ICE-MDV were isolated and the Zhongshan site where *Chlamydomonas* ICE-L was isolated.

macro-photosynthetic organisms as well as terrestrial plants. Since we can not cover all aspects of cold adaptation of plants to polar environments, we direct the reader to several excellent books (Whitton and Potts, 2000; Margesin et al., 2008; Vincent, 2007; Seckbach, 2007) and reviews (Morgan-Kiss et al., 2006; Dolhi et al., 2013; Vincent, 2000, 2007; Zakhia et al., 2008; Priscu et al., 1998; Mock and Thomas, 2008; Lyon and Mock, 2014; Kennicutt et al. 2014, 2015; Xavier et al., 2016) that have been published on adaptation of eukaryotic and prokaryotic organisms to polar environments. Below, we summarize the major photosynthetic adaptations that contribute to photoprotection, the maintenance of photostasis and adaptation of photopsychrophilic unicellular green algae, as well as photopsychrotolerant cyanobacteria, macroalgae and terrestrial plants to Antarctic and Arctic environments.

3.1. *Permanently ice-covered lakes - a model photopsychrophilic green alga*

Chlamydomonas sp. UWO241 isolated from Lake Bonney, Antarctica (Fig. 4) was originally named *Chlamydomonas subcaudata* (Morgan et al., 1998; Gudynaite-Savitch et al. 2006, 2007) which was subsequently changed to *Chlamydomonas raudensis* UWO241 (Pocock et al., 2004). However, RAPD analyses (Gupta, 2013) combined with independent re-sequencing of nuclear rDNA (18S and 28S) and the plastid-encoded large subunit of Rubisco (rbcL), confirmed that UWO241 is a distinct species from SAG49.72 positioned in the Moewusinia clade of the Chlamydomonadales. Henceforth, this Antarctic photopsychrophile was renamed *Chlamydomonas sp.* UWO241 (Possmayer et al., 2016). Most recently, UWO241 has been renamed *Chlamydomonas priscuii*.

UWO241 can exist either as a single, biflagellate, motile cell (Fig. 5a, b, d, f) or as a collection of 4–16 individual cells called a palmelloid enclosed by a limiting membrane (Fig. 5c,d,e). The growth data (Fig. 5A and B) confirm that UWO241 is photopsychrophilic since it does not grow above 20 °C but is resilient to light levels that are at least 5-fold higher than the natural light levels of Lake Bonney. Furthermore, shifting UWO241 from a permissive growth temperature of 10 °C to a non-permissive growth temperature of 24 °C causes cell death over time as measured by SYTOX-Green staining (Fig. 5). Interestingly, UWO241 was more sensitive to cell death at 24 °C in the light than in the dark at 24 °C supporting the role of light and photostasis as critical determinants for the survival from stress of this photopsychrophile (Fig. 5).

UWO241 maintains a comparable energy balance as that of a mesophile albeit under drastically different thermodynamic constraints (Szyszka et al., 2007). As discussed below, we suggest that is partly accounted for by the reorganization of the structure of the photosynthetic apparatus of UWO241 relative to the model mesophile *C. reinhardtii* (Szyszka-Mroz, 2015, 2019). The reorganization of the photosynthetic apparatus in UWO241 is illustrated by comparing the 77K fluorescence emission spectra and thylakoid polypeptides of UWO241 with those of the mesophile *C. reinhardtii* (Fig. 6). As expected, the mesophile exhibits two major emission bands: one at about 685nm associated with PSII and another at about 715nm associated with PSI. In contrast, UWO241 consistently exhibits a very distinctive 77K emission

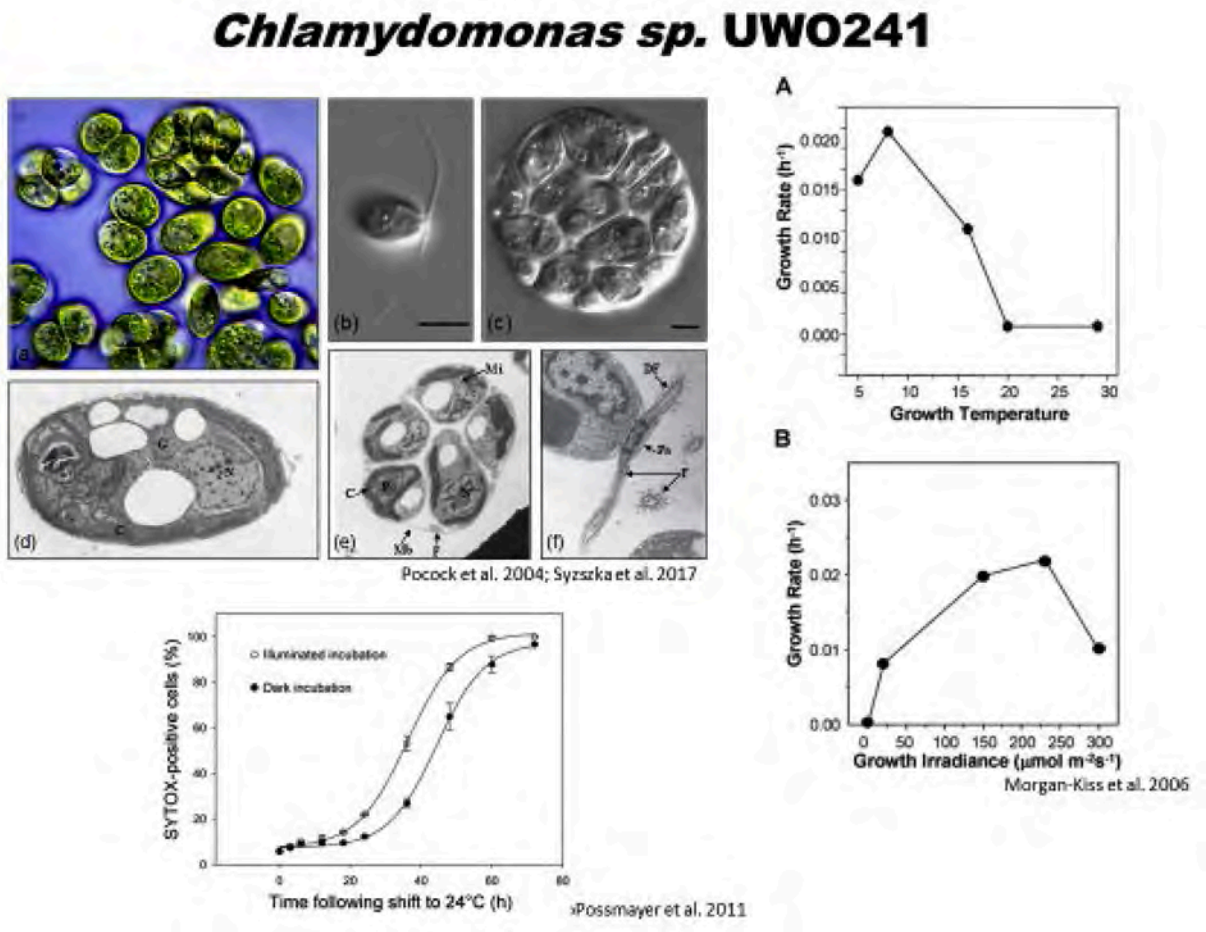


Fig. 5. Light and transmission electron micrographs of UWO241. (a) Light microscopic image of UWO24. (b and c) Images of a biflagellate, single cell (b) and a multicellular palmelloid (c). (d, e, f) TEM cross-section of s single cell. (e), a palmelloid and (f) flagella of UWO241. **(A)** Growth temperature response of UWO241. **(B)** Light response curve for the growth rate of UWO241. **(C)** The effects of a temperature shift on the viability of UWO241 based on Sytox- Green fluorescence staining.

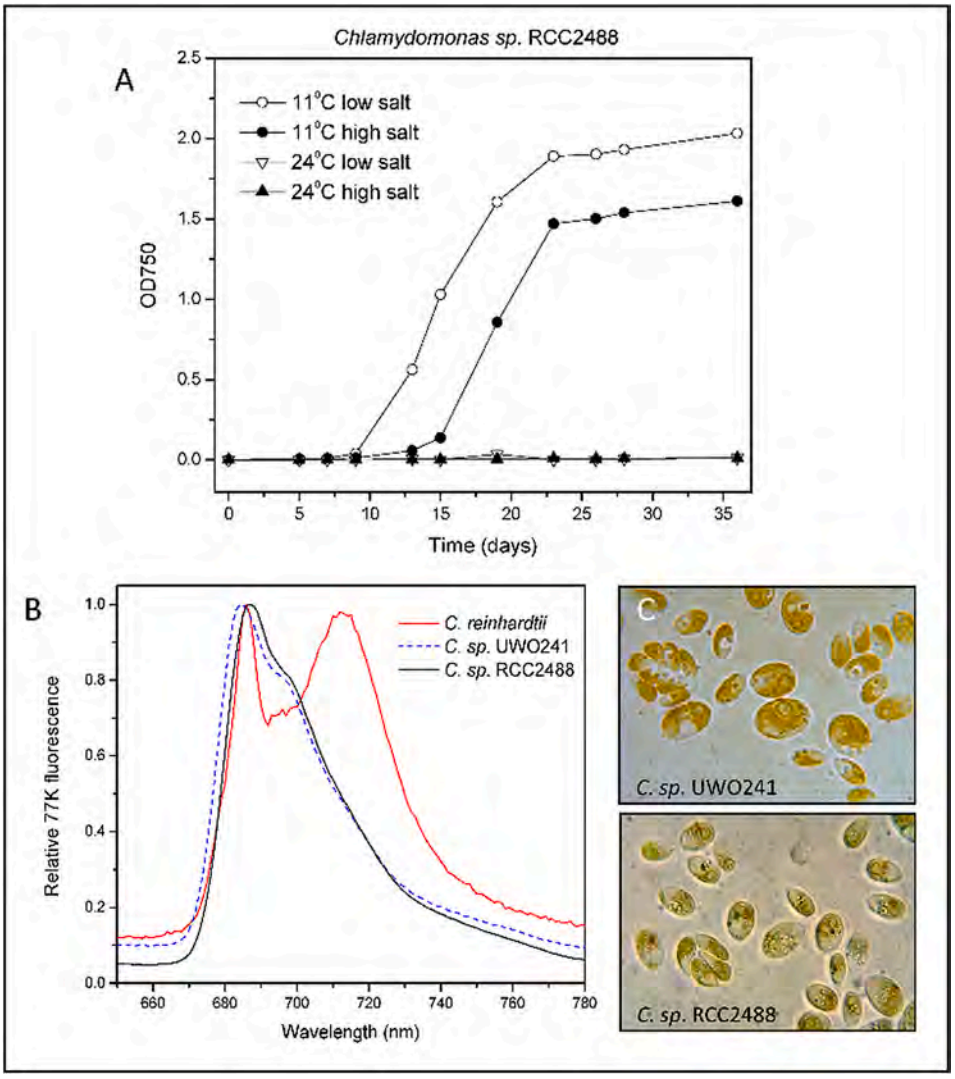


Fig. 6. Fluorescence emission spectra of the photosynthetic apparatus of *Chlamydomonas reinhardtii, Chlamydomonas sp* UWO241 and *Chlamydomonas sp* RCC2488. (A) Growth curves of Arctic isolate, *Chlamydomonas sp* RCC2488. (B) 77K fluorescence emission spectra of the mesophile, *Chlamydomonas reinhardti* (solid red), the Antarctic psychrophile, *Chlamydomonas sp* UWO241 and the Arctic psychrophile, *Chlamydomonas sp* RCC2488. (C) Light microscopic images of UWO241 and RCC2488.

spectrum characterized by the absence of the prominent PSI emission band even though PSI is present and functional (Kalra et al., 2020; Morgan et al., 1998; Morgan-Kiss et al., 2005; Szyszka-Mroz et al. 2015, 2019; Cook et al., 2019). This novel 77K fluorescence emission spectrum can be accounted for, at least in part, by the following: (1) a reduction and/or absence of 7 of the 11 Lhca polypeptides normally associated with PSI (Morgan et al., 1998); (2) the presence of a novel PSI-Cytb6/f supercomplex (Fig. 7) which appears to be important in the regulation of cyclic electron flow around PSI (CEF) (Kalra et al., 2020; Szyszka-Mroz et al., 2015) and (3) a major reorganization in the distribution of PSI-LHCI and PSII-LHCII complexes within thylakoid membranes based on digitonin fraction experiments combined with immunoblot analyses (Szyszka-Mroz et al., 2019), and last, an unusually low Chla/b ratio of 1.8–2.0 (Morgan et al., 1998). Typically plants and green algae exhibit a Chla/b ratio of about 3.0 when grown under optimal conditions (Hopkins and Hüner, 1999). We note with interest that a photopsychrophilic, Arctic isolate (*Chlamydomonas sp. RCC2488*) exhibits comparable 77K emission spectra to that of UWO241 (Fig. 6). Further research is required to determine whether the Arctic photopsychrophile exhibits a similar reorganization of its photosynthetic apparatus as reported for UWO241.

State transitions are essential for the maintenance of photostasis and photoprotection during acclimation to a fluctuating light environment for all known green algae and terrestrial plants (Supplementary Fig. 3). The molecular mechanism is governed by the reversible phosphorylation of LHCII that is regulated by the thylakoid protein kinases, Stt7 and Stl1, in *C. reinhardtii* and by STN7 and STN8, in *Arabidopsis thaliana* (Rochaix, 2014; Wunder et al., 2013; Pesaresi et al., 2011). These protein kinases sense excitation pressure, that is, the reduction state of the intersystem PETC (Allen et al., 1981; Oxborough et al., 1987; Allen, 1992; Bennett, 1991; Zer and Ohad, 2003). An enhanced reduction state of the intersystem PETC induces the phosphorylation of a mobile population of LHCII. This results in the disengagement of phosphorylated LHCII from PSII and its subsequent migration in the plane of the thylakoid membrane to become physically associated with PSI (Supplementary Fig. 3). Thus, state transitions represent a mechanism to modulate the energy distribution between PSII and PSI in a co-ordinated manner under fluctuating light conditions for photoprotection from EEE and attempts to maintain photostasis by adjusting σ_{PSII} to maximize rates of photosynthetic electron transport and CO_2 assimilation.

Since UWO241 exits in a relatively constant but low light environment conditions during 6 months of austral summer (Morgan-Kiss et al., 2006), is the capacity for short-term state transitions essential for the survival of UWO241 in Lake Bonney? UWO241 consistently fails to exhibit classic state transitions assessed as a change in the ratio of the PSII/PSI emission bands in 77K fluorescence emission spectra regardless of conditions used to induce them (Fig. 8) (Morgan-Kiss et al. 2001, 2005; Szyszka et al., 2007; Szyszka-Mroz et al., 2019; Gudynaite-Savitch, 2006, 2007; Kalra and Morgan-Kiss, unpublished). This is a novel

