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Review article

Photosynthetic adaptation and multicellularity in the Antarctic psychrophile, *Chlamydomonas priscuii*

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ABSTRACT

Acclimation, adaptation and survival in persistent cold polar environments are complex phenomena associated with myriad molecular, biochemical and physiological mechanisms. The psychrophile, *Chlamydomonas priscuii*, is endemic to Lake Bonney, Antarctica. Adaptation to its extreme polar environment includes homeoviscous adaptation of membranes, maintenance of energy balance through photostasis and surface area to volume ratio. In addition to these mechanisms, this psychrophile can exist in culture as motile, single cells or as immobile, multicellular palmelloids. Comparative biochemical, physiological, microscopic and spectroscopic analyses of purified single cells and palmelloids indicate that the conversion of single cells to multicellular palmelloids alters the composition and organization of the photosynthetic apparatus. This enhances photoprotection of the photosynthetic apparatus from light and low temperature stress by minimizing potential cellular energy imbalances and safely dissipating excessive excitation energy by nonphotochemical quenching mechanisms. In addition to decreased susceptibility to predation, enhanced photoprotection from photoinhibition associated with palmelloid formation may be a complementary, selective, evolutionary advantage for the induction of multicellularity in green algae.

1. Introduction

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 [1]. Consequently, they are important components that govern global carbon balance and moderate the impact of global climate change on the biosphere.

These vast cold, Arctic and Antarctic ecosystems sequester at least 32 % of the total global CO_2 annually in the form of "blue carbon" [2,3]. As illustrated in Fig. 1, the aquatic photosynthetic productivity, estimated by chlorophyll *a* (Chla) concentration, is highest globally in the North Pacific, the North Atlantic and the Southern Ocean and is an order of magnitude more productive than the tropical regions of the Pacific and the Atlantic Oceans (Fig. 1). It is thought that the immense areas of these polar aquatic ecosystems more than compensates for the low species diversity with respect to their contributions as sinks for global photosynthetic CO_2 assimilation compared to the tropical terrestrial ecosystems [2–5]. In addition to the polar Atlantic and Southern Oceans, permanently ice-covered lakes are characteristic of continental Antarctica [3–6]. Notwithstanding their important contributions to global CO_2 sequestration, these micro-organisms that dominate the polar oceans and permanently ice-covered lakes present in continental Antarctic represent some of the least studied organisms on our planet [6–10].

The ecosystem services provided by the polar photoautotrophs are a consequence of the light- and temperature-dependent process of photosynthesis which is essential for the maintenance and regulation of energy flow for the whole planet. This is achieved through the transformation of energy in the form of sunlight into biomass energy. This photosynthetic ecosystem service is reflected in the distribution of biomass on Earth. Plants and micro-organisms represent about 82 % and 17 % respectively of Earth's total biomass [11]. The latter includes the photosynthetic micro-organisms such as algae and cyanobacteria that

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dominate our vast oceans, lakes, rivers and streams. Energy from the Sun through the process of photosynthesis generated the 550 gigatons (Gt) of carbon biomass present on Earth today over millions of years of evolution.

Despite climate change and global warming, our planet remains a rather cold place [12]. Oceans that cover approximately 70 % of the Earth's surface have characteristic temperatures of ≤5 °C. The polar Arctic and Antarctic regions constitute approximately 20 % of the surface area. Finally, the mountainous, alpine regions of the world constitute about another 5 % of the Earth's surface [12]. However, the study of non-model terrestrial and aquatic life endemic to polar regions provides an exceptional opportunity to understand the basis of novel adaptations to these extreme environments, which are not necessarily accessible through research focussed on model systems [14–31].

2. Photosynthetic adaptation to extreme polar environments

2.1. Cell membranes and cold adaptation

Poikilotherms, including photoautotrophs (plants, green algae, cyanobacteria) as well as heterotrophs (e.g. bacteria, fungi, reptiles, and fish) are unable to control their cellular temperature which is strictly dependent upon the vagaries of the ambient environment. Cellular function and compartmentation are strictly dependent upon the presence of cell membranes. However, changes in temperature can severely impact membrane stability and function [5,29–32]. To ensure the stability and function of these cellular membranes in response to cold temperature, poikilothermic organisms must adjust membrane lipid and fatty acid composition to maintain membrane fluidity in the cold. This response is called homeoviscous adaptation which, in plants, algae and cyanobacteria, generally has been focussed on modulation of the membrane lipid and the acyl chain composition in response to cold stress and cold acclimation [32–44,46,47].

The Antarctic psychrophile, *C. priscuii*, cultured at its optimum low growth temperature (8 °C) exhibits homeoviscous adaptation when compared to the model mesophile cultured at its optimum growth temperature (29°); indeed, there is a 1.44 higher unsaturation index for *C. priscuii* (2.74) compared to *C. reinhardtii* (1.90) [48]. This probably contributes to a greater membrane fluidity at low temperature in the psychrophile than in the mesophile. Thylakoid membrane stability as a function of temperature can be assessed by monitoring the change in background Chla fluorescence yield (Fo) [49–52]. The critical temperature for a change in membrane stability in *C. priscuii* (40 °C), was 10° lower than that for *C. reinhardtii* (50 °C) which is consistent with the observed differences in unsaturation index [48].

