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Photosynthetic responses in *Phaeocystis antarctica* towards varying light and iron conditions

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Abstract The effects of iron limitation on photoacclimation to a dynamic light regime were studied in *Phaeocystis antarctica*. Batch cultures were grown under a sinusoidal light regime, mimicking vertical mixing, under both iron-sufficient and -limiting conditions. Iron-replete cells responded to changes in light intensity by rapid xanthophyll cycling. Maximum irradiance coincided with maximum ratios of diatoxanthin/diadinoxanthin (dt/dd). The maximum quantum yield of photosynthesis (F_v/F_m) was negatively related to both irradiance and dt/dd. Full recovery of F_v/F_m by the end of the light period suggested successful photoacclimation. Iron-limited cells displayed characteristics of high light acclimation. The ratio of xanthophyll pigments to chlorophyll *a* was three times higher compared to iron-replete cells. Down-regulation of photosynthetic activity was moderated. It is argued that under iron limitation cells maintain a permanent state of high energy quenching to avoid photoinhibition during exposure to high irradiance. Iron-limited cells could maintain a high growth potential due to an increased absorption capacity as recorded by in vivo absorption, which balanced a decrease in F_v/F_m. The increase in the chlorophyll *a*-specific absorption cross section was related to an increase in carotenoid pigments and a reduction in the package effect. These experiments show that *P. antarctica* can acclimate successfully to conditions as they prevail in the Antarctic ocean, which may explain the success of this species.

Keywords Fluorescence · Iron · Light · *Phaeocystis* · Pigments · Xanthophyll cycling

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Introduction

In the Southern Ocean, the factors light and iron exert synergistic growth control on microalgae (De Baar et al. 2005). In vast areas, iron concentrations are often too low to support growth (Martin et al. 1990; van Leeuwe et al. 1997). In addition, frequent wave action induces deep vertical mixing of the water column. Consequently, its planktonic inhabitants are subject to a highly dynamic light regime (Mitchell and Brody 1991). Under these conditions, the ability to photoacclimate determines the growth success of algae. Since iron exerts control on various photosynthetic processes, its low ambient

concentration may impede photoacclimation (Greene et al. 1991; van Leeuwe and De Baar 2000). Yet, the impact of iron limitation on photoacclimation has so far received little attention.

Photoacclimation to a dynamic light regime involves optimisation of the photosystems in such a way that energy generation and utilisation are in balance (Kana et al. 1997). Conditions of rapid vertical mixing require that cells can acclimate directly to changes in light intensity that range from almost darkness to excessively high irradiance levels. Dim light conditions deep in the water column necessitate an extensive light-harvesting complex, whereas high irradiance levels at the surface require small complexes that are resistant to photodamage. When more energy is generated than can be utilised for growth, photodamage can occur (Demmig-Adams and Adams 1996). Under variable light conditions, periods between low- and high-light conditions are usually too short for acclimation by de novo synthesis of light-harvesting or photoprotective pigment-protein complexes, respectively. Moreover, de novo synthesis is a costly process. Cells that are subjected to variable light conditions will therefore benefit from flexible photosystems (see Muller et al. 2001 for review). Processes involved in photoacclimation on short time scales (minutes) are energy-dependent quenching (qE) and state-transition quenching (qT). These processes vary with species (e.g. van Leeuwe et al. 2005). Green flagellates possess adaptable photosystems that support the rapid down-regulation of photosynthetic activity by xanthophyll pigment cycling and state transitions. In these organisms, alternative quenching processes that involve mobility of the photosynthetic membranes (Anderson et al. 1995) may also play a role, but are not well described. In contrast, rapid photoacclimation in diatoms is limited to xanthophyll cycling. This appears to be related to a more-homogeneous, and therefore less-flexible, organisation of the thylakoid membranes of diatoms