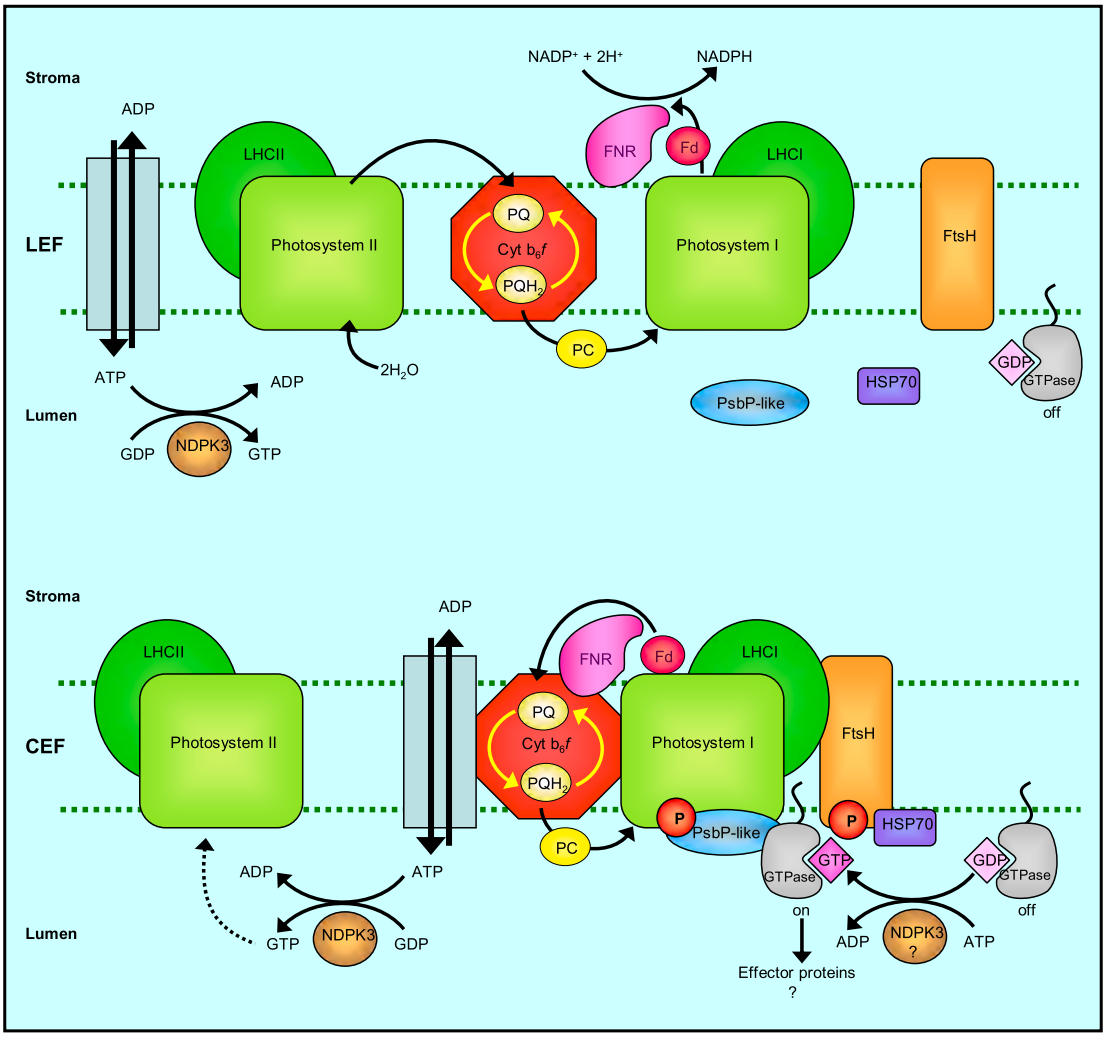


Fig. 7. Model illustrating the organization of UWO241 PSI-Cytb6/f supercomplex. **(TOP).** Model of the typical organization of the eukaryotic PETC illustrating normal linear electron flow (LEF) and other proteins of the chloroplast thylakoid membrane. In LEF, photons absorbed by the light harvesting complex (LHCII) are transferred to the photosystem II reaction centre which results in the photo-oxidation of P680 to P680+ + e. P680+ is reduced back to P680 by the oxidation of water and the release of oxygen. Electrons obtained from the photo-oxidation of photosystem II are transferred to plastocyanin (PC) via the plastoquinone pool (PQ) and the Cytb6f complex. Light absorbed by the light harvesting complex of photosystem I (LHCI) is transferred to the photosystem I reaction centre which results in the photo-oxidation of P700 to P700+ + e. This electron is used to reduce NADP + to NADPH via ferredoxin (Fd)- FNR complex and consumed to fix CO2 via the Calvin-Benson-Bassham cycle. LEF generates a proton motive force (pmf) across the thylakoid membrane consumed by the chloroplast ATP synthase complex (grey box) to generate the ATP required for CO2 fixation by the Calvin-Benson-Bassham cycle in the stroma. **(BOTTOM)** Proposed model illustrating the reorganization of PETC and PSI of UWO241 into a PSI-Cytb6f-supercomplex. The PSI-Cytb6f supercomplex stimulates cyclic electron flow (CEF) via Fd, the PQ pool, and PC and around PSI which regulates the distribution of reductant between pmf (solid black arrows) for CO2 fixation by the Calvin-Benson-Bassham cycle (broken black arrow). P illustrates the protein phosphorylation sites detected in the PsbPlike and the FtSH subunits of UWO241–PSI-Cytb6f supercomplex. NDPK3, PsbP-like protein, HSP70, heat shock protein 70, FtSH, ATP-dependent Zn-metlloprotease; ATP translocase. All subunits illustrated in the model were identified after purification of the PSI-Cytb6/f supercomplex initially by sucrose density centrifugation followed by 2D IEF-SDS-PAGE and the subsequent identification of individual polypeptides by liquid chromatography-IEF-nanotandem mass spectrometry (Szyszka-Mroz et al., 2015).

feature of this photopsychrophile even though it is able to maintain high rates of photosynthesis at low growth temperature (Pocock et al., 2007). The lack of state transitions in UWO241 was correlated with an unusual Cytf/b6 complex in which the Cyt f is 7kD smaller than that of *C. reinhardtii* based on SDS-PAGE despite the fact that both proteins show 79% identity in amino acid sequence and are of comparable calculated molecular masses based on the gene sequences for *petA*. Furthermore, the photopsychrophilic form of Cyt f was less heat stable than that of *C. reinhardtii* (Gudynaite-Savitch et al., 2006). It was hypothesized that the inability to undergo state transitions in UWO241 was due to the presence of its unique Cyt f. However, the *C. reinhardtii ΔpetA* mutant transformed with *petA* from UWO241 retained the capacity to undergo state transitions comparable to WT indicating that the novel Cyt f of UWO241 did not explain the inability of UWO241 to undergo classic state transitions Gudynaite-Savitch (2006); Gudynaite-Savitch (2007). Thus, it appears that a capacity for photoprotection through classic short-term state transitions is not essential for the survival of UWO241 in Lake Bonney.

The photopsychrophilic chlorophyte, *Chlorella sp*. strain BI was isolated from a pond on the Ross Ice Shelf near Bratina Island, Antarctica (Fig. 4). Phylogenetic analyses placed this strain in the Chlorella clade (Morgan-Kiss et al., 2008). However, unlike UWO241, *Chlorella sp*. strain BI exhibits the capacity for classic short-term state transitions as does the photopsychrophile, *Chlamydomonas* ICE-MVD (Fig. 8). Clearly, the absence of short-term state transitions are not prerequisites for photopsychrophily in eukaryotic algae. This may reflect the very different habitats and ecosystems occupied by UWO241, *Chlorella sp*. strain BI and *Chlamydomonas* ICE-MVD.

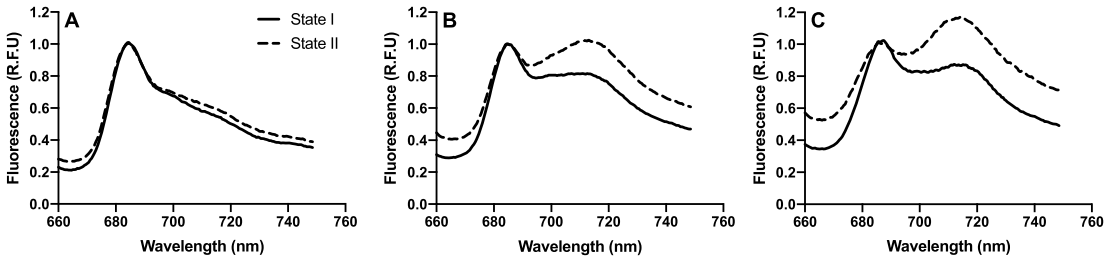


Fig. 8. Low temperature (77K) fluorescence spectra of the three different *Chlamydomonas* spp. under state I and state II conditions. Cultures were grown in Bold's Basal media at their respective optimal temperatures (Photopsychrophiles (UWO241 and ICE-MDV) at 8 °C and mesophile *C. reinhardtii* at 23 °C). State transitions were induced using chemical inhibitors DCMU (State I, solid line) and FCCP (State II, dashed line) as described before (Iwai et al., 2010). Low temperature fluorescence spectra (Chl a) were recorded for each strain and condition. Fluorescence values are shown as relative fluorescence units (R.F.U). PSII and PSI fluorescence maxima are at 685 nm and 715 nm, respectively. During transition to state 2, PSI fluorescence increases due to migration of LHCII towards PSI. UWO241 (A); ICE-MDV (B); *C.reinhardtii* (C).

Nevertheless, we were surprised to discover that despite the inability to undergo classic state transitions, the UWO241 genome and proteome clearly exhibit the presence of *Stt7* and *Stl1* (Szyszka-Mroz et al., 2019; Zhang et al., 2021). Consistent with adaptation to its low temperature environment, the extent of thylakoid protein phosphorylation in UWO241 was highest at 5 °C but was inhibited at 25 °C whereas the opposite was observed for the mesophile, *C. reinhardtii* (Szyszka-Mroz et al., 2019). The kinase domain of the UWO241 Stt7 (Fig. 9) exhibited significant structural alterations which were interpreted to indicate its predisposition to function maximally at low temperature and exhibit minimal sensitivity to the known protein kinase inhibitor, staurosporine, compared to that of *C. reinhardtii* (Szyszka-Mroz et al., 2019). Furthermore, the complement of light harvesting polypeptides and PSII core polypeptdes phosphorylated was distinct in UWO241 compared to *C. reinhardtii*. In addition, UWO241 exhibited novel phosphorylation sites including distinct subunits of the PSI-Cytf/b6 supercomplex not observed in the mesophile. Furthermore, the phosphorylation status of these subunits combined with the requirement for high salt governed the stability of the PSI-Cytf/b6 supercomplex and the rates of CEF in UWO241 (Szyszka-Mroz et al., 2019; Kalra et al., 2020). UWO241 Stt7/Stl1 kinases are examples of membrane-associated, cold-adapted, enzymes that function optimally at cold temperatures but are inhibited at high temperatures (Aquist et al., 2017). Hepworth et al. (2021) suggest that the novel PSI-supercomplexes observed in green algae such as *C. reinhardtii* (Takahashi et al., 2013; Iwai et al., 2010) and UWO241 (Szyszka-Mroz et al., 2019; Kalra et al., 2020) may govern the ratio of CEF/LEF in green algae (Fig. 1B). Thus, the structure and function of the PSI-Cytf/b6 supercomplex as well as the cold adapted properties of the UWO241 Stt7/Stl1 kinases appear to be important in the manitenance of photostasis in UWO241 by regulating the ratio of CEF/LEF. Whether this is true of all photopsychrophiles has yet to be determined.

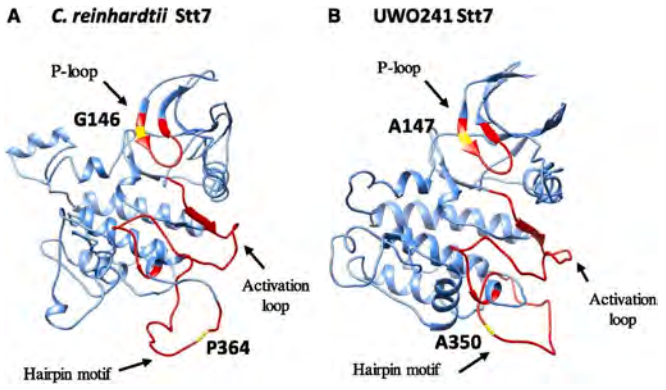


Fig. 9. Predicted 3-D structures of Stt7 kinase domains in *C. reinhardtii* (A) and UWO241 (B). The important domains in each case are shown in red and highlighted with a black arrow. The critical residues that differ between *C. reinhardtii* and UWO241 are shown in yellow and labeled.

Fig. 1 illustrates the important role of photosynthetic ferredoxins (Fd) in governing the distribution of electrons from PSI to various essential metabolic sinks in cyanobacteria, green algae and plants (Knaff, 1996; McKay et al., 1999; Boehm et al., 2015; Schorsch et al., 2018). Recently, a global interaction Fd network was identified for *C. reinhardtii* providing myriad putative roles for this protein in redox metabolism, carbohydrate modification, fatty acid biosynthesis, hydrogen production, nitrogen and sulfur metabolism, state transitions, and dark anoxia (Peden et al., 2013). PETF (Fd1) represents about 98% of all transcribed *Fd* genes in *C. reinhardtii* (Terauchi et al., 2009). However, ferredoxin from UWO241 is adapted to function in cold environments (Cvetkovska et al., 2018) since the purified enzyme exhibited highest structural stability and activity at 10 °C but is more labile at temperatures greater than 40 °C than that of *C. reinhardtii*. Transcriptome as well as polypeptide analyses indicated that, in contrast to other photoautotrophs, UWO241 expressed and accumulated two forms of Fd: Fd-1A and Fd-1B (Cvetkovska et al., 2018). Genomic comparisons of UWO241 Fd-1A and Fd-1B with 21 other Fd from green algae, diatoms, terrestrial plants and cyanobacteria indicated that all Fd were highly conserved at the primary protein sequence (Fig. 10). The predicted amino acid sequence indicated that the mesophilic *C. reinhardtii* and the photopsychrophilic UWO241 Fd differed by 11 amino acids which occur in regions distant from the active site and involved in Fe binding and protein-protein interactions (Fig. 10). It is interesting to note that such differences in predicted amino acid sequences can lead to such significant differences in temperature stability and activity. Although these observations for Fd in UWO241 are consistent with those of other psychrophilic as well as thermophillic enzymes examined to date (Feller and Gerday, 2003; D'Amico et al., 2006; Aquist et al., 2017; Rainer, 2000; Pinney et al., 2021) the precise molecular mechanism that underly these properties remains an enigma. However, it may, in part, reflect epistatic effects of amino acid residues (Starr and Thornton, 2016). Thus, UWO241 Fd-1 is unique among psychrophilic proteins since it appears not only to exhibit enhanced activity and structural stability at low temperature, it also accumulates to levels twice that observed for Fd1 in mesophilic *C. reinhardtii*. This combination of increased τ^{-1} and increased "n" for UWO Fd-1 may contribute to the higher capacity for photosynthetic electron transport and the maintenance of photostasis under its natural cold environment by enhancing sink capacity as estimated by n (τ^{-1}).

In addition to adaptation to constant light levels during austral summer, UWO241 is also adapted to 6 months of darkness during austral winter. UWO241 exhibits a shade-adapted state and maintains normal Chl levels during the dark austral winter months (Morgan-Kiss et al. 2006, 2015). This is unusual since most terrestrial plants become etiolated when exposed to prolonged darkness (Nemhauser and Chory, 2009). Despite being adapted to seasonal, prolonged darkness, UWO241 is able to maintain high levels of Chl a and Chl b during the austral

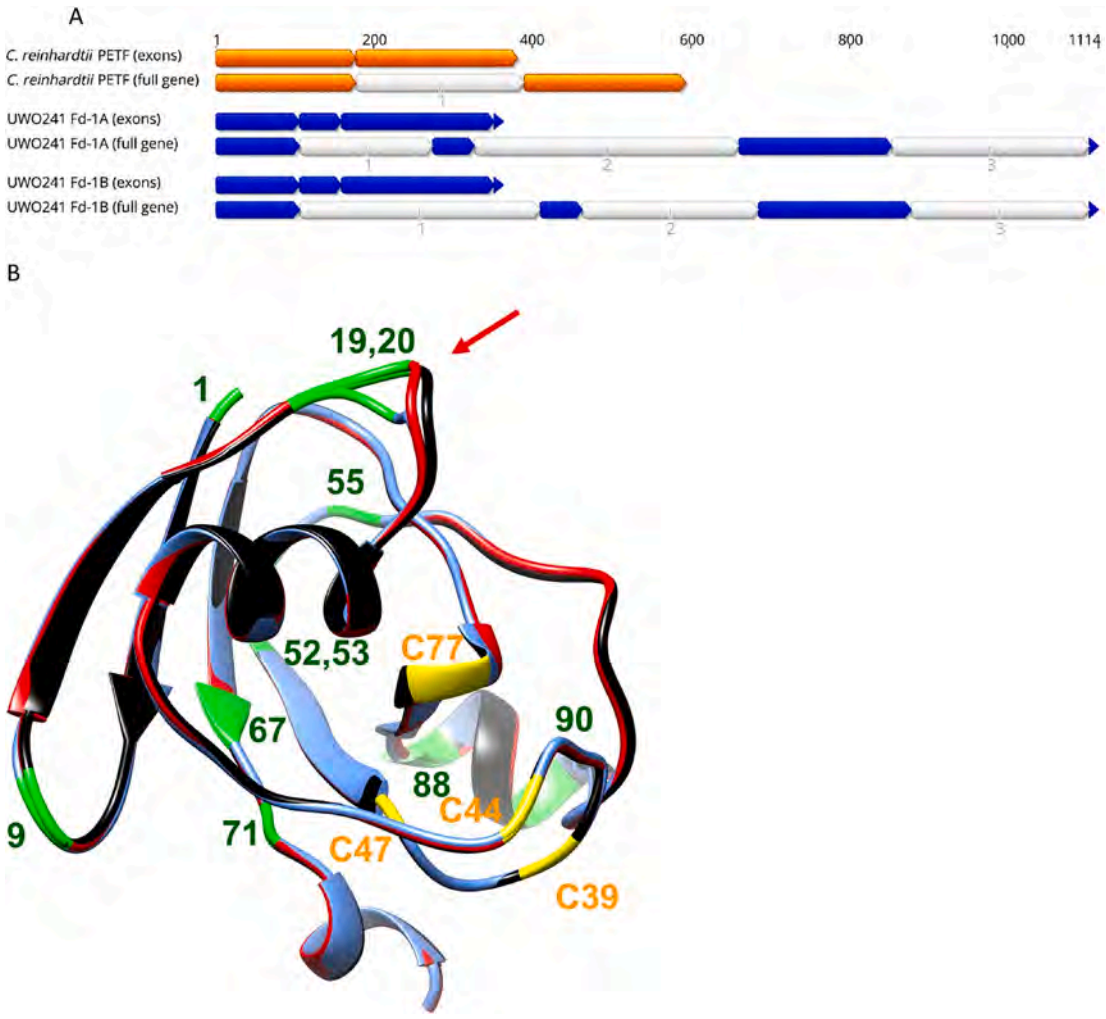


Fig. 10. A. Comparative gene organization of ferredoxin in *Chlamydomonas reinhardtii* and *Chlamydomonas sp* UWO241. (A) Graphical representation of the gene structure of photosynthetic ferredoxin genes in the psychrophile *Chlamydomonas sp*. UWO241 and the mesophile *Chlamydomonas reinhardtii*. In all cases, the non-coding intron sequences are shown in white and sequentially numbered, while the protein coding exon sequences are shown in color (orange for *C. reinhardtii*, and blue for UWO241). Both the full gene and the concatenated exonic sequences are shown, demonstrating the difference in gene structure between the two organisms. (B) Comparative 3-D structures of ferredoxin based on genome sequence data of *Chlamydomonas reinhardtii* and *Chlamydomonas sp* UWO241. Predicted tertiary structure of the two ferredoxin (Fd) isoforms from Chlamydomonas sp. UWO241 (Fd-1A in red; Fd-1B in black) superimposed on the structure of photosynthetic Fd (PETF) from *Chlamydomonas reinhardtii* (blue). The structure of *C. reinhardtii* PETF was obtained from PDB (ID: 2mh7). Fd-1A and Fd- 1B were modeled based on homologous proteins using the PHYRE2 Engine. The positions of the conserved cysteine residues involved in coordination of the [2Fe–2S] cluster are labeled and highlighted in yellow. The residues that are different between sequences are labeled and highlighted in green.

winter period (Morgan-Kiss et al., 2015). We note with interest that the diatom, *Phaeodactylum tricornutum*, grown under control temperatures also maintains a functional photosynthetic apparatus during exposure to dark periods coupled with rapid recovery upon re-illumination (Nymark et al. 2013).