2.2. Photostasis and cold adaptation

Non-model organisms from the extreme polar habitats represent successful adaptation to life at the edge [5,28,52]. With respect to temperature adaptation, organisms are typically classified as either eurythermic or stenothermic. The former reflects organisms that can tolerate a wide temperature range whereas the latter can tolerate a much narrower range [53]. The Antarctic green alga, *C. priscuii*, is unique compared to the model green alga, *C. reinhardtii*, because the former is an extremophile that is adapted to persistent and consistent low temperature, high salt and low daily light levels, combined with extreme annual variation in photoperiod [5,28]. In addition, *C. priscuii* is a photopsychrophile (photosynthetic psychrophile) [53] that is obligately adapted to low temperature (0–12 °C) and will die at temperatures ≥ 20 °C [5,54]. Photopsychrophiles are photoautrophs which distinguishes them from all other heterotrophic psychrophiles including fungi [55,56] and bacteria [30,57–59]. However, not all photosynthetic polar micro-organisms are stenothermic psychrophiles. Many polar microbes

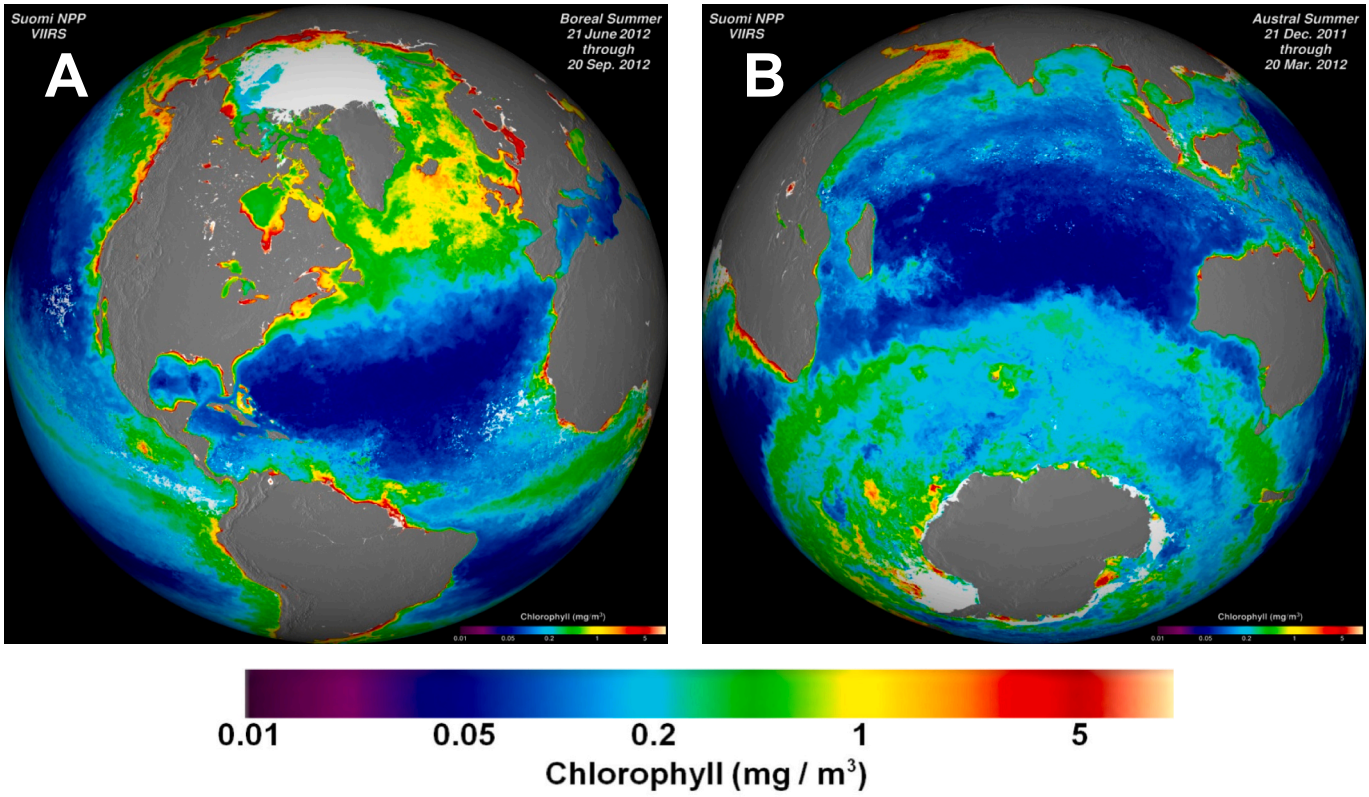

Fig. 1. Global aquatic chlorophyll concentrations. A - Northern hemisphere; B - Southern hemisphere.
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are psychrotolerant eurytherms and, thus, abide a much wider range of temperatures than stenothermic psychrophiles [61,62].

For both psychrophilic or psychrotolerant organisms, 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-dependent, redox reactions associated with photosynthetic electron transport and the soluble stromal enzymes involved in CO_2 assimilation through the Calvin-Benson-Bassham Cycle (CBB). The CBB consumes ATP and photosynthetic reductants to reduce C, N and S required for cellular maintenance, growth, development and reproduction. A major challenge for all polar photoautotrophs is to balance the flow of energy from the source, in the form of absorbed photons involved in photosynthetic photochemistry, to the metabolic sinks. These sinks consume the energy in the biochemical, enzyme-catalyzed reactions generating metabolites needed for growth, development, and reproduction in a thermodynamically challenging habitat [63–69]. The maintenance of cellular energy balance in photosynthetic organisms is referred to as photostasis [64,65,70,71] and is required to minimize the production of reactive oxygen species (ROS) and reduce the potential for oxidative damage. However, ROS are two-faced Janus. Not only does their accumulation during stress result in cellular damage, but ROS are also important stress-related signalling molecules [72–74].

As summarized in Table 1, myriad mechanisms have evolved in terrestrial plants and aquatic algae in response to cold adaptation and the attainment of photostasis. These include regulation of the absorption of light through modulation of the *physical size* of the light harvesting complexes associated with the photosystems via redox regulation of transcription of nuclear *Lhcb* genes [27,75–79], the transition between typical linear electron flow (LEF) through PSII and PSI versus PSI cyclic electron flow (CEF) as well as the reduction of O_2 via the plastid terminal oxidase (PTOX) in the process of chlororespiration [21,80–95]. In addition, state transitions, governed by redox regulated phosphorylation-dephosphorylation of PSII light harvesting polypeptides, control the energy distribution between PSII and PSI to fine tune photosynthesis and are considered essential in photoprotection of the photosynthetic apparatus from excessive excitation energy (EEE) [89] in plants and green algae [90–95].

Additional photoprotective mechanisms have evolved that govern the partitioning of energy between photochemical versus non-photochemical quenching (NPQ) to dissipate EEE safely as heat via photosystem II (PSII) light harvesting antennae and the xanthophyll cycle [96–103]. The induction of xanthophyll cycle activity affects the *functional size* of the photosystem light harvesting complexes through the conversion of the light harvesting carotenoid violaxanthin to the energy dissipating carotenoids antheraxanthin and zeaxanthin which reduces the photosynthetic efficiency of light absorption and ensures the safe dissipation of EEE as heat through NPQ [65,104–106,108–110]. Although the cost of these photoprotective mechanisms is a general decrease in photosynthetic light absorption efficiency, the benefits include enhanced probability of survival associated with short-term acclimation and long-term adaptation of photosynthetic organisms to EEE to reduce sensitivity to photoinhibition induced upon exposure to various stress conditions [111–117].

The regulation of photosynthetic electron flow, state transitions and energy partitioning contribute to the attainment of photostasis by protecting the photosynthetic apparatus from potential photodamage due to exposure to EEE in extreme environments. This includes restructuring and reorganizing the photosynthetic apparatus which is governed by redox retrograde signalling to regulate the expression of photosynthetic nuclear genes in plants and algae [118–125]. This usually affects changes in phenotype as reflected in major changes in pigmentation in algae such as *C. vulgaris* [25,26], *C. reinhardtii* [84,110], *D. tertiolecta* [116–118], *D. salina* [27,119,120] as well as the filamentous cyanobacterium, *Plectonema boryanum* [121,122]. The phenotypic changes

Table 1
Proposed cellular/molecular mechanisms of cold adaptation in psychrophilic (cold-adapted) microorganisms.

	Proposed cold-adaptation functions	References
Proteins/enzymes	Maintenance of adequate metabolic flux	Szyszka-Mroz et al. [129] Feller et al. [185] Devos et al. [186] Miyazaki et al. [187] Feller and Gerday [188] Casanueva et al. [13] Paredes et al. [189] Siddiqui et al. [29]
Lipids, membrane fatty acids, unsaturated fatty acids long-chain polyunsaturated fatty acids (LC-PUFA)	Maintenance of membrane fluidity	Russell and Fukunaga [191] Morgan-Kiss et al. [48] Mock and Kroon [192] Králová [198] Hassan et al. [194]
Photosynthetic apparatus	Maintenance of light harvesting capacity and photosynthetic electron flow	Szyszka-Mroz et al. [128] Cvetkovska et al. [158] Morgan et al. [48] Mock and Valentin [196] Mock and Hock [195] Morgan-Kiss et al. [5] Zhang et al. [194]
Pigments: carotenoids	Modulation of membrane fluidity Photoprotection Antioxidants	Chattopadhyay et al. [200] Jagannadham et al. [198] Leya et al. [199] Dieser et al. [201] Shen et al. [202]
Compatible solutes	Osmoprotection against freezing induced osmotic stress, desiccation protection against freezing induced desiccation, cryopreservation	Ghobakhlou et al. [203] Fonseca et al. [204] Goordial et al. [205] Raymond et al. [206]
Antifreeze proteins Ice-nucleating proteins	Ice growth and recrystallisation inhibition Extracellular ice crystal nucleation	Gilbert et al. [207] Muryoi et al. [208] Raymond et al. [209] Bar Dolev et al. [210]
Chaperones	Maintenance of protein folding and stability Destabilisation of RNA/DNA secondary structures	Tosco et al. [211] Yoshimune et al. [212] Romero-Romero et al. [213] Collins and Gerday [214] Cvetkovska et al. [54]