A rate-limiting step in chlorophyll biosynthesis in eukaryotic photoautotrophs is the conversion of protochlorophyllide to chlorophyllide. LPOR is the light-dependent and DPOR is the dark-independent protochlorophyllide oxidoreductase that catalyzes this reaction (Reinbothe and Reinbothe, 1996). However, the three genes (*chlL*, *chlN*, and *chlB*) that encode DPOR are absent not only from the UWO241 genome but also absent from its plastome and mitochondrial genome (Cvetkovska et al., 2019). In contrast, 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 UWO241. Thus, it appears that UWO241 does have a functional Chl biosynthetic pathway that is totally dependent on LPOR but has lost DPOR even though this alga is exposed to prolonged annual seasonal darkness.

How can this astonishing conundrum be rationalized? At 17m below the bottom of the ice cover where UWO241 was isolated, Lake Bonney exhibits extremely high O_2 concentrations (Morgan-Kiss et al., 2006). DPOR is very sensitive to O_2 concentrations due the presence of an essential Fe–S cluster which is not present in LPOR. Consequently, we hypothesize that the evolutionary elimination of DPOR from UWO241 would not result in a deleterious effect on UWO241. This may explain the absence of *chlL*, *chlN*, or *chlB* genes in UWO241 (Cvetkovska et al., 2019). To validate this hypothesis with respect O_2 concentrations and the absence of DPOR, more phototrophs from Lake Bonney must be examined. Furthermore, the mechanism by which UWO241 represses the process of etiolation in the dark and maintain normal Chl levels has yet to be elucidated.

What physiological and biochemical adaptations allow UWO241 to persist through such a prolonged dark period? To address this question, an exquisite field experiment was performed by Morgan-Kiss and colleagues (2015) in which laboratory cultures of UWO241 placed in dialysis bags containing water from Lake Bonney were transferred back into Lake Bonney and suspended at a depth of 17 m to allow the

photopsychrophile to respond to the natural light, temperature and dissolved ions of Lake Bonney. Physiological and molecular analyses of the transplanted UWO241 cultures were compared with the natural phytoplankton community of Lake Bonney during a period of 6-weeks during the natural transition from the light period of austral summer to the darkness of austral winter (Morgan-Kiss et al., 2015). During this transition, the UWO monocultures ceased CO_2 fixation with a concomitant down-regulation of the Rubisco gene, *rbcL*, as well as the gene encoding the PSII reaction centre polypeptide, *psbA*. These trends were matched in the natural phytoplankton community of Lake Bonney (Morgan-Kiss et al., 2015). It was concluded that the transplanted cultures of UWO241 shifted from a light-adapted state to a shade-adapted state during the transition to polar night. This is consistent with the previously proposed model for dark adaptation in this polar alga (Morgan-Kiss et al. 2006, 2015; Mock and Thomas, 2008). The processes involved in the reactivation and the induction of photosynthesis in the transition from the darkness of austral winter to the light conditions of austral summer to maintain photostasis remain to be elucidated. A limiting factor in acquiring the necessary data under natural conditions is the logistical problem of safely gaining access to Lake Bonney during this transition period in the Antarctic. However, results from lab-controlled approaches can be integrated with exciting new technologies which utilize automated sampling to gain year-round access to the native phytoplankton communities living in polar lakes such as Lake Bonney. It was recently reported that unlike strict photoautotrophic algae such as UWO241, that the diatom, *Fragilariopsis cylindrus,* can switch to alternative modes of energy acquisition and continue to grow even during the polar night (Kennedy et al., 2019; Gray et al., 2020).

3.2. Coastal polar macro-algae

In Antarctic and Arctic coastal regions, macro-algae represent key members of these shallow marine ecosystems (Wiencke and Hop, 2016). Coastal kelp beds represent prominent and vital components of these cold, benthic ecosystems. Kelp is sessile and consequently differ from unicellular, motile microbial green algae such as UWO241 discussed above. How do sessile, cold tolerant Arctic kelp such as *Saccharina latissama* respond to light and temperature stress? Although *Saccharina latissama* is cold tolerant, photosynthesis was most sensitive to the exposure of *S. latissama* to elevated light levels combined with *high* temperature (Heinrich et al., 2012). Polar kelp such as *S. latissama* are certainly photopsychrotolerant but given its sensitivity to high temperature *S. latissma* appears to be stenothermic. Is *S. latissma* photopsychrophilic? We are unaware of any published data for Arctic *S. latissama* that distinguishes a photopsychrophilic nature from that of photopsychrotolerance.

Nonetheless, the published photosynthetic responses of *S. latissama* indicate that the maintenance of photostasis during exposure to EEE caused by high light combined with high temperature plays an important role in the survival of this macro-alga to changes in temperature and light (Heinrich et al., 2012). For example, photoacclimation of *S. latissama* suppresses the accumulation of nuclear transcripts encoding light harvesting polypeptides combined with alterations in the pigment content and composition (Heinrich et al., 2012). Unfortunately, in this transcriptomic study, no data are available regarding changes in light harvesting polypeptide levels. Assuming that changes in mRNA levels were correlated with suppressed light harvesting polypeptide accumulation, these data are consistent with suggestion that *S. latissama* maintains photoprotection and photostasis, during abiotic stress, in part, by decreasing σ_{PSII} and therefore decreasing photosynthetic efficiency to protect its photosynthetic apparatus from EEE.

3.3. Polar cyanobacteria

Although cyanobacteria, like plants and green algae, are oxygenic and exhibit similar photosystems (PSI and PSII), phycobilisomes are the light harvesting pigment-protein complexes that service these two photosystems (Fig. 1A). Phycobilisomes consist of protein-bound phycoerythyrin, phycocyanin and allophycocyanin. Phenotypic plasticity as reflected in alterations in pigmentation of cyanobacteria represents a photoprotective response to EEE and is, in part, a consequence of altered structure and composition of the phycobilisomes which reduces the light harvesting efficiency of cyanobacteria to maintain photostasis by adjusting σ_{PSII} (Miskiewicz et al. 2000, 2002; Bailey et al., 2008; Grossman et al. 1993, 1994; Hüner et al., 2012; Wilson et al., 2006). In addition to adjustment of phycobilisomes in response to EEE, many aquatic cyanobacteria contain an orange carotenoid protein (OCP) to quench the excess energy absorbed by the phycobilisome which increases non-photochemical energy dissipation in the form of heat and photoprotection from EEE (Fig. 2) (Kirilovsky, 2007, 2015).

Phormidium subfuscum isolated from a microbial mat in an Antarctic lake on the McMurdo ice-shelf and *Phormidium tenue* isolated from the rock surface in an Arctic river bed, exhibited remarkable plasticity with respect to growth and photosynthetic responses to temperature. Even though both species originated from a polar environment, *Phormidium tenue* exhibits eurythermic growth response whereas *Phormidium subfuscum* is stenothermic (Tang and Vincent, 1999). This differential growth response was consistent with a greater capacity to adjust photosynthetic performance over a wider temperature range in *P. tenue* than *P. subfuscum* even though both species originated from a polar environment. Thus, a eurythermal acclimation strategy may provide an advantage in a daily fluctuating environment whereas a stenothermal strategy may provide a significant benefit in environments characterized by relatively constant seasonal temperatures such as exhibited in perennially ice-covered lakes of Antarctica (Morgan-Kiss et al., 2006).

The phenotypic and photosynthetic response of *P. tenue* to low temperature to maintain photostasis include adjustments in pigment content and composition as well as decreases in σ_{PSII}. These are consistent with the responses of the eurythermal green algae, *Chlorella vulgaris* and *Duneliella salina* (Krol et al., 1997; Maxwell et al. 1994, 1995a, 1995b) as well as the eurythermal filamentous cyanobacterium, *Plectonema boryanum* (Miskiewicz et al. 2000, 2002) at low temperature. In addition, Antarctic cyanobacteria accumulate carotenoids combined with increased levels of UV-absorbing compounds (Tang et al., 1997; Tang and Vincent, 1999; Vincent, 2000, 2007; Ivanov et al., 2000; Miskiewicz et al., 2002; Zakhia et al., 2008) similar to that reported for Antarctic marco-algae (Hoyer et al., 2001). We suggest that these observed adjustments in σ_{PSII} and UV-absorbing compounds are photoprotective mechanisms that help to explain the dominance of cyanobacteria and coastal kelp in these cold Antarctic and Arctic aquatic ecosystems (Tang and Vincent, 1999; Nadeau and Castenholz, 2000; Vincent, 2000; Wiencke and Hop, 2016).

3.4. Polar terrestrial plants

Terrestrial vegetation in maritime ecosystems of the Antarctic peninsula is dominated by mosses and lichens which are poikilohydric and therefore, metabolically active only when in the hydrated state (Schroeter et al., 2017). Brophytes tend to dominate this maritime ecosystem whereas lichens tend to dominate the drier, Antarctic ecosystems where light coupled with the extreme low temperatures is a major seasonal stress (Schroeter et al., 2017). At southern latitudes greater than 60° S, approximately 111 species of bryophytes have been identified (Perara-Castro et al., 2021). Endemic mosses are exposed to extreme low temperature coupled with freezing conditions during most of their life cycle (Perara-Castro et al., 2021). The comprehensive study of Perara-Castro et al. (2021) assessed the mechanism(s) that 15 bryophyte species on Livingston Island, Antarctica, employed to protect their photosynthetic apparatus from EEE for long-term survival. Although survival to freezing in the hydrated state varied depending on the species, in the dehydrated state the analyzed species were able to survive a temperature of −20 °C (Perara-Castro et al. (2021). In the hydrated

state, these Antarctic bryophytes down-regulated PSII activity and adjusted σ_{PSII} through reaction center quenching (Perara-Castro et al. (2021) (Fig. 2) as a major mechanism for photoprotection and energy balance and the attainment of photostasis (Ö;quist et al., 1992; Ivanov et al., 2003; Ö;quist and Hüner, 2003). Reversible dehydration appears to be a prominent protective mechanism for many Antarctic mosses and lichens to avoid light stress. However, in contrast to most Antarctic bryophytes, low temperature combined with light does not appear to be a problem for the Antarctic moss, *Bryum argenteum* (Schroeter et al., 2012). This species constitutively exhibits high levels of the xanthophyll cycle pigments (Schroeter et al., 2012) which protects the photosynthetic apparatus from EEE through nonphotochemical dissipation (Fig. 2) and modulation of σ_{PSII}.

Lichens are composed of a fungal mycobiont which lives symbiotically with a photobiont, either a green alga or a cyanobacterium (Colesie et al., 2018). Seasonal adjustments in lichen photosynthesis appears to be governed mainly by temperature and light (MacKenzie et al., 2002). However, the response of lichens to long-term environmental change is complex due to their slow growth rates coupled with their longevity and exposure to many successive seasonal cycles (Schroeter et al., 2017; Colesie et al., 2018). Respiration represents a major sink [n (τ^{-1})] in cellular energy balance and photostasis [(σ_{PSII}) (E_k)=n (τ^{-1})]. Energy homeostasis in lichens involves the balance between the response of respiratory loss of CO_2 of the heterotrophic mycobiont and the response of photosynthetic CO_2 uptake of the photobiont. Colesie et al., (2018) reported that increased respiration in 3 lichens examined was not associated with any respiratory down regulation during long-term exposure to elevated temperatures. Thus, surprisingly, the three lichens examined failed to show respiratory thermal acclimation typically observed in terrestrial plants (Atkin and Tjoelker, 2003; Way and Yamori, 2014). Clearly, Antarctic mosses and lichens have evolved several different photoprotective mechanisms to ensure survival in this extreme environment (Schroeter et al. 2012, 2017; Colesie et al., 2018; Perara-Castro et al., 2021).

There are only two angiosperms endemic to the Antarctic continent, *Colobanthus quitensis* (Kunth) Bartl., a dicot (Supplementary Fig. 1A) and *Deschampsia antarctica* Desv., a monocot (Supplementary Fig. 1B) found in the maritime Antarctic peninsula, 68°42' S (Fig. 4). Both terrestrial angiosperms grow and photosynthesize during austral summer when the mean temperature is about 3 °C but remain under the snow and dormant during the austral winter (Bascunan-Godoy et al., 2006; Bravo and Griffith, 2005; Bravo et al., 2001). The light-dependent photosynthetic reduction of O_2 (Fig. 1B) represents an alternative pathway for the consumption of photosynthetically-generated electrons (Asada, 1994; Fryer et al., 1998; Ort, 2001; Stepien and Johnson, 2009; Queval and Foyer, 2012; Ivanov et al., 2012; Johnson and Stepien, 2016) and photoprotection upon exposure to EEE (Ort and Baker, 2002) to maintain photostasis by the enhancing sink capacity [n (τ^{-1})]. However, the reduction of O_2 may generate reactive oxygen species (ROS) which contribute to oxidative damage. Recently, it was reported that the accumulation of ROS at low temperature as well as exposure to UV-B radiation caused significant genetic damage in *Colobanthus quitensis* and *Deschampsia antarctica* under natural Antarctic field conditions (Acuña-Rodríguez et al., 2021). Therefore, use of O_2 as an alternative electron acceptor must be accompanied by the concomitant accumulation of antioxidants to mitigate potential oxidative damage (Asada, 1994). However, ROS may also provide protection through their positive roles in signal transduction networks induced by myriad environmental stresses (Karpinski et al., 1999; Baxter et al., 2014; Dietz et al., 2016; Foyer et al., 2017).

The PETC in *C. quitensis* was reported to be insensitive to changes in O_2 concentrations indicating that O_2 was not utilized as an alternative photosynthetic electron acceptor (Fig. 1B) in *C. quitensis*, whereas, approximately 30% of its PETC activity was linked to the reduction of oxygen in *D. antarctica* (Perez-Torres et al. 2004, 2007). Thus, *C. quitensis* appeared to be more dependent on NPQ for photoprotection (Fig. 2) which affects σ_{PSII} from EEE whereas *D. antarctica* increased sink capacity [n (τ^{-1})] by using O_2 as an alternative electron acceptor (Ort and Baker, 2002) indicating that these two polar terrestrial plants appear to be dependent on different photoprotective mechanisms to maintain photostasis and survive the harsh terrestrial Antarctic environment.