reflect photosynthetic acclimation characterized by decreases in total Chl, increases in the ratio of Chla/b and lower levels of light harvesting or phycobilisome polypeptides resulting in a decrease in the efficiency of photosynthetic light absorption.

A novel feature of the Antarctic psychrophile, *Chlamydomonas priscuii*, is that it exhibits minimal phenotypic changes in pigmentation in response changes in light levels or exposure to low temperature [5,11,123] compared to model plants such as *Arabidopsis thaliana* [124] and mesophilic green algae such as *C. reinhardtii* [84,110], *C. vulgaris* [25,26], *D. tertiolecta* [124–126] and *D. salina* [27,127,128]. Furthermore, *C. priscuii* is deficient in the capacity to perform state transitions [5,11,125,126]. This deficiency may be a consequence of an altered thylakoid protein kinase required for thylakoid protein phosphorylation [127–130] which preferentially phosphorylates a subunit of a PSI-Cytb6/f supercomplex which governs the high rates of PSI cyclic electron flow in *C. priscuii*. This is not observed in other model plant or green algal systems [135–137]; however, a similar deficiency in state transitions was observed for the Arctic psychrophile, *Chlamydomonas malina*. Notably, the Antarctic psychrophile, *Chlamydomonas* sp. ICE-MVD, was able to perform classic state transitions like the mesophile *C. reinhardtii* [11]. Clearly, the inability to perform state transitions is not a general characteristic of photopsychrophily in polar green algae. In addition to these novel characteristics, *C. priscuii* also exhibits a weak phototactic response compared to either the mesophile, *C. reinhardtii*, and the Antarctic psychrophile, ICE-MVD [130]. This weak phototactic response in *C. priscuii* is associated with a reduction in the repertoire of genes encoding photoreceptors important in phototaxis as well as its unusually small eyespot [130]. ICE-MVD exhibited a much stronger phototactic response than *C. priscuii*, the authors concluded that a weak phototactic response is not a characteristic of psychrophily, but rather, probably reflects shade-adaptation of *C. priscuii* to its natural, Lake Bonney habitat [130].

We suggest that homeoviscous adaptation and the maintenance of photostasis is essential for polar algae to survive life at the edge.

3. Multicellularity

Myriad acclimation strategies have evolved to enhance survival to environmental stress (Table 1). However, the intensity combined with the time-period over which an algal culture is exposed to a particular environmental stress is also a crucial factor that will ultimately determine survival. Are there alternative mechanisms to homeoviscous adaptation, phototaxis and photostasis that algae exploit to acclimate and adapt to conditions of prolonged stress? When the physiological and molecular mechanisms are no longer sufficient to protect against a particular stress, some algae have evolved higher-order, developmental strategies for survival through the conversion of single cells into either multicellular aggregates and/or multicellular structures called palmelloids [131–137]. The conversion of a motile, single cell to either an immobile, cellular aggregate consisting of hundreds of cells or a multicellular palmelloid consisting of 2 to 16 individual cells has been interpreted to represent stages in the onset of multicellularity in the evolution of eukaryotes [136–138]. In bacteria, cyclic di-GMP has been shown to regulate the transition from a motile lifestyle to a non-motile, sessile lifestyle important in the formation of complex biofilms [139–143]. Recently, the advent of complex cell architecture has also been reported in the Asgard archaea, *Candidatus Lokiarcheaum ossiferum*, from which it is suggested that multicellular eukaryotes may have emerged [144].

The transition from a single cell to a colonial palmelloid is the result of abnormal cell division and flagellar structure [145,146], which can be induced by various stress conditions including pollutants, low pH, temperature and oxidative stress [147–155]. Chloroplatinic acid induces palmelloid formation in *Chlamydomonas eugamentos* by inhibiting the release of cells from the mother cell after cell division [152]. Interestingly, the cold-adapted Arctic strain of *Haematococcus pluvialis* exists predominantly as an organized palmelloid [156]. It appears that any abrupt deviation from the optimal growth conditions potentially induces a transition from single cells to palmelloids and colonial aggregates in green algae. For example, exposure of the mesophile, *C. reinhardtii*, to a lower than the optimal growth temperature induces palmelloid formation whereas shifting the psychrophile, *C. priscuii*, to supra-optimal temperatures induces palmelloid formation (Figs. 2, 3) [157]. Most recently, it was reported that *C. reinhardtii* also forms palmelloids in response to salt stress [159,160]. Thus, we suggest that, in general, any prolonged environmental perturbation may impose a selective pressure for the transition to multicellularity in green algae.