Eutrema salsugineum (Supplementary Fig. 1C), previously named *Thellungiella salsuginea,* is a cold-tolerant halophyte native to the Arctic and its Yukon ecotype can be found growing in the Takhini salt flats (60°51.292N 135°43.042W) near Whitehorse, Yukon Territory, Canada (Griffith et al., 2007). Since this species is a close relative of *Arabidopsis thaliana,* the Yukon (Griffith et al., 2007) and Shandong ecotypes (Stepien and Johnson, 2009) of *Eutrema salsugineum* are considered excellent model systems for comparative analyses to elucidate the genetic, molecular and biochemical basis of plant stress tolerance (Griffith et al., 2007; Kazachkova et al., 2018). *Eutrema* is generally more tolerant than *Arabidopsis* to a number of abiotic stresses (Kazachkova et al., 2018) including freezing (Griffith et al., 2007), N-deficiency (Kant et al., 2008), and phosphate stress (Velasco et al., 2016). *Eutrema* vs Arabidopsis is another excellent example of the usefulness of exploiting non-model systems in comparison with model biological systems to address the mechanisms that underlie plant stress, acclimation and adaptation to extreme environments.

With respect to photostasis, Stepien and Johnson (2009) compared the photosynthetic performance of the Shandong ecotype of *E. salsugineum* with WT *Arabidopsis thaliana* with respect to salt stress. Photosynthetic CO_2 assimilation in WT Arabidopsis was inhibited with a concomitant decrease in rates of LEF due to feedback inhibition of photosynthesis as a consequence of lower sink activity [n (τ^{-1})] upon exposure to high salt. To compensate for this limitation in LEF, WT Arabidopsis exhibited enhanced PSI CEF (Fig. 1B) in combination with a stimulation of NPQ (Fig. 2) to dissipate excess absorbed light as heat to protect the photosynthetic apparatus from EEE under salt stress (Stepien and Johnson, 2009) and consequently maintain photostasis. In contrast, *Eutrema salsugineum* exhibited minimal inhibition of photosynthetic CO_2 assimilation combined with minimal induction of either CEF or NPQ due to its ability to continue to consume photosynthetically-generated electrons even upon exposure to EEE due to its high sink capacity [n (τ^{-1})]. In addition, *Eutrema salsugineum* showed elevated levels of PTOX, the plastid terminal oxidase, which oxidizes the PQ pool by reducing O_2 to water (Fig. 1B) which minimizes the accumulation of ROS (Aluru and Rodermel, 2004; Streb et al., 2005; McDonald et al., 2011; Nawrocki et al., 2015; Johnson and Stepien, 2016). Resilience to either low temperature, in the case of *D. antarctica* (Perez-Torres et al., 2007), or high salt in the case of *Eutrema salsugineum* (Stepien and Johnson, 2009; Johnson and Stepien, 2016) may, in part, be accounted for by the ability to utilize O_2 rather than CO_2 as a terminal photosynthetic electron acceptor (Fig. 1B) to maintain photostasis.

The high-latitude boreal forests of North America and Eurasia cover approximately 1.3 billion hectares and store up to 33% of all terrestrial carbon on Earth. Consequently, this boreal ecosystem is crucial in governing the global carbon cycle in response to climate change (Way and Oren, 2010). Boreal forests of the northern hemisphere consist of both deciduous and evergreen species which exhibit quite distinct strategies as discussed in detail elsewhere (Öquist and Hüner, 2003; Way and Oren, 2010; Way and Yamori, 2014). Due to the seasonal fluctuations in temperature from summer to winter, needles of boreal evergreens are exposed to EEE because they continue to absorb light during the winter even though most of this absorbed energy cannot be used productively due to the low temperature-induced inhibition of photosynthetic CO_2 assimilation (Ensminger et al., 2004; Ivanov et al., 2001; Krivosheeva et al., 1996; Öquist, 1983; Öquist and Huner, 1991; Oquist and Hüner, 2003; Öquist and Martin, 1986; Sveshnikov et al., 2006; Stinziano et al., 2015; Way and Sage, 2008; Busch et al., 2009; Fréchette et al., 2015; Chang et al., 2021). Boreal evergreens develop frost hardiness or freezing tolerance which enables them to survive extreme winter

conditions by exploiting two primary environmental cues. First, the shortened photoperiod in late summer and autumn induces dormancy which terminates active growth. Second, this is coupled to low, freezing temperatures in the fall and winter that induce maximum frost hardiness within the genetically determined limitations of individual species. Thus, the mechanism employed by boreal evergreens to protect the overwintering photosynthetic apparatus includes down regulation photosynthetic efficiency (σ_{PSII}) by converting PSII reaction centres from energy transformers to energy quenchers dissipating EEE safely as heat through non-photochemical processes associated primarily with PSII reaction centres rather than a complete dependence on the xanthophyll cycle associated with PSII light harvesting complexes (Fig. 2) (Ivanov et al., 2001, 2003; Chang et al., 2021; Verhoeven, 2014; Fréchette et al., 2016; Ö;quist and Hüner, 2003). In the spring, quenched PSII reaction centers are converted back to energy transformers to provide the necessary energy for growth and development (Ö;quist and Hüner, 2003). The reversible interconversion between PSII energy transformers vs energy quenchers contributes to photoprotection and photostasis during the overwintering season in these boreal evergreens by modulating σ_{PSII}.

We note with interest that, although the Antarctic angiosperms, mosses, lichens, Arctic boreal forest evergreens as well as *Eutrema salsugineum* are generally considered extremophiles, we find no published experimental evidence to indicate that these photoautotrophs or any terrestrial plant species, for that matter, have been designated as photopsychrophilic despite their apparent adaptation to natural and extreme cold habitats. We conclude that similar to polar cyanobacteria (Tang and Vincent, 1999; Vincent, 2007) and the macro-alga, *S. latissima* (Schroeter et al. 2012, 2017), these Antarctic and Arctic terrestrial plant species are probably photopsychrotolerant rather than photopsychrophilic from which we conclude that photopsychrophily is not an essential adaptive strategy for the survival of polar terrestrial plants.

4. Phylogeny of photopsychrophily

It has been proposed that fragmentation of the original supercontinent, Gondwana, was accompanied by successive widespread glaciation events of the Earth (Hoffman et al., 1998). Kirschvink et al. (2000) hypothesized that this extensive glaciation lead to a "snowball Earth" in which the oceans were ice covered. It has been suggested that these successive glaciation events followed by extreme greenhouse conditions ("hot house") provided selective pressure on the evolution of life on Earth (Hoffman et al., 1998; Kirschvink et al., 2000). Prokaryotic organisms which dominated the Neoproterozoic era 1000 to 500 million years ago survived these extremely stressful glaciation events which gave rise to the evolution of red and green algae prior to the terminal glaciation event (Hofmann et al., 1990). A "succession of snowball glaciations must have imposed an intense environmental filter, resulting in a series of genetic 'bottleneck and flush' cycles" (Hofmann et al., 1990) which may have resulted in small populations or demes (Carson, 1987) of microbes that led to the evolution of psychrophiles and photopsychrophiles (Morgan-Kiss et al., 2008).

The Chlorophyta harbour more than a third of all confirmed photopsychrophiles of which 23 species can be placed in the order Chlamydomonadales (Fig. 11). Presently, researchers are employing shotgun environmental sequencing to characterize algal communities from cold environments (Bielewicz et al., 2011; Dolhi et al., 2013; Li et al., 2016). Cold-adapted Chlamydomonadales can be found in a number of polar and alpine environments, such as ice-covered lakes, sea ice, transitory meltwater ponds, and snowfields (Morgan-Kiss et al., 2006; Cvetkovska et al., 2017). At present, only about 93 confirmed algal photopsychrophilic species have been identified which include unicellular as well as macroalgal species which span green algae, rhodophytes, stramenopiles, and dinoflagellates (Fig. 11). This supports the thesis that photopsychrophily has probably evolved independently several times during eukaryotic algal evolution. However, establishing the number of times that photopsychrophily has arisen during algal evolution is not straightforward. This is a consequence of the minimal information available on the exact number of photopsychrophilic species within individual groups as well as their phylogenetic relationships. In addition, it is difficult to determine whether the shift to cold tolerance over evolutionary time was gained independently in multiple lineages or

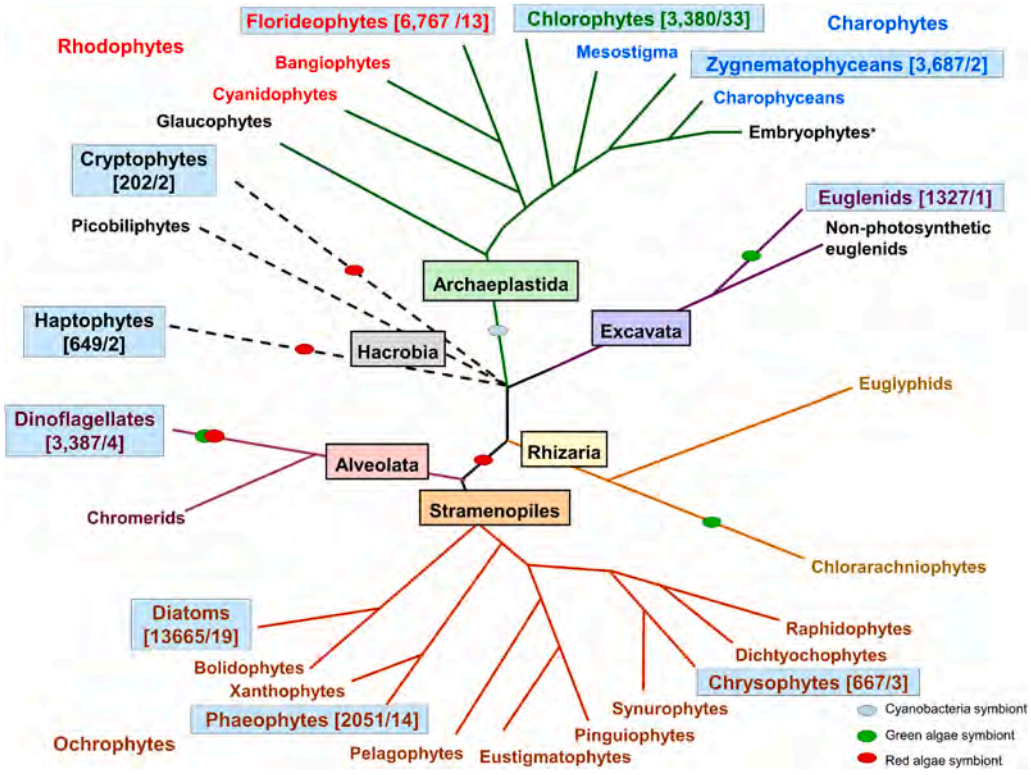


Fig. 11. Tree of eukaryotes highlighting lineages harboring known psychrophilic algae. Only major eukaryotic groups containing plastid-bearing photosynthetic organisms are shown. The branching pattern does not necessarily represent relationships between lineages. The dotted lines represent uncertain relationships and conflicting positions within the tree. The lineages containing psychrophiles are boxed in [total number of species/known number of psychrophilic species]. The branch containing the embryophyte lineage (marked with *) contains several species that are adapted to permanently cold environments, such as the Antarctic plants *Deschampsia antarctica* (Gramineae) and *Colobanthus quitensis* (Caryophyllene). These species, while permanently adapted to the cold, do not fit the definition of psychrophiles.

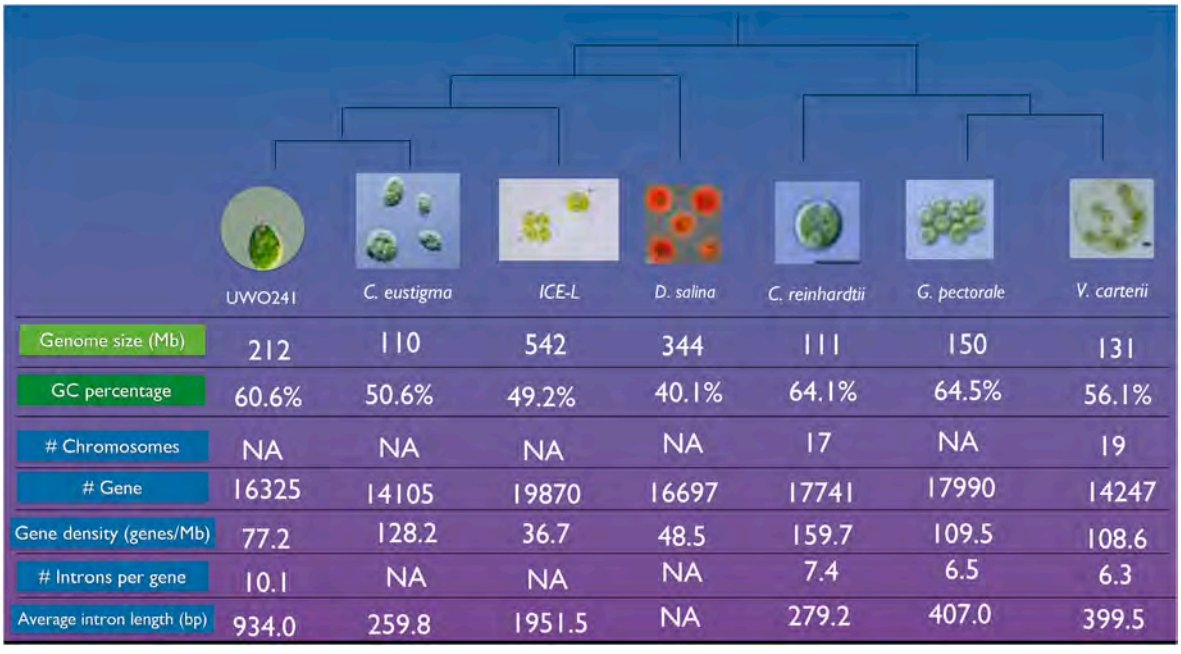
whether it represents an ancestral state. However, given the small number of photopsychrophilic species in any given family, we suggest that it is unlikely that the origin of algal photopsychrotolerance and photopsychrophily is ancestral.

5. Comparative genomics of eukaryotic photopsychrophiles

Compared to the plethora of genome sequences available in the molecular ecology of prokaryotes (Pinney et al., 2021), the genomic data base for eukaryotic microbes is substantially smaller (Keeling et al., 2014). Furthermore, the genomic data base available for photopsychrophiles is even more restricted. We highlight the novel genomic characteristics of confirmed green algal photopsychrophiles *Chlamydomonas sp. UWO241* (Zhang et al., 2021), *Chlamydomonas ICE-L* (Zhang et al., 2020) with the genomes of the mesophilic green algae, *C. reinhardtii, C,eustigma*, *G. pectorale* and *V. carteri* (Fig. 12; Fig. 13). ICE-L is the major contributor to primary productivity of the Antarctic sea ice ecosystem (Arrigo et al. 1997, 2012) in contrast to UWO241 which exists in the water column below the permanently ice-covered Lake Bonney. In addition, we include a brief comparison with the genome of the Antarctic psychrophilic diatom, *Fragilariopsis cylindrus* (Mock and Valentin, 2004; Mock et al., 2017) as well as the photopsychrotolerant, Antarctic green alga, *Coccomyxa subellipsoidea* (Blanc et al., 2012) (Fig. 12; Fig. 13).