Experimental evidence indicates that one evolutionary advantage of either cell aggregation or palmelloid formation is decreased susceptibility to predation by rotifers and other natural predators compared to the single cell state [136,137,148,149,153,154]. Exciting new evidence has been uncovered by de Carpentier et al. [136,137] elucidating the underlying molecular mechanism of cell aggregation in *C. reinhardtii*. The response of this model mesophile, to abiotic stress is to induce a collective behaviour between individual single cells to form large, random cell aggregates that protect the cells from heat shock. De Carpentier et al. [136,137] generated a family of socializer (*saz*) mutants of *C. reinhardtii* that aggregate spontaneously. Using a multi-omics approach, they showed that the observed cell aggregation is a result of genetic reprogramming and substantial modification of the secretome rather than passive agglutination. Exposure of WT cells to the media of *saz1* cells after those cells had been removed induced aggregation in WT cells. Analyses of the media of *saz1* cells indicated the presence of pherophorins, matrix metalloproteinases, serine-proline-rich proteins and lysis oxidases. Three pherophorin mutants (*phc30*, *phc41* and *phc50*) failed to aggregate and it was concluded that specific pherophorins are involved in the aggregation process in *C. reinhardtii*. Furthermore, the two pherophorin mutants (*phc28* and *phc35*) aggregated spontaneously [137], indicating that the products of these genes inhibit aggregation. These results provide key insights into the mechanisms and genes involved in the origins of multicellularity in green algae [138–141]. However, organization of single cells into a multicellular palmelloid must reflect a developmental response that is distinct from the apparent random aggregation reported by de Carpentier et al. [136,137]. Recent results show that, although the psychrophilic *C. priscuii* forms

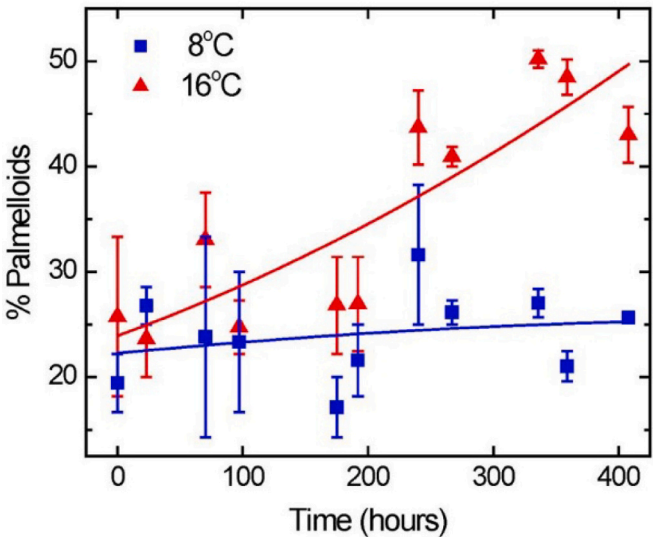

Fig. 2. The effect of temperature on palmelloid formation in C. priscuii. *C. priscuii* was cultured at either 8 °C (blue, controls) or 16 °C (red, temperature stress) as described in detail in [157]. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