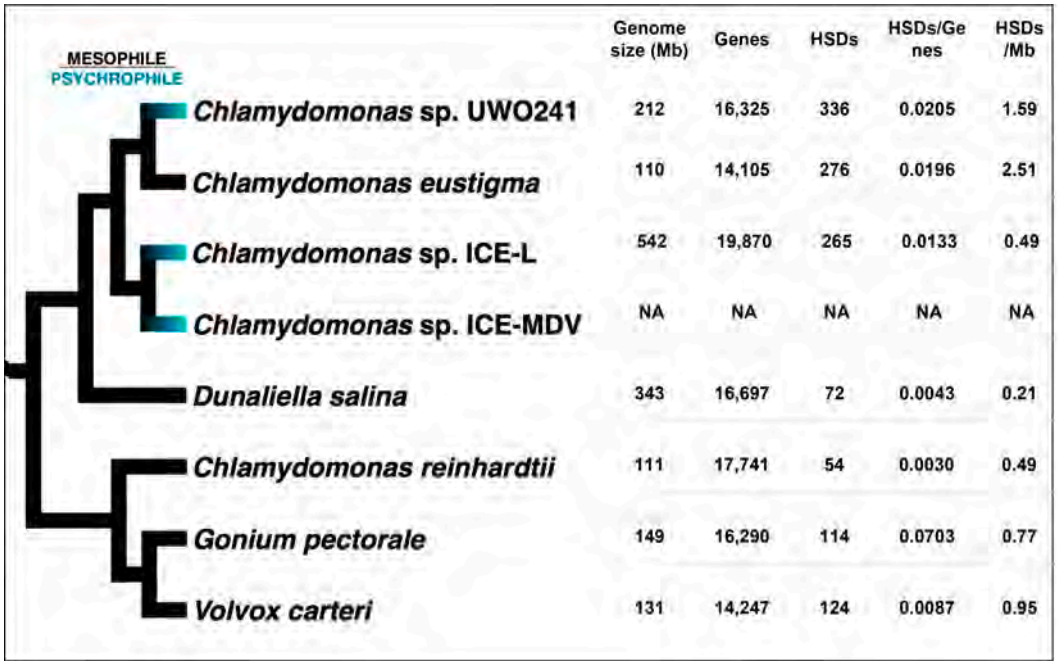
Our discussion is focused on four novel genomic characteristics putatively identified for photopsychrophilic green algae. First, the genome size of the two photopsychrophilic green algae, *Chlamydomonas sp. UWO241* and *Chlamydomonas ICE-L* is at least twice the size of the model mesophile, *C. reinhardtii* (Fig. 12; Fig. 13). Second, this is correlated with a relative gene density (gene/Mb) for UWO241 and ICE-l that is 30–60% lower on average than the 4 mesophiles *C. reinhardtii, C,eustigma*, *G. pectorale* and *V. carteri* even though the total number of genes in these genomes varied by only 8–12%. This lower gene density may be accounted for, in part, by an increase in the number of introns per gene (Fig. 12) as illustrated for Fd in UWO241 (Fig. 10A). Although *D. salina* is a mespohile, it is a halophilic extremophile and exhibits a gene density similar to that of the extremophiles, UWO241 and ICE-L (Fig. 12). Third, the presence of highly similar duplicates (HSD) in the genomes of *Chlamydomonas sp. UWO241* and *Chlamydomonas ICE-L* is 3 to 4-fold higher than that observed for the mesophiles examined (Fig. 13). The widespread gene duplication in UWO241 is unmatched in any chlorophyte genome studied to date totaling 1339 gene copies of HSDs (Zhang et al., 2021). Furthermore. the exonic sequences of more than half of the HSDs in UWO241 are under strong purifying selection based on low (<1.0) nonsynonymous to synonymous substitution rates (dN/dS), ranging from 0 to 0.5 (Zhang et al., 2021). Many of the HSDs in UWO241 are indistinguishable from each other at the amino acid level, and 65 HSDs exhibit identical nucleotide coding regions (Zhang et al., 2021). Epistasis with respect to protein amino acid sequence refers to the subtle impacts of residue-residue interactions that can occur either locally or at a distance that can affect protein folding and catalytic activity (Starr and Thornton, 2016). Thus, the observed changes in the temperature-dependent activities and structural stability reported for Fd1 and Stt7 from UWO241 may be epistatic in nature. However, the role of protein epistasis in protein evolution (Starr and Thornton, 2016) indicates that our attempts to link changes in gene sequence due to the evolution of photosychrophiles to changes in the protein primary structure and to adaptive changes in the structure and function of enzymes and proteins is much more complex than previously assumed by a strictly reductionist genomic approach.

Fourth, another novel feature of the green algal photopsychrophilic genomes is the presence of genes encoding no fewer than 37 ice-binding proteins (IBPs) of bacterial origin in UWO241 (Zhang et al., 2021) versus 12 in ICE-L (Zhang et al., 2020). These IBPs were presumably acquired by horizontal gene transfer (HGT). These data for UWO241 are among largest number of IBPs ever recorded in a photosynthetic protist (Zhang et al., 2021). The existence of IBPs in genomes is thought to be an adaptation to polar environments (Raymond and Kim, 2012). This may be expected in a species such as ICE-L that lives in the Antarctic sea ice where cells will be exposed to frequent freezing and thawing events (Zhang et al., 2020). Ice binding proteins inhibit ice recrystallization and include antifreeze proteins (AFP) which inhibit growth of ice crystals within the cytoplasm thus protecting cells from freezing damage (Griffith and Yaish, 2004; Griffith et al., 2005; Wisniewski et al., 2018). However, UWO241 exists within the Lake Bonney water column below the ice cover that remains at 5 °C year-round and therefore never freezes. Thus, the potential adaptive role of IBPs in UWO241 remains unclear. We suggest that the large number of genes encoding IBPs in



	UWO241	C. eustigma	ICE-L	D. salina	C. reinhardtii	G. pectorale	V. carterii
Genome size (Mb)	212	110	542	344	111	150	131
GC percentage	60.6%	50.6%	49.2%	40.1%	64.1%	64.5%	56.1%
# Chromosomes	NA	NA	NA	NA	17	NA	19
# Gene	16325	14105	19870	16697	17741	17990	14247
Gene density (genes/Mb)	77.2	128.2	36.7	48.5	159.7	109.5	108.6
# Introns per gene	10.1	NA	NA	NA	7.4	6.5	6.3
Average intron length (bp)	934.0	259.8	1951.5	NA	279.2	407.0	399.5

Fig. 12. Comparative genomics of green algal species. Top illustrates the phylogeny of the illustrated species and light microscopic images of each species.



	Genome size (Mb)	Genes	HSDs	HSDs/Genes	HSDs/Mb
Chlamydomonas sp. UWO241	212	16,325	336	0.0205	1.59
Chlamydomonas eustigma	110	14,105	276	0.0196	2.51
Chlamydomonas sp. ICE-L	542	19,870	265	0.0133	0.49
Chlamydomonas sp. ICE-MDV	NA	NA	NA	NA	NA
Dunaliella salina	343	16,697	72	0.0043	0.21
Chlamydomonas reinhardtii	111	17,741	54	0.0030	0.49
Gonium pectorale	149	16,290	114	0.0703	0.77
Volvox carteri	131	14,247	124	0.0087	0.95

Fig. 13. Comparative data illustrating the proportions of Highly Similar Duplicates (HSDs) in green algal species.

UWO241 may be a reflection of its ancestry rather than adaptation to its current environment. Alternatively, IBPs may have a unique but unknown function in UWO241. Further research is required to unravel this enigma.

Regulation of cell membrane viscosity by modulation of membrane lipid unsaturation is a major response to acclimation and adaptation to low temperature in all organisms (Browse et al., 1991; Nishida and Murata et al., 1996; Murata and Los, 1997; Siegenthaler and Tremolieres, 1998; Ivanov et al., 2012). Consistent with this role of membrane lipid unsaturation is the presence of expanded gene families associated with fatty acid unsaturation in ICE-L resulting in high levels of polyunsaturated fatty acids (PUFA) presumably to enhance membrane lipid viscosity at the consistent low temperature (Zhang et al., 2020). This is supported by earlier studies which reported differential expression of several fatty acid desaturases in ICE-L in response to salinity (An et al., 2013; He et al., 2019).

Fragilariopsis cylindrus is a photopsychrophilic diatom (Supplementary Fig. 2A) which represents the primary producer in the Southern Ocean for which it is considered an indicator species (Mock et al., 2017). Its 61.1 Mb genome is 4–8 times smaller than either UWO241 or ICE-L but consists of more genes (21,066) than either green algal photopsychrophile (Fig. 12) (Mock et al., 2017). Despite its smaller genome size, 29% of the *Fragilariopsis cylindrus* genes are represented by divergent alleles which indicates a high level of gene duplication (Proulx and Phillips, 2006). Thus, gene duplication appears to be a consistent feature of photopsychrophiles. Furthermore, like the two green algal photopsychrophiles, a family of 11 ice-binding proteins of bacterial origin are present in the genome of *Fragilariopsis cylindrus* presumably acquired through HGT (Mock et al., 2017).

Coccomyxa subellipsoidea C-169 is a small (3–9 μm), free-living, unicellular green alga (Supplementary Fig. 2B) with an optimal growth temperature of 20 °C isolated from Antarctic algal peat. This Antarctic green alga represents the first polar eukaryotic green alga to have its genome sequenced (Blanc et al., 2012). In contrast to the other Antarctic algae and *Fragilariopsis cylindrus* discussed above, *C. subellipsoidea* C-169 is classified as photopsychrotolerant rather than photopsychrophilic. Its 48.8 Mb genome size is similar to that of *Fragilariopsis cylindrus* but between 77 and 91% smaller than either green algal photopsychrophile (Fig. 12). Similar to the photopsychrophiles, *Coccomyxa subellipsoidea* C-169 exhibits marked gene duplication (7.2%) but approximately 50% fewer protein-encoding genes (9,851) (Blanc et al., 2012) than either the photopsychrophilic green algae or *Fragilariopsis cylindrus*.

Our genomic analyses of indicate that genetic redundancy may be a hallmark of not only of photopsychrophily but also photopsychrotolerance and adaptation to high salt environments. We hypothesize that genetic redundancy may be a prevalent characteristic of all photopsychrophilic and photopsychrotolerant extremophiles. However, given the limited number of published genome sequences presently available, more genome sequences of photosynthetic extremophiles from various habitats is required to validate this hypothesis.

6. Summary

An impressive biodiversity of algae and cyanobacteria dominate Antarctic and Arctic aquatic life. Although lichens and mosses dominate the Antarctic terrestrial landscape, angiosperms are represented by only two species, one monocot and one dicot. Our survey of photosynthetic adaptation in these organisms indicate that photoprotection and the maintenance of photostasis is an essential characteristic of photoautotrophic polar life whether terrestrial plant, or aquatic alga or photosynthetic prokaryote and irrespective of whether they are photopsychrophilic or photopsychrotolerant. The down-regulation of photosynthetic efficiency through modulation of σ_{PSII} by adjustments in either nonphotochemical quenching or the physical size of the light harvesting complexes, or enhancing sink capacity [n (τ^{-1})] by using O_2 as an alternative electron acceptor appear to be prominent photoprotective strategies that govern photostasis and photosynthetic adaptation to polar ecosystems. The mechanism employed appears to be species-dependent. However, these mechanisms for photoprotection and photostasis in response to environmental stress are not unique to polar organisms but are also prevalent in many mesophilic photoautotrophs (Demmig-Adams and Adams, 1996; Hüner et al., 2003; Horton and Ruban, 2005). This is consistent with the metaphor of evolution as a pliable "tinkerer" (Kohalmi, 2017) rather than a "ridged master".

These functional mechanisms are correlated with genome expansion and the genetic redundancy of the photosychrophiles and photopsychrotolerant species examined despite drastic differences in genome

size. We suggest that the combination of the maintenance of energy balance through an array of photoprotective mechanisms and the inherent genetic redundancy of photopsychrophilic and photopsychrotolerant species examined may confer the necessary resilience to survive the harsh polar environments.

Despite the requirement for the maintenance of photostasis, the evidence presented indicate that the enigma of photopsychrophily and photopsychrotolerance can not be explained by the presence of a single gene or molecular key or even a single gene family. Rather, photopsychrophily and photopsychrotolerance appear to be the result of a complex integration of myriad adaptations at various levels of cellular organization that evolved to allow survival in an extreme polar environment. Consequently, we suggest that photopsychrophily and photopsychrotolerance represent *emergent properties* of evolution in these extremely cold environments.

7. Future directions

A crucial limitation in the unravelling of the enigma of photopsychrophily and psychrotolerance is the lack of a sufficient number of sequenced genomes of Antarctic and Arctic photopsychrophilic and photopsychrotolerant species. Overcoming this limitation in the future is of paramount importance. This should contribute to understanding the link(s) between gene sequences, protein amino acid sequences, inherent protein temperature stability/activity and their link to low temperature adaptation.

Given the impact of present global warming on the Arctic and Antarctic ecosystems, further research should be focussed on the ability of photopsychrophiles and psychrotolerant polar species to adapt and survive elevated temperatures.

The ease with which eukaryotic photosynthetic model systems such as *Chlamydomonas reinhardtii* (Rochaix, 2014) and *Arabidopsis thaliana* (Kazachkova et al., 2018) can be cultured and genetically manipulated continues to be of critical importance in the identification of putative 'molecular keys' to unlock basic molecular mechanisms of cellular development and reproduction, photosynthesis, respiration and energy metabolism. Given that photopsychrophily and photopsychrotolerance appear to be emergent properties, the identification of non-model systems such as *Chlamydomonas sp* UWO241, *Chlamydomonas ICE-L* and *Fragilariopsis cylindrus* through which photopsychrophilic mutants can potentially be generated will be increasingly important to validate present assumptions linking the evolutionary significance to alterations in gene sequences. We can begin to address the genetic basis of photopsychrophily through mutational analyses and genome editing approaches using CRISPR-cas9 technology. However, it is essential that such a reductionist approach be combined with a systems approach that includes studies at the population level under controlled laboratory as well as natural field conditions (Kennicutt II et al., 2014; Kennicutt et al., 2015; Xavier et al., 2016; Morgan-Kiss et al., 2015).

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jplph.2021.153557.

References

Acuña-Rodríguez, I.S., Zúñiga-Venegas, L.A., Molina-Montenegro, M.A., 2021. Genotoxicity of oxidative stress and UV-B radiation in Antarctic vascular plants. Polar Biol. 44, 1029–1036.
Adams III, W.W., Demmig-Adams, B., 1993. In: Yamamoto, H.Y., Smith, C.M. (Eds.), Energy Dissipation and Photoprotection in Leaves of Higher Plants. Photosynthetic Responses to the Environment, vol. 8. Amer Soc Plant Physiol., pp. 27–36
An, M., Mou, S., Zhang, X., Zheng, Z., Ye, N., Wang, D., Zhang, W., Miao, J., 2013. Expression of fatty acid desaturase genes and fatty acid accumulation in *Chlamydomonas sp*. ICE-L under salt stress. Bioresour. Technol. 149, 77–83.
Allen, J.F., 1992. Protein phosphorylation in regulation of photosynthesis. Biochim. Biophys. Acta 1098, 275–335.
Allen, J.F., Bennett, J., Steinback, K.E., Arntzen, C.J., 1981. Chloroplast protein phosphorylation couples plastoquinone redox state to distribution of excitation energy between photosystems. Nature 291, 21–25.
Aluru, M.R., Rodermel, S.R., 2004. Control of chloroplast redox by the IMMUTANS terminal oxidase. Physiol. Plantarum 120, 4–11.
Aquist, J., Isaksen, G.V., Brandsdal, B.O., 2017. Computation of enzyme cold adaptation. Nature Rev. Chem. 1, 1–14.
Aro, E.-M., Virgin, I., Andersson, B., 1993. Photoinhibition of photosystem II. Inactivation, protein damage and turnover. Biochim. Biophys. Acta Bioenerg. 1143, 113–134.
Arrigo, K.R., Perovich, D.K., Pickart, R.S., Brown, Z.W., van Dijken, G.L., Lowry, K.E., Mills, M.M., Palmer, M.A., Balch, W.M., Bahr, F., Bates, N.R., Benitez-Nelson, C., Bowler, B., Brownlee, E., Ehn, J.K., Frey, K.E., Garley, R., Laney, S.R., Lubelczyk, L., Mathis, J., Matsuoka, A., Mitchell, B.G., Moore, G.W.K., Ortega-Retuerta, E., Pal, S., Polashenski, C.M., Reynolds, R.A., Schieber, B., Sosik, H.M., Stephens, M., Swift, J. H., 2012. Massive phytoplankton blooms under Arctic sea ice. Science 336, 1408.
Arrigo, K.R., Worthen, D.L., Lizotte, M.P., Dixon, P., Dieckmann, G., 1997. Primary production in Antarctic sea ice. Science 276, 394. https://doi.org/10.1126/science.276.5311.394.
Asada, K., 1994. Mechanisms for scavenging reactive molecules generated in chloroplasts under light stress. In: Baker, N.R., Bowyer, J.R. (Eds.), Photoinhibition of Photosynthesis- from Molecular Mechanisms to the Field. Bios Scientific, Oxford, UK, pp. 129–142.
Atkin, O., Tjoelker, M.G., 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. Trends Plant Sci. 8, 343–351.
Atkins, P., 2010. The Laws of Thermodynamics. A Very Short Introduction. Oxford University Press.
Bailey, S., Grossman, A., 2008. Photoprotection in cyanobacteria: regulation of light harvesting. Photochem. Photobiol. 84, 1410-142.
Baker, N.R., 2008. Chlorophyll fluorescence: a probe of photosynthesis in vivo. Annu. Rev. Plant Biol. 59, 89–113.
Bakermans, C., 2012. Psychrophiles: life in the cold. In: Aniton, R.P. (Ed.), Extremophiles: Micrbiology and Biotechnology. Caister Academic Press, pp. 53–76.
Bascunan-Godoy, L., Uribe, E., Zuniga-Feest, A., Corcuera, L., Bravo, L., 2006. Low temperature regulates sucrose-phosphate synthase activity in *Colobanthus quitensis* (Kunth) Bartl. by decreasing its sensitivity to Pi and increased activation by glucose-6-phosphate. Polar Biol. 1–7.
Baxter, A., Mittler, R., Suzuki, N., 2014. ROS as key players in plant stress signalling. J. Exp. Bot. 65, 1229–1240.
Bennett, J., 1991. Protein phosphorylation in green plant chloroplasts. Annu. Rev. Plant Physiol. Plant Mol. Biol. 42, 281–311.
Bhaya, D., Schwarz, R., Grossman, A.R., 2000. Molecular responses to environmental stress. In: Whitton, B.A., Potts, M. (Eds.), The Ecology of Cyanobacteria. Kluwer Academic, Dordrecht, pp. 397–442.
Bielewicz, S., Bell, E., Kong, W., Friedberg, I., Priscu, J.C., Morgan-Kiss, R.M., 2011. Protist diversity in a permanently ice-covered Antarctic Lake during the polar night transition. ISME J. 5, 1559–1564.
Blanc, G., Agarkova, I., Grimwood, J., Kuo, A., Brueggeman, A., Dunigan, D.D., Gurnon, J., Ladunga, I., Lindquist, E., Lucas, S., Pangilinan, J., Pröschold, T., Salamov, A., Schmutz, J., Weeks, D., Yamada, T., Lomsadze, A., Borodovsky, M., Claverie, J.-M., Grigoriev, I.V., Van Etten, J.L., 2012. The genome of the polar eukaryotic microalga Coccomyxa subellipsoidea reveals traits of cold adaptation. Genome Biol. 13, R39.
Bligh, J., Johnson, K.G., 1973. Glossary of terms for thermal physiology. J. Appl. Physiol. 35, 941–961.
Boehm, M., Alahuhta, M., Mulder, D.W., Peden, E.A., Long, H., Brunecky, R., Lunin, V.V., King, P.W., Ghirardi, M.L., Dubini, A., 2015. Crystal structure and biochemical characterization of Chlamydomonas FDX2 reveal two residues that, when mutated, partially confer FDX2 the redox potential and catalytic properties of FDX1. Photosynth. Res. 128, 45–57.
Bravo, L.A., Griffith, M., 2005. Characterization of antifreeze activity in Antarctic plants. J. Exp. Bot. 56, 1189–1196.
Bravo, L.A., Ulloa, N., Zuniga, G.E., Casanova, A., Corcuera, L.J., Alberdi, M., 2001. Cold resistance in Antarctic angiosperms. Physiol. Plantarum 111, 55–65.
Browse, J., Somerville, C., 1991. Glycerolipid synthesis: biochemistry and regulation. Annu. Rev. Plant Physiol. Plant Mol. Biol. 42, 467–506.