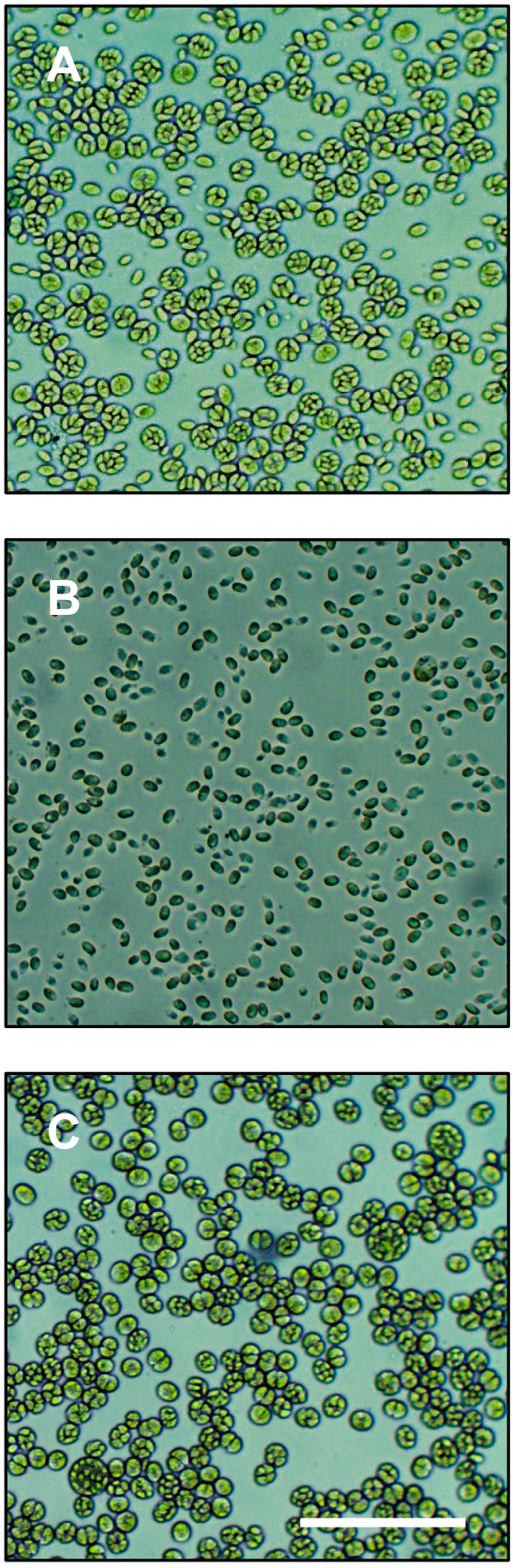

Fig. 3. Light microscope images of *C. priscuii* control cells (A), isolated single cells (B) and isolated palmelloids (C). Magnification 40×, scale bars 100 μm (A, B and C).

palmelloids, it does not aggregate upon exposure to salt stress in contrast to *C. reinhardtii* (Fig. 4). However, *C. priscuii* does have a vegetative lytic enzyme (VLE) gene, homologous to that of *C. reinhardtii* and this gene appears to be complete and is present in three distinct copies in the *C. priscuii* genome [12a]. Thus, it would appear that *C. priscuii* has the potential to aggregate similar to *C. reinhardtii* but is inhibited from doing so. Further research is required to elucidate the regulation and molecular basis of palmelloid formation versus cellular aggregation in *C. priscuii*.

3.1. Multicellularity and the surface area to volume ratio

The growth rates of unicellular algal species are generally believed to depend on physiological, metabolic and environmental factors (temperature, salinity, etc.). In addition, several studies have shown that cell size is also a major factor for growth by its dependence on the surface area to volume (S/V) ratio and hence the rate of nutrient uptake [161,162]. Furthermore, it was hypothesised that the balance of selective pressures affecting S/V ratio is critical in aqueous environments, where autotrophic algal species compete for nutrients absorbed through their surface membranes [161–163]. Indeed, a positive correlation between growth rates, nutrient uptake, temperature, carbon assimilation, the maximum photosynthetic rate and S/V ratio has been reported in various algal species [163–171].

The origin and evolution of organismal complexity (i.e., the transition from unicellular to multicellular) have been studied extensively and require several selective and mechanistic prerequisites (see [176] for a review). Several previous studies [171–181], have shown that single-cell organisms can readily evolve multicellularity when subjected to the right environmental selective pressures [182]. It has been reported that the appearance of a multicellular structures derived from a unicellular one was accompanied by a remarkable change in *Chlamydomonas*-specific and volvocine-specific cell cycle and reproductive gene expression patterns [179].

The transition from motile unicellular organisms to colonial and/or larger multicellular aggregates is accompanied by a variety of requirements and ultimately has benefits and costs. Commonly, various environmental selective pressures are assumed to be the driving force for unicellular organisms to increase in size. The general constraint limiting the increase of cell size is the decrease in the surface to volume ratio (S/V ratio), which reduces the exchange of nutrients and thus the growth rates of the cells [181–184]. To avoid these constraints, several unicellular organisms including various algal species developed the strategy of holding the mitotic products (daughter cells) together by extracellular material, thus increasing in size by forming aggregates/palmelloids without significant alterations in S/V ratio of the individual cells [180–188]. However, forming a group (aggregates/palmelloids) would decrease the S/V ratio of the newly formed multicellular structure which was referred to as the “transport limitation” and was viewed as a general aspect of evolutionary transitions by Solari et al. [184]. Thus, the metabolic and viability constraints in larger structures (colonies/palmelloids) might provide a strong enough selective pressure to push the organismal design to germ-soma differentiation and higher complexity [29,184,185,187–189,191–193].

3.2. Multicellularity and photoprotection

Axenic cultures of *C. priscuii* propagated at low temperatures (4–10 °C) under continuous light represent a typical mixture of 20 % nonmotile palmelloids and 80 % motile single cells (Fig. 3) [157]. Compared to single cells, palmelloids of *C. priscuii* show decreased levels of the PSII light-harvesting complex II (LHCII) proteins consistent with a 2-fold higher Chl a/b ratio during growth at 16 °C than growth at 8 °C [157] which reduces light absorption efficiency. This is reflected in comparative difference 77 K fluorescence emission spectroscopy of *C. priscuii* single cells compared to palmelloids [157]. This spectroscopic