Busch, F., Hüner, N.P.A., Ensminger, I., 2009. Biochemical constrains limit the potential of the photochemical reflectance index as a predictor of effective quantum efficiency of photosynthesis during the winter spring transition in Jack pine seedlings. Funct. Plant Biol. 36, 1016–1026.
Carson, H.L., 1987. The genetic system, the deme, and the origin of species. Annu. Rev. Genet. 21, 405–423.
Casanueva, A., Tuffin, M., Cary, C., Cowan, D.A., 2010. Molecular adaptations to psychrophily: the impact of 'omic' technologies. Trends Microbiol. 18, 374–381.
Chang, C.Y., Bräutigam, K., Hüner, N.P.A., Ensminger, I., 2021. Champions of winter survival: cold acclimation and molecular regulation of cold hardiness in evergreen conifers. New Phytol. 229, 675–691.
Chory, J., Wu, D., 2001. Weaving the complex web of signal transduction. Plant Physiol. 125, 77–80.
Chown, S.L., Clarke, A., Fraser, C.I., Cary, S.C., Moon, K.L., McGeoch, M.A., 2015. The changing form of Antarctic biodiversity. Nature 522, 431–438.
Chrismas, N., Anesio, A., Sanchez-Baracaldo, P., 2015. Multiple adaptations to polar and alpine environments within cyanobacteria: a phylogenomic and Bayesian approach. Front. Microbiol. 6 article 01070.
Coleine, C., Stajich, J.E., Zucconi, L., Onofri, S., Selbmann, L., 2020. Sun exposure drives Antarctic cryptoendolithic community structure and composition. Polar Biol. 43, 607–615.
Colesie, C., Büdel, B., Hurry, V., Green, T.G.A., 2018. Can Antarctic lichens acclimatize to changes in temperature? Global Change Biol. 24, 1123–1135.
Collins, T., Roulling, F., Piette, F., Marx, J.-C., Feller, G., Gerday, C., D'Amico, S., 2008. Fundamentals of cold-adapted enzymes. In: Schinner, F., Marx, J.-C., Gerday, C. (Eds.), Psychrophiles from Biodiversity to Biotechnology (Margesin R. Springer-Verlag, Berlin, pp. 211–227.
Cook, G., Teufel, A., Kalra, I., Wang, X., Priscu, J., Morgan-Kiss, R., 2019. The Anarctic psychrophiles *Chlamydomonas spp.* UWO241 and ICE-MDV exhibit differential restructuring of photosystem I in response to iron. Photosynth. Res. https://doi.org/10.1007/s11120-019-00621-0.
Cvetkovska, M., Hüner, N.P.A., Smith, D.R., 2017. Chilling out: the evolution and diversification of psychrophilic algae with a focus on Chlamydomonadales. Polar Biol. 40, 1169–1184.
Cvetkovska, M., Orgnero, S., Hüner, N.P.A., Smith, D.R., 2019. The enigmatic loss of light-independent chlorophyll biosynthesis from an Antarctic green alga in a light-limited environment. New Phytol. 222, 651–656.
Cvetkovska, M., Szyszka-Mroz, B., Possmayer, M., Pittock, P., Lajoie, G., Smith, D.R., Hüner, N.P.A., 2018. Characterization of photosynthetic ferredoxin from the Antarctic alga *Chlamydomonas sp*. UWO241 reveals novel features of cold adaptation. New Phytol. 219, 588–604.
D'Amico, S., Marx, J.-C., Feller, G., Gerday, C., 2006. Psychrophilic microorganisms: challenges for life. EMBO Rep. 7, 385–389.
Demmig-Adams, B., Adams III, W.W., 1996. The role of xanthophyll cycle carotenoids in the protection of photosynthesis. Trends Plant Sci. 1, 21–26.
Dietz, K.-J., Mittler, R., Noctor, G., 2016. Recent progress in understanding the role of reactive oxygen species in plant cell signaling. Plant Physiol. 171, 1535–1539.
Dolhi, J.M., Maxwell, D.P., Morgan-Kiss, R.M., 2013. Antarctic *Chlamydomonas raudensis*: an emerging model for cold adatptation of photosynthesis. Extremophiles 17, 711–722.
Durnford, D.G., Falkowski, P.G., 1997. Chloroplast redox regulation of nuclear gene transcription during photoacclimation. Photosynth. Res. 53, 229–241.
England, J., 2020. Every Life Is on Fire- How Thermodynamics Explains the Origins of Living Things. Basic Books, New York.
Ensminger, I., Busch, F., Hüner, N.P.A., 2006. Photostasis and cold acclimation: sensing low temperature through photosynthesis. Physiol. Plantarum 126, 28–44.
Ensminger, I., Sveshnikov, D., Campbell, D.A., Funk, C., Jansson, S., Lloyd, J., Shibistova, O., Öquist, G., 2004. Intermittent low temperatures constrain spring recovery of photosynthesis in boreal Scots pine forests. Global Change Biol. 10, 995–1008.
Falkowski, P.G., Chen, Y.-B., 2003. Photoacclimation of light harvesting systems in eukaryotic algae. In: Green, B.R., Parson, W.W. (Eds.), Advances in Photosynthesis and Respration Light Harvesting Systems in Photosynthesis, vol. 13. Kluwer Academic Publishers, Dordrecht, pp. 423–447.
Feller, G., Gerday, C., 1997. Psychrophilic enzymes: molecular basis of cold adaptation. Cell. Mol. Life Sci. 53, 830–841.
Feller, G., Gerday, C., 2003. Psychrophilic enzymes: hot topics in cold adaptation. Nat. Rev. Microbiol. 1, 200–208.
Foyer, C.H., Ruban, A.V., Noctor, G., 2017. Viewing oxidative stress through the lens of oxidative signalling rather than damage. Biochem. J. 474, 877.
Fréchette, E., Chang, C.Y.-Y., Ensminger, I., 2016. Photoperiod and temperature constraints on the relationship between the photochemical reflectance index and the light use efficiency of photosynthesis in *Pinus strobus*. Tree Physiol. 36, 311–324.
Fréchette, E., Wong, C.Y.S., Junker, L.V., Chang, C.Y.-Y., Ensminger, I., 2015. Zeaxanthin-independent energy quenching and alternative electron sinks cause a decoupling of the relationship between the photochemical reflectance index (PRI) and photosynthesis in an evergreen conifer during spring. J. Exp. Bot. 66, 7309–7323.
Fryer, M.J., Andrews, J.R., Oxborough, K., Blowers, D.A., Baker, N.R., 1998. Relationship between CO_2 assimilation, photosynthetic electron transport, and active O_2 Metabolism in leaves of maize in during periods of low temperature. Plant Physiol. 116, 571–580.
Fujita, Y., Murakami, A., Aizawa, K., Ohki, K., 1994. Short-term and long-term adaptation of the photosynthetic apparatus: homeostatic properties of thylakoids. In: Bryant, D.A. (Ed.), The Molecular Biology of Cyanobacteria, Advances in Photosynthesis, vol. 1. Kluwer Academic, Dordrecht, pp. 677–692.
Gooseff, M.N., Barrett, J.E., Adams, B.J., Doran, P.T., Fountain, A.G., Lyons, W.B., McKnight, D.M., Priscu, J.C., Sokol, E.R., Takacs-Vesbach, C., Vandegehuchte, M.L., 2017. Decadal ecosystem response to an anomalous melt season in a polar desert in Antarctica. Nature Ecol. Evol. 1, 1334–1338.
Gray, A., Krolikowski, M., Fretwell, P., Convey, P., Peck, L.S., Mendelova, M., et al., 2020. Remote sensing reveals Antarctic green snow algae as important terrestrial carbon sink. Nat. Commun. 11, 2527.
Gray, M.W., 2017. Lynn Margulis and the endosymbiont hypothesis: 50 years later. Mol. Biol. Cell 28, 1285–1287.
Griffith, M., Yaish, M.W.F., 2004. Antifreeze proteins in overwintering plants: a tale of two activities. Trends Plant Sci. 9, 399–405.
Griffith, M., Lumb, C., Wiseman, S.B., Wisniewski, M., Johnson, R.W., Marangoni, A.G., 2005. Antifreeze proteins modify the freezing process in planta. Plant Physiol. 138, 330–340.
Griffith, M., Timonin, M., Wong, A.C.E., Gray, G.R., Akhter, S.R., Saldanha, M., Rogers, M.A., Weretilnyk, E.A., Moffatt, B., 2007. *Thellungiella*: an Arabidopsis-related model plant adapted to cold temperatures. Plant Cell Environ. 30, 529–538.
Griffiths, H.J., Anker, P., Linse, K., Maxwell, J., Post, A.L., Stevens, C., Tulaczyk, S., Smith, J.A., 2021. Breaking all the rules: the first recorded hard substrate sessile benthic community far beneath an Antarctic ice shelf. Front. Mar. Sci. 8 article 642040.
Grossman, A.R., 2021. 2021. Moving toward more model algae. J. Phycol. 57, 51–53.
Grossman, A.R., Schaefer, M.R., Chiang, G.G., Collier, J.L., 1993. The phycobilisome, a light-harvesting complex responsive to environmental conditions. Microbiol. Rev. 57, 725–749.
Grossman, A.R., Schaefer, M.R., Chiang, G.G., Collier, J.L., 1994. The responses of cyanobacteria to environmental conditions: light and nutrients. In: Bryant, D.A. (Ed.), Advances in Photosynthesis. The Molecular Biology of Cyanobacteria, vol. 1. Kluwer Academic, Dordrecht, pp. 641–675.
Grossman, A.R., Mackey, K.R.M., Bailey, S., 2010. A perspective on photosynthesis in oligotrophic oceans: hypothesis concerning alternate routes of electron flow. J. Phycol. 46, 629–634.
Gudynaite-Savitch, L., Gretes, M., Morgan-Kiss, R., Savitch, L., Simmonds, J., Kohalmi, S., Hüner, N.P.A., 2006. Cytochrome f from the Antarctic psychrophile, *Chlamydomonas raudensis* UWO 241: structure, sequence, and complementation in the mesophile, *Chlamydomonas reinhardtii*. Mol. Genet. Genom. 275, 387–398.
Gudynaite-Savitch, L., Loiselay, C., Savitch, L.V., Simmonds, J., Kohalmi, S., Choquet, Y., Hüner, N.P.A., 2007. The small domain of cytochrome f from the psychrophile, *Chlamydomonas raudensis* UWO 241, modulates the apparent molecular mass and decreases the accumulation of cytochrome f in the mesophile, *Chlamydomaonas reinhardtii*. Biochem. Cell. Biol. 85, 616–627.
Gupta, R., 2013. Genome Profiling of Two Strains of the Green Alga *Chlamydomonas Raudensis*. MSc Thesis, University of Western Ontario, p. 65pp.
He, Y., Zheng, Z., An, M., Chen, H., Qu, C., Liu, F., Wang, Y., Miao, J., Hou, X., 2019. Molecular cloning and functional analysis of a Δ 12-fatty acid desaturase from the Antarctic microalga Chlamydomonas sp. ICE-L. Biotech. 9, 1–9.
Heinrich, S., Valentin, K., Frickenhaus, S., Wiencke, C., 2012. Transcriptomic analysis of acclimation to temperature and light stress in *Saccharina latissima* (Phaeophyceae). PLoS One 7 e44342-e44342.
Hendrickson, L., Furbank, R.T., Chow, W.S., 2004. A simple alternative approach to assessing the fate of absorbed light energy using chlorophyll fluorescence. Photosynth. Res. 82, 73–81.
Hepworth, C., Wood, W.H.J., Emrich-Mills, T.Z., Proctor, M.S., Casson, S., Johnson, M.P., 2021. Dynamic thylakoid stacking and state transitions work synergistically to avoid acceptor-side limitation of photosystem I. Nature Plants 7, 87–93.
Hochachka, P., Somero, G.N., 1973. Strategies of Bichemical Adaptation. WB Saunders, Philadelphia, USA.
Hochachka, P.W., Somero, G.N., 2002. Biochemical Adaptation. Mechanisms and Process in Physiological Evolution. Oxford University Press Inc, New York, NY, USA).
Hoffman, P.F., Kaufman, A.J., Halverson, G.P., Schrag, D.P., 1998. A neoproterozoic snowball earth. Science 281, 1342. https://doi.org/10.1126/science.281.5381.1342.
Hofmann, H.J., Narbonne, G.M., Aitken, J.D., 1990. Ediacaran remains from intertillite beds in northwestern Canada. Geology 18, 1199–1202.
Hollis, L., Hüner, N.P.A., 2014. Retrograde operational sensing and signalling pathways maintain photostasis in green algae, cyanobacteria and terrestrial plants. Trends Photochem. Photobiol. 16, 47–61.
Hopkins, W.G., Hüner, N.P.A., 2009. Introduction to Plant Physiology, fourth ed. Wiley and Sons.
Horton, P., Ruban, A., 2005. Molecular design of the photosystem II light-harvesting antenna: photosynthesis and photoprotection. J. Exp. Bot. 56, 365–373.
Hoyer, K., Savall, T., Wiencke, C., 2001. Photoprotective substances in Antarctic macroalgae and thier variation with respect to depth distribution, different tissues and developmental stages. Mar. Ecol. Prog. Ser. 211, 117–129.
Hüner, N.P.A., Dahal, K., Bode, R., Kurepin, L.V., Ivanov, A.G., 2016. Photosynthetic acclimation, vernalization, crop productivity and 'the grand design of photosynthesis. J. Plant Physiol. 203, 29–43.
Hüner, N.P.A., Dahal, K., Hollis, L., Bode, R., Rosso, D., Krol, M., Ivanov, A.G., 2012. Chloroplast redox imbalance governs phenotypic plasticity: the "grand design of photosynthesis" revisited. Front. Plant Physiol. 3 article 255.
Hüner, N.P.A., Öquist, G., Sarhan, F., 1998. Energy balance and acclimation to light and cold. Trends Plant Sci. 3, 224–230.
Hüner, N.P.A., Öquist, G., Melis, A., 2003. Photostasis in plants, green algae and cyanobacteria: the role of light harvesting antenna complexes. In: Green, B.R., Parson, W.W. (Eds.), Advances in Photosynthesis and Respiration Light Harvesting