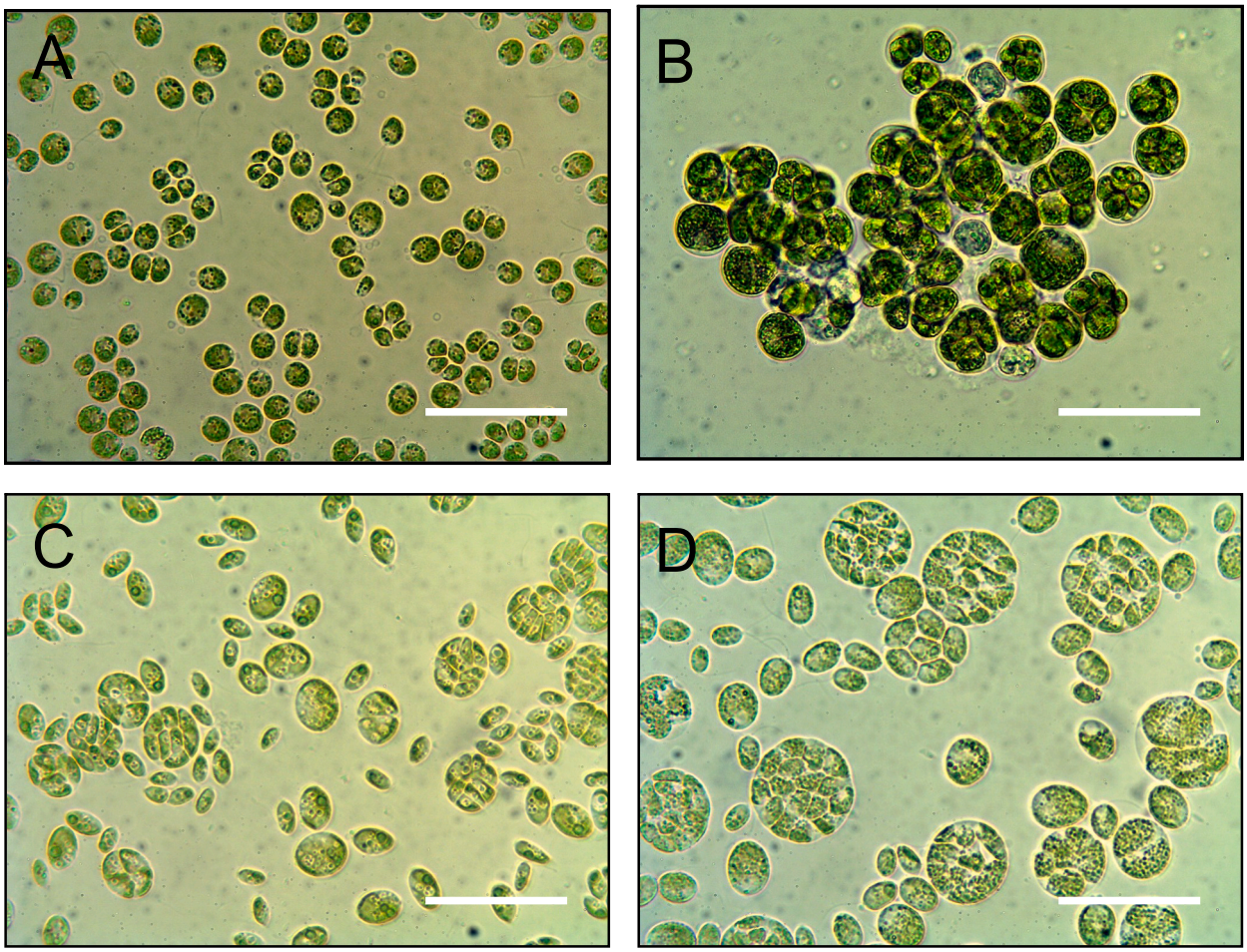

Fig. 4. Light microscope images of *Chlamydomonas reinhardtii* cultures grown in Bold's Basal medium (BBM), supplemented with 25 mM NaCl (A) and 200 mM NaCl (B). *Chlamydomonas priscuii* cultures grown in BBM, supplemented with 25 mM NaCl (C) and 700 mM NaCl (D). Magnification 40×. Scale bars, 20 μm.

technique is very sensitive to changes in the pigment and polypeptide compositions as well as the organization of PSII and PSI and their functional interactions [50–52]. Thus, surprisingly, the transition from single cells to multicellular palmelloids appears to result in detectable alterations in the organization and composition of the PSI and PSII pigment-protein complexes [157].

Comparative room temperature Chla fluorescence induction combined with 77 K Chla fluorescence emission spectroscopic analyses of isolated cells and palmelloids indicated that, although the maximum PSII photochemical efficiency, measured as Fv/Fm, was comparable for isolated single cells and isolated palmelloids, excitation pressure, measured as 1-qL, was lower in palmelloids than single cells [157] consistent with an increased capacity to dissipate EEE in palmelloids compared to single cells. This differential level of excitation pressure was associated with 50 % higher light saturated rates of ETR in palmelloids relative to single cells exposed to high light at low temperature. The decreased sensitivity to high light was by enhanced non-regulated dissipation of EEE (ΦNO) presumable through reaction centre quenching rather than normal antenna quenching via the xanthophyll cycle [63,64]. Functionally, the temperature-induced morphological transition of *C. priscuii* from a single to a multicellular state alters the composition and organization of the photosynthetic apparatus which predisposes it to dissipate EEE via non-regulated dissipation of excess absorbed energy [157]. Thus, single cells are morphologically and photosynthetically distinct from the single cells enclosed within a palmelloid. We suggest that in addition to decreased susceptibility to predation, palmelloid formation results in photoprotection from photoinhibition under EEE conditions. Thus, palmelloid formation may be an additional selective criterion for multicellularity in some green algae which has not been considered previously, to our knowledge. However, the molecular mechanism underlying the observed alterations in the organization of the photosynthetic apparatus in response to the transition of single cells to multicellular palmelloids remains to be elucidated (Fig. 5).

4. Conclusions

Cold adaptation of *C. priscuii* is dependent upon the combination of homeoviscous adaptation combined with the maintenance of photostasis and optimum S/V ratio. The exposure of *C. priscuii*, to increased growth temperatures close to non-permissive conditions (18–20 °C) is stressful for this stenothermic psychrophile. In response to this temperature stress, *C. priscuii*, shifts its morphology from motile, single cells to immobile, multicellular palmelloids which protects its photosynthetic apparatus from EEE by reducing light absorption efficiency by decreasing the abundance of the PSII light-harvesting complexes coupled with enhanced energy dissipation of excess absorbed light via NO quenching mechanisms. Thus, an advantage of palmelloid formation is decreased susceptibility to stress-induced photoinhibition [157] while maintaining an optimum S/V ratio. We suggest that in addition to decreased susceptibility to predation [144,145,148,149,153,154], enhanced photoprotection from photoinhibition associated with palmelloid formation may contribute an evolutionary advantage for the induction of multicellularity in some green algae.

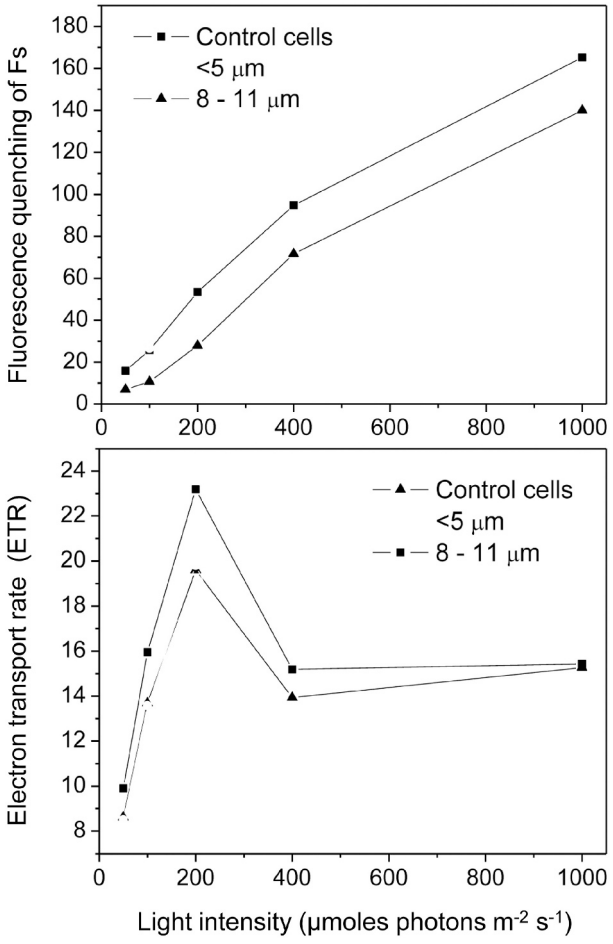

Fig. 5. Palmelloids of *C. priscuii* exhibit a decreased sensitivity to light. Isolated single cells (control cells, <5 μm) and isolated palmelloids (8–11 μm) were purified from *C. priscuii* cultures exposed to increasing light intensity. Photosynthetic performance was assessed by quenching of room temperature Chla fluorescence (Fs) and light saturated electron transport rates (ETR). Data are from [157].

CRediT authorship contribution statement

Conceptualization of the research by NPAH, AG and BS-M. Low temperature (77 K) chlorophyll fluorescence spectral analyses and room temperature chlorophyll fluorescence induction performed and analyzed by AG. Culturing of algae by BS-M, AG, VK and HL. Separation of single cells and palmelloids by BS-M, VK. Light microscopy and analyses by BS-M, VK. DRS performed the comparative genomic analyses. NPAH wrote the initial and the final drafts which were edited by all co-authors prior to submission.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Norman Huner reports financial support was provided by Natural Sciences and Engineering Research Council of Canada.

Data availability

Data will be made available on request.

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