Antennas in Photosynthesis, vol. 13. Kluwer Academic Publishers, Dordrecht, pp. 401–421.
Ivanov, A.G., Miskiewicz, E., Clarke, A.K., Greenberg, B.M., Huner, N.P., 2000. Protection of photosystem II against UV-A and UV-B radiation in the ücyanobacterium *Plectonema boryanum*: the role of growth temperature and growth irradiance. Photochem. Photobiol. 72, 772–779.
Ivanov, A.G., Sane, P., Hurry, V., Krol, M., Sveshnikov, D., Hüner, N.P.A., et al., 2003. Low-temperature modulation of the redox properties of the acceptor side of photosystem II: photoprotection through reaction centre quenching of excess energy. Physiol. Plantarum 119, 376–383.
Ivanov, A.G., Sane, P.V., Zeinalov, Y., Malmberg, G., Gardestrom, P., Hüner, N.P.A., Öquist, G., 2001. Photosynthetic electron transport adjutments in overwintering Scots pine (*Pinus sylvestris* L). Planta 213, 575–585.
Ivanov, A.G., Sane, P.V., Simidjiev, I., Park, Y.-I., Hüner, N.P.A., Öquist, G., 2012. Restricted capacity for PSI-dependent cyclic electron flow in *petE* mutant compromises the ability for acclimation to iron stress in Synechococcus sp. PCC 7942 cells. Biochim. Biophys. Acta Bioenerg. 1871, 1277–1284.
Iwai, M., Takizawa, K., Tokutsu, R., Okamuro, A., Takahashi, Y., Minagawa, J., 2010. Isolation of the elusive supercomplex that drives cyclic electron flow in photosynthesis. Nature 464, 1210–1213.
Jackson, E.E., Hawes, I., Jungblut, A.D., 2021. 16S rRNA gene and 18S rRNA gene diversity in microbial mat communities in meltwater ponds on the McMurdo Ice Shelf, Antarctica. Polar Biol. 44, 823–836.
Johnson, G.N., Stepien, P., 2016. Plastid terminal oxidase as a route to improving plant stress tolerance: known knowns and known unknowns. Plant Cell Physiol. 57, 1387–1396.
Jung, H.-S., Chory, J., 2010. Signaling between chloroplasts and the nucleus: can a systems biology approach bring clarity to a complex and highly regulated pathway? Plant Physiol. 152, 453–459.
Kalra, I., Wang, X., Cvetkovska, M., Jeong, J., McHargue, W., Zhang, R., Hüner, N.P.A., Yuan, J.S., Morgan-Kiss, R., 2020. *Chlamydomonas* sp. UWO 241 exhibits high cyclic electron flow and rewired metabolism under high salinity. Plant Physiol. 183, 588–601.
Kant, S., Bi, Y.-M., Weretilnyk, E., Barak, S., Rothstein, S.J., 2008. The Arabidopsis halophytic relative *Thellungiella halophila* tolerates nitrogen-limiting conditions by maintaining growth, nitrogen uptake, and assimilation. Plant Physiol. 147, 1168.
Karpinski, S., Reynolds, H., Karpinska, B., Wingsle, G., Creissen, G., Mullineaux, P., 1999. Systemic signaling and acclimation in response to excess excitation energy in Arabidopsis. Science 284, 654–657.
Kashefi, K., Lovley, D.R., 2003. Extending the upper temperature limit for life. Science 301, 934.
Kazachkova, Y., Eshel, G., Pantha, P., Cheeseman, J.M., Dassanayake, M., Barak, S., 2018. Halophytism: what have we learnt from Arabidopsis thaliana: relative model systems? Plant Physiol. 178, 972–988.
Keeling, P.J., Burki, F., Wilcox, H.M., Allam, B., Allen, E.E., Amaral-Zettler, L.A., Armbrust, E.V., Archibald, M., Bharti, A.K., Bell, C.J., Beszteri, B., Bidle, K.D., Cameron, C.T., Campbell, L., Caron, D.A., Cattolico, R.A., Collier, J.L., Coyne, K., Davy, S.K., Deschamps, P., 2014. The Marine Microbial Eukaryote Transcriptome Sequencing Project (MMETSP): illuminating the functional diversity of eukaryotic life in the oceans through transcriptome sequencing. PLoS Biol. 12, 1–6.
Kennedy, F., Martin, A., Bowman, P., Wilson, R., McMinn, A., 2019. Dark metabolism: a molecular insight into how the Antarctic sea-ice diatom *Fragilariopsis cylindrus* survives long-term darkness. New Phytol. 223, 675–691.
Kennicutt II, M.C., Chown, S.L., et al., 2014. Polar research: six priorities for Antarctic science. Nature 512, 523–525.
Kennicutt, M.C., Chown, S.L., Cassano, J.J., et al., 2015. A roadmap for Antarctic and Southern Ocean science for the next two decades and beyond. Antarct. Sci. 27, 3–18.
Kirilovsky, D., 2007. Photoprotection in cyanobacteria: the orange carotenoid protein (OCP)-related non-photochemical-quenching mechanism. Photosynth. Res. 93, 7–16.
Kirilovsky, D., 2015. Modulating energy arriving at photochemical reaction centers: orange carotenoid protein-related photoprotection and state transitions. Photosynth. Res. 126, 3–17.
Kirschvink, J.L., Eric, J.G., Bertani, L.E., Nicholas, J.B., Jens, G., Linda, N.M., Rachel, E. S., 2000. Paleoproterozoic snowball earth: extreme climatic and geochemical global change and its biological consequences. Proc. Natl. Acad. Sci. U.S.A. 97, 1400–1405.
Knaff, D.B., 1996. Ferredoxin and ferredoxin-dependent enzymes. Advances in Photosynthesis. In: Ort, D.R., Yocum, C.F. (Eds.), Oxygenic Photosynthesis: the Light Reactions, vol. 4. Kluwer Academic, Dordrecht, pp. 333–361.
Kohalmi, S.E., Clayton, E.J., 2017. Tinker, tailor, soldier, enzyme. Nature Plants 3, 848–849.
Krause, G.H., Weis, E., 1991. Chlorophyll fluorescence and photosynthesis: the basics. Annu. Rev. Plant Physiol. Plant Mol. Biol. 42, 313–349.
Kramer, D.M., Evans, J.R., 2011. The importance of energy balance in improving photosynthetic productivity. Plant Physiol. 155, 70–78.
Kramer, D.M., Johnson, G., Kiirats, O., Edwards, G.E., 2004. New fluorescence parameters for the determination of Q_A redox state and excitation energy fluxes. Photosynth. Res. 79, 209–218.
Krivosheeva, A., Tao, D.-L., Ottander, C., Wingsle, G., Dube, S.L., Öquist, G., 1996. Cold acclimation and photoinhibition of photosynthesis in Scots pine. Planta 200, 296–305.
Krol, M., Maxwell, D.P., Hüner, N.P.A., 1997. Exposure of *Dunaliella salina* to low temperature mimics the high light-induced accumulation of carotenoids and the carotenoid binding protein (Cbr). Plant Cell Physiol. 38, 213–216.
Li, W., Podar, M., Morgan-Kiss, R.M., 2016. Ultrastructural and single-cell-level characterization reveals metabolic versatility in a microbial eukaryote community from an ice-covered Antarctic lake. Appl. Environ. Microbiol. 82, 3659–3670.
Liu, C., Huang, X., Wang, X., Zhang, X., Li, G., 2006. Phylogenetic studies on two strains of Antarctic ice algae based on morphological and molecular characteristics. Phycologia 45, 190–198.
Long, S.P., Humphries, S., Falkowski, P.G., 1994. Photoinhibition of photosynthesis in nature. Annu. Rev. Plant Physiol. Plant Mol. Biol. 45, 633–662.
Lyon, B.R., Mock, T., 2014. Polar microalgae: new approaches to an extreme and changing environment. Biology 3, 56–80.
MacKenzie, T.D., Krol, M., Hüner, N.P.A., Campbell, D.A., 2002. Seasonal changes in chlorophyll fluorescence quenching and the induction and capacity of photoprotective xanthophyll cycle in *Lobaria pulmonaria*. Can. J. Bot. 80, 255–261.
Margesin, R., Schinner, F., Marx, J.-C., Gerday, C., 2008. Psychrophiles: from Biodiversity to Biotechnolgy. Springer-Verlag, Berlin.
Maxwell, D.P., Falk, S., Hüner, N.P.A., 1995a. Photosystem II excitation pressure and development of resistance to photoinhibition I. LHCII abundance and zeaxanthin content in Chlorella vulgaris. Plant Physiol. 107, 687–694.
Maxwell, D.P., Falk, S., Trick, C.G., Hüner, N.P.A., 1994. Growth at low temperature mimics high-light acclimation in *Chlorella vulgaris*. Plant Physiol. 105, 535–543.
Maxwell, D.P., Laudenbach, D.E., Hüner, N.P.A., 1995b. Redox regulation of light-harvesting complex II and *cab* mRNA abundance in *Dunaliella salina*. Plant Physiol. 109, 787–795.
Maxwell, K., Johnson, G.N., 2000. Chlorophyll fluorescence—a practical guide. J. Exp. Bot. 51, 659–668.
McDonald, A.E., Ivanov, A.G., Bode, R., Maxwell, D.P., Rodermel, S.R., Hüner, N.P.A., 2011. Flexibility in photosynthetic electron transport: the physiological role of plastoquinol terminal oxidase (PTOX). Biochim. Biophys. Acta Bioenerg. 1807, 954–967.
McKay, R.M.L., La Roche, J., Yakunin, A.F., Durnford, D.G., Geider, R.J., 1999. Accumulation of ferredoxin and flavodoxin in a marine diatom in response to Fe. J. Phycol. 35, 510–519.
Melis, A., 1998. Photostasis in plants. In: Photostasis and Related Phenomena (Williams and Thistle. Plenum Press, New York, pp. 207–220.
Melis, A., 1999. Photosystem-II damage and repair cycle in chloroplasts: what modulates the rate of photodamage *in vivo*. Trends Plant Sci. 4, 130–135.
Miskiewicz, E., Ivanov, A.G., Hüner, N.P.A., 2002. Stoichiometry of the photosynthetic apparatus and phycobilisome structure of the cyanobacterium *Plectonema boryanum* UTEX 485 are regulated by both light and temperature. Plant Physiol. 130, 1414–1425.
Miskiewicz, E., Ivanov, A.G., Williams, J.P., Khan, M.U., Falk, S., Hüner, N.P.A., 2000. Photosynthetic acclimation of the filamentous cyanobacterium, *Plectonema boryanum* UTEX 485, to temperature and light. Plant Cell Physiol. 41, 767–775.
Mock, T., Thomas, D.N., 2008. Microalgae in polar regions: linking functional genomics and physiology with environmental conditions. In: Margesin, R., Schinner, F., Marx, J.-C., Gerday, C. (Eds.), Psychrophiles from Biodiversity to Biotechnology. Springer-Verlag, Berlin, pp. 285–312.
Mock, T., Otillar, R.P., Strauss, J., et al., 2017. Evolutionary genomics of the cold-adapted diatom *Fragilariopsis cylindrus*. Nature 541, 536–540.
Mock, T., Valentin, K., 2004. Photosynthesis and cold acclimation: molecular evidence from a polar diatom. J. Phycol. 40, 732–741.
Morgan-Kiss, R.M., Ivanov, A.G., Hüner, N.P.A., 2001. The antarctic psychrophile, *Chlamydomonas subcaudata*, is deficient in state I-state II transitions. Planta 214, 435–445.
Morgan-Kiss, R.M., Lizotte, M.P., Kong, W., Priscu, J.C., 2016. Photoadaptation to the polar night by phytoplankton in a permanently ice-covered Anarctic lake. Limnol. Oceanogr. 61, 3–13.
Morgan-Kiss, R.M., Ivanov, A.G., Modla, S., Czymmek, K., Hüner, N.P.A., Priscu, J.C., Lisle, J.T., Hanson, T.E., 2008. Identity and physiology of a new psychrophilic eukaryotic green alga, *Chlorella sp.*, strain BI, isolated from a transitory pond near Bratina Island, Antarctica. Extremophiles 12, 701–711.
Morgan-Kiss, R.M., Ivanov, A.G., Pocock, T., Krol, M., Gudynaite-Savitch, L., Hüner, N.P. A., 2005. The Antarctic psychrophile, *Chlamydomonas raudensis* Ettl (UWO241) (Chlorophyceae, Chlorophyta), exhibits a limited capacity to photoacclimate to red light. J. Phycol. 41, 791–800.
Morgan-Kiss, R.M., Priscu, J.C., Pocock, T., Gudynaite-Savitch, L., Hüner, N.P.A., 2006. Adaptation and acclimation of photosynthetic microorganisms to permanently cold environments. Microbiol. Mol. Biol. Rev. 70, 222–252.
Morgan, R.M., Ivanov, A.G., Priscu, J.C., Maxwell, D.P., Hüner, N.P.A., 1998. Structure and composition of the photochemical apparatus of the Antarctic green alga, *Chlamydomonas subcaudata*. Photosynth. Res. 56, 303–314.
Morita, R.Y., 1975. Psychrophilic bacteria. Bacteriol. Rev. 39, 144–167.
Murata, N., Los, D.A., 1997. Membrane fluidity and temperature perception. Plant Physiol. 115, 875–879.
Murata, N., Takahashi, S., Nishiyama, Y., Allakhverdiev, S.I., 2007. Photoinhibition of photosystem II under environmental stress. Biochim. Biophys. Acta Bioenerg. 1767, 414–421.
Mykytczuk, N.C.S., Foote, S.J., Omelon, C.R., Southam, G., Greer, C.W., Whyte, L.G., 2013. Bacterial growth at −15°C;molecular insights from the permafrost bacterium Planococcus halocryophilus Or1. ISME J. 7, 1211–1226.
Nadeau, T.L., Castenholz, R.W., 2000. Characterization of psychrophilic oscillatorians (cyanobacteria) from Antarctic meltwater ponds. J. Phycol. 36, 914–923.
Nawrocki, W.J., Tourasse, N.J., Taly, A., Rappaport, F., Wollman, F.-A., 2015. The plastid terminal oxidase: its elusive function points to multiple contributions to plastid physiology. Annu. Rev. Plant Biol. 66, 49–74.
Nelson, N., 2011. Photosystems and global effects of oxygenic photosynthesis. Biochim. Biophys. Acta Bioenerg. 1807, 856–863.
Nemhauser, J.L., Chory, J., 2009. Photomorphogenesis. In: The Arabidopsis Book. The Arabidopsis Book. The American Society of Plant Biologists, pp. 1–12.

Neukermans, G., Oziel, L., Babin, M., 2018. Increased intrusion of warming Atlantic water leads to rapid expansion of temperate phytoplankton in the Arctic. Global Change Biol. 24, 2545–2553.
Nishida, I., Murata, N., 1996. Chilling sensitivity in plants and cyanobacteria: the crucial contribution of membrane lipids. Annu. Rev. Plant Physiol. Plant Mol. Biol. 47, 541–2553.
Nott, A., Jung, H.-S., Koussevitzky, S., Chory, J., 2006. Plastid-to-nucleus retrograde signalling. Ann. Rev.Plant Biol. 57, 739–759.
Obryk, M.K., Doran, P.T., Friedlaender, A.S., Gooseff, M.N., Li, W., Morgan-Kiss, R.M., Priscu, J.C., Schofield, O., Stammerjohn, S.E., Steinberg, D.K., Ducklow, H.W., 2016. Responses of Antarctic marine and freshwater ecosystems to changing ice conditions. Bioscience 66, 864–879.
Öquist, G., 1983. Effects of low temperature on photosynthesis. Plant Cell Environ. 6, 281–301.
Öquist, G., Chow, W.S., Anderson, J.M., 1992. Photoinhibition of photosynthesis represents a mechanism for long-term regulation of photosystem II. Planta 186, 450–460.
Öquist, G., Hüner, N.P.A., 2003. Photosynthesis of overwintering evergreen plants. Annu. Rev. Plant Biol. 54, 329–355.
Öquist, G., Hüner, N.P.A., 1991. Effects of cold acclimation on the susceptibility of photosynthesis to photoinhibition in Scots pine and in winter and spring cereals: a fluorescence analysis. Funct. Ecol. 5, 91–100.
Öquist, G., Martin, B., 1986. Cold climates. In: Baker, N.R., Long, S.P. (Eds.), Photosynthesis in Contrasting Environments, vol. 7. Elsevier, New York, pp. 237–293.
Ort, D., Baker, N.R., 2002. A photoprotective role for O_2 as an alternative electron sink in photosynthesis? Curr. Opin. Plant Biol. 5, 193–198.
Ort, D.R., 2001. When there is too much light. Plant Physiol. 125, 29–32.
Osmond, C.B., 1994. What is photoinhibition? Some insights from comparison of shade and sun plants. In: Baker, N.R., Bowyer, J.R. (Eds.), Photoinhibition of Photosynthesis-From Molecular Mechanisms to the Field. Bios Scientific Publishers, Oxford UK, pp. 1–24.
Oxborough, K., Lee, P., Horton, P., 1987. Regulation of thylakoid protein phosphorylation by high-energy-state quenching. FEBS Lett. 221, 211–214.
Peden, E.A., Boehm, M., Mulder, D.W., Davis, R., Old, W.M., King, P.W., Ghirardi, M.L., Dubini, A., 2013. Identification of global ferredoxin interaction networks in Chlamydomonas reinhardtii. J. Biol. Chem. 288, 35192–35209.
Petrou, K., Hill, R., Brown, C.M., Campbell, D.A., Doblin, M.A., Ralph, P.J., 2010. Rapid photoprotection in sea-ice diatoms from the East Antarctic pack ice. Limnol. Oceanogr. 55, 1400–1407.
Petrou, K., Hill, R., Doblin, M.A., McMinn, A., Johnson, R., Wright, S.W., Ralph, P.J., 2011. Photoprotection of sea-ice microalgal communities from the east Antarctic pack ice. J. Phycol. 47, 77–86.
Perez-Torres, E., Bravo, L.A., Corcuera, L.J., Johnson, G.N., 2007. Is electron transport to oxygen an important mechanism in photoprotection? Contrasting responses from Antarctic vascular plants. Physiol. Plantarum 130, 185–194.
Perera Castro, A., Flexas, J., González-Rodríguez, A., Fernandez-Marin, B., 2021. Photosynthesis on the edge: photoinhibition, desiccation and freezing tolerance of Antarctic bryophytes. Photosynth. Res. 149, 135–153.
Perez-Torres, E., Dinamarca, J., Bravo, L., Corcuera, L., 2004. Responses of *Colobanthus quitensis* (Kunth) Bartl. to high light and low temperature. Polar Biol. 27, 183–189.
Pesaresi, P., Pribil, M., Wunder, T., Leister, D., 2011. Dynamics of reversible protein phosphorylation in thylakoids of flowering plants: the roles of STN7, STN8 and TAP38. Biochim. Biophys. Acta 1807, 887–896.
Pfannschmidt, T., 2003. Chloroplast redox signals: how photosynthesis controls its own genes. Trends Plant Sci. 8, 33–41.
Pfannschmidt, T., Yang, C., Peter, N., Chong, K., 2012. The hidden function of photosynthesis: a sensing system for environmental conditions that regulates plant acclimation responses. Protoplasma 249, 125–136.
Pinney, M.M., Mokhtari, D.A., Akiva, E., Yabukarski, F., Sanchez, D.M., Liang, R., Doukov, T., Martinez, T.J., Babbitt, P.C., Herschlag, D., 2021. Parallel molecular mechanisms for enzyme temperature adaptation. Science 371, eaay2784.
Pocock, T., Lachance, M.-A., Proschold, T., Priscu, J.C., Kim, S.S., Hüner, N.P.A., 2004. Identification of a psychrophilic green alga from Lake Bonney Antarctica : *Chlamydomonas raudensis* ettl. (UWO 241) *chlorophyceae*. J. Phycol. 40, 1138–1148.
Pocock, T.H., Koziak, A., Rosso, D., Falk, S., Hüner, N.P.A., 2007. *Chlamydomonas raudensis* (UWO 241), *Chlorophyceae,* exhibits the capacity for rapid D1 repair in response to chronic photoinhibition at low temperature. J. Phycol. 43, 924–936.
Possmayer, M., Gupta, R.K., Szyszka-Mroz, B., Maxwell, D.P., Lachance, M.A., Hüner, N. P.A., Smith, D.R., 2016. Resolving the phylogenetic relationship between *Chlamydomonas sp*. UWO 241 and *Chlamydomonas raudensis* SAG49.72 (*Chlorophyceae*) with nuclear and plastid DNA sequences. J. Phycol. 52, 305–310.
Priscu, J.C., Fritsen, C.H., Adams, E.E., Giovannoni, J., Paerl, H.W., McKay, C.P., Doran, P.T., Gordon, D.A., Lanoil, B.D., Pinckney, J.L., 1998. Perennial Antarctic lake ice: an oasis for life in a polar desert. Science 280, 2095–2098.
Proulx, S.R., Phillips, P.C., 2006. Allelic divergence precedes and promotes gene duplication. Evolution 60, 881–892.
Queval, G., Foyer, C.H., 2012. Redox regulation of photosynthetic gene expression. Phil. Trans. Biol. Sci. 367, 3475–3485.
Rainer, J., 2000. Do ultrastable proteins from hyperthermophiles have high or low conformational rigidity? Proc. Natl. Acad. Sci. Unit. States Am. 97, 2962–2964.
Raymond, J.A., Kim, H.J., 2012. Possible role of horizontal gene transfer in the colonization of sea ice by algae. PLoS One 7 e35968-e35968.
Reinbothe, S., Reinbothe, C., 1996. Regulation of chlorophyll biosynthesis in angiosperms. Plant Physiol. 111, 1–7.
Rochaix, J.-D., 2014. Regulation and dynamics of the light-harvesting system. Annu. Rev. Plant Biol. 65, 287–309.
Rogers, A.D., 2007. Evolution and biodiversity of Antarctic organisms: a molecular perspective. Phil. Trans. Roy. Soc. B 362, 2191–2214.
Sabine, C.L., Feely, R.A., Gruber, N., Key, R.M., Lee, K., Bullister, J.L., Wanninkhof, R., Wong, C.S., Wallace, D.W.R., Tilbrook, B., Millero, F.J., Peng, T.-H., Kozyr, A., Ono, T., Rios, A.F., 2004. The oceanic sink for anthropogenic CO_2. Science 305, 367.
Sagan, L., 1967. On the origin of mitosing cells. J. Theor. Biol. 14, 225–274.
Schorsch, M., Kramer, M., Goss, T., Eisenhut, M., Robinson, N., Osman, D., Wilde, A., Sadaf, S., Brückler, H., Walder, L., Scheibe, R., Hase, T., Hanke, G.T., 2018. A unique ferredoxin acts as a player in the low-iron response of photosynthetic organisms. Proc. Natl. Acad. Sci. Unit. States Am. 115, E12111–E12120.
Schreiber, U., Schliwa, U., Bilger, W., 1986. Continuous recording of photochemical and non-photochemical chlorophyll fluorescence quenching with a new type of modulation fluorometer. Photosynth. Res. 10, 63–73.
Schroedinger, E., 1947. What Is Life? the Physical Aspect of the Living Cell. Cambridge University Press, p. p184.
Schroeter, B., Green, T.G.A., Kulle, D., Pannewitz, S., Schlensog, M., Sancho, L.G., 2012. The moss *Bryum argenteum* var. muticum Brid. is well adapted to cope with high light in continental Antarctica. Antarct. Sci. 24, 281–291.
Schroeter, B., Green, T.G.A., Pintado, A., Türk, R., Sancho, L.G., 2017. Summer activity patterns for mosses and lichens in Maritime Antarctica. Antarct. Sci. 29, 517–530.
Seckbach, J., 2007. Algae and Cyanobacteria in Extreme Environments. Springer, Dordrecht.
Siddiqui, K.S., Williams, T.J., Wilkins, D., Yau, S., Allen, M.A., Brown, M.V., Lauro, F.M., Cavicchioli, R., 2013. Psychrophiles. Ann. Rev. Earth Planet Sci. 41, 87–115.
Siddiqui, K.S., Cavicchioli, R., 2006. Cold-adapted enzymes. Ann.Rev. Biochem. 75, 403–433.
Siegenthaler, P.-A., Tremolieres, A., 1998. Role of acyl lipids in the function of photosynthetic membranes in higher plants. In: Siegenthaler, P.-A. (Ed.), Advances in Photosynthesis and Respiration. Lipids in Photosynthesis: Structure, Function and Genetics, vol. 6. Kluwer Academic Publishers, Dordrecht, pp. 145–173.
Somero, G.N., 2004. Adaptation of enzymes to temperature: searching for basic "strategies.". Comp. Biochem. Physiol., B 139, 321–333.
Sommers, P., Darcy, J.L., Gendron, E.M.S., Stanish, L.F., Bagshaw, E.A., Porazinska, D.L., Schmidt, S.K., 2017. Diversity patterns of microbial eukaryotes mirror those of bacteria in Antarctic cryoconite holes. FEMS Microbiol. Ecol. 94, fix167.
Starr, T.N., Thornton, J.W., 2016. Epistasis in protein evolution. Protein Sci. 25, 1204–1218.
Stepien, P., Johnson, G.N., 2009. Contrasting responses of photosynthesis to salt stress in the glycophyte Arabidopsis and the halophyte Thellungiella: role of the plastid terminal xxidase as an alternative electron sink. Plant Physiol. 149, 1154–1165.
Stinziano, J.R., Hüner, N.P.A., Way, D.A., 2015. Warming delays autumn declines in photosynthetic capacity in a boreal conifer, Norway spruce (*Picea abies*). Tree Physiol. 35, 1303–1313.
Streb, P., Josse, E.-M., Gallouet, E., Baptist, F., Kuntz, M., Cornic, G., 2005. Evidence for alternative electron sinks to photosynthetic carbon assimilation in the high mountain plant species *Ranunculus glacialis*. Plant Cell Environ. 28, 1123–1135.
Sutherland, D.L., Howard-Williams, C., Ralph, P., Hawes, I., 2020. Environmental drivers that influence microalgal species in meltwater pools on the McMurdo Ice Shelf, Antarctica. Polar Biol. 43, 467–482.
Sveshnikov, D., Ensminger, I., Ivanov, A.G., Campbell, D.A., Lloyd, J., Funk, C., Hüner, N.P.A., Öquist, G., 2006. Excitation energy partitioning and quenching during cold acclimation in Scots pine. Tree Physiol. 26, 325–336.
Szyszka-Mroz, B., Cvetkovska, M., Ivanov, A.G., Smith, D.R., Possmayer, M., Maxwell, D. P., Hüner, N.P.A., 2019. Cold-adapted protein kinases and thylakoid remodeling impact energy distribution in an Antarctic psychrophile. Plant Physiol. 180, 1291–1309.
Szyszka-Mroz, B., Pittock, P., Ivanov, A.G., Lajoie, G., Hüner, N.P.A., 2015. The Antarctic psychrophile *Chlamydomonas sp*. UWO 241 preferentially phosphorylates a photosystem I-cytochrome b6/f supercomplex. Plant Physiol. 169, 717–736.
Szyszka, B., Ivanov, A.G., Hüner, N.P.A., 2007. Psychrophily is associated with differential energy partitioning, photosystem stoichiometry and polypeptide phosphorylation in *Chlamydomonas raudensis*. Biochim. Biophys. Acta Bioenerg. 1767, 789–800.
Takahashi, H., Clowez, S., Wollman, F.-A., Vallon, O., Rappaport, F., 2013. Cyclic electron flow is redox-controlled but independent of state transition. Nat. Commun. 4, 2954.
Tanaka, R., Tanaka, A., 2007. Tetrapyrrole biosynthesis in higher plants. Annu. Rev. Plant Biol. 58, 321–346.
Tang, E.P.Y., Tremblay, R., Vincent, W.F., 1997. Cyanobacterial dominance of polar freshwater ecosystems - high-latitude mat-formers adapted to low temperature. J. Phycol. 33, 171–181.
Tang, E.P.Y., Vincent, W.F., 1999. Strategies of thermal adaptation by high-latitude cyanobacteria. New Phytol. 142, 315–323.
Terauchi, A.M., Lu, S.-F., Zaffagnini, M., Tappa, S., Hirasawa, M., Tripathy, J.N., Knaff, D.B., Farmer, P.J., Lemaire, S.D., Hase, T., Merchant, S.S., 2009. Pattern of expression and substrate specificity of chloroplast ferredoxins from Chlamydomonas reinhardtii. J. Biol. Chem. 284, 25867–25878.
Terrado, R., Scarcella, K., Thaler, M., Vincent, W.F., Lovejoy, C., 2013. Small phytoplankton in Arctic seas: vulnerability to climate change. Biodiversity 14, 2–18.
Thomas, D.N., Dieckmann, G.S., 2002. Antarctic sea ice–a habitat for extremophiles. Science 295, 641.
Velasco, V.M.E., Mansbridge, J., Bremner, S., Carruthers, K., Summers, P.S., Sung, W.W. L., Champigny, M.J., Weretilnyk, E.A., 2016. Acclimation of the crucifer *Eutrema*

salsugineum to phosphate limitation is associated with constitutively high expression of phosphate-starvation genes. Plant Cell Environ. 39, 1818–1834.
Verhoeven, A.S., 2014. Sustained energy dissipation in winter evergreens. New Phytol. 201, 57–65.
Vincent, W., 2000. Cyanobacterial dominance in the polar regions. In: Whitton, B.A., Potts, M. (Eds.), The Ecology of Cyanobacteria. Kluwer Academic, Dordrecht, pp. 321–340.
Vincent, W.F., 2007. Cold tolerance in cyanobacteria and life in the cryosphere. In: Seckbach, J. (Ed.), Algae and Cyanobacteria in Extreme Environments. Springer, Dordrecht, pp. 289–301.
Way, D.A., Oren, R., 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. Tree Physiol. 30, 669–688.
Way, D.A., Sage, R.F., 2008. Elevated growth temperatures reduce the carbon gain of black spruce [*Picea mariana* (Mill.) B.S.P.]. Global Change Biol. 14, 624–636.
Way, D.A., Yamori, W., 2014. Thermal acclimation of photosynthesis: on the importance of adjusting our definitions and accounting for thermal acclimation of respiration. Photosynth. Res. 119, 89–100.
Whitton, B.A., Potts, M., 2000. The Ecology of Cyanobacteria: Their Diversity in Time and Space. Kluwer Academic, Dordrecht.
Wiencke, C., Hop, H., 2016. Ecosystem Kongsfjorden: new views after more than a decade of research. Polar Biol. 39 https://doi.org/10.1007/s00300-016-2032-9.
Wilson, K.E., Ivanov, A.G., Öquist, G., Grodzinski, B., Sarhan, F., Hüner, N.P.A., 2006. Energy balance, organellar redox status and acclimation to environmental stress. Can. J. Bot. 1355–1370.
Wisniewski, M., Nassuth, A., Arora, R., 2018. Cold hardiness in trees: a mini-review. Front. Plant Sci. 9 article 1394.
Woodson, J.D., Chory, J., 2008. Coordination of gene expression between organellar and nuclear genomes. Nat. Rev. Genet. 9, 383–395.
Wunder, T., Xu, W., Liu, Q., Wanner, G., Leister, D., Pribil, M., 2013. The major thylakoid protein kinases STN7 and STN8 revisited: effects of altered STN8 levels and regulatory specificities of the STN kinases. Front. Plant Physiol. 4 article 417.
Wynn-Williams, D.D., 2000. Cyanobacteria in deserts- life at the limit? In: Whitton, B.A., Potts, M. (Eds.), The Ecology of Cyanobacteria. Kluwer Academic, Dordrecht, pp. 341–366.
Xavier, J.C., Brandt, A., Ropert-Coudert, Y., Badhe, R., Gutt, J., Havermans, C., Jones, C., Costa, E.S., Lochte, K., Schloss, I.R., Kennicutt II, M.C., Sutherland, W.J., 2016. Future challenges in Southern Ocean ecology research. Front. Marine Sci. 3 article 94.
Yumoto, I., 2013. Cold Adapted Microorganisms. Caister Academic Press, UK.
Zakhia, F., Jungblut, A.-D., Taton, A., Vincent, W., Wilmotte, A., 2008. In: Margesin, R., Schinner, F., Marx, J.-C., Gerday, C. (Eds.), Cyanobacteria in Cold Ecosystems. Psychrophiles from Biodiversity to Biotechnology. Springer-Verlag, Berlin, pp. 121–135.
Zer, H., Ohad, I., 2003. Light, redox state, thylakoid-protein phosphorylation and signaling gene expression. Trends Biochem. Sci. 28, 467–470.
Zhang, X., Cvetkovska, M., Morgan-Kiss, R., Hüner, N.P.A., Smith, D.R., 2021. Draft genome sequence of the Antarctic green alga. Chlamydomonas sp. UWO241. iScience. https://doi.org/10.1016/j.isci.2021.102084.
Zhang, Z., Qu, C., Yao, R., Nie, Y., Xu, C., Miao, J., Zhong, B., 2019. The parallel molecular adaptations to the Antarctic cold environment in two psychrophilic green algae. Genome Biol Evol 11, 1897–1908.
Zhang, Z., Qu, C., Zhang, K., He, Y., Zhao, X., Yang, L., Zheng, Z., Ma, X., Wang, X., Wang, W., Wang, K., Li, D., Zhang, L., Zhang, X., Su, D., Chang, X., Zhou, M., Gao, D., Jiang, W., Leliaert, F., Bhattacharya, D., De Clerck, O., Zhong, B., Miao, J., 2020. Adaptation to extreme Antarctic environments revealed by the genome of a sea ice green alga. Curr. Biol. 30, 3330–3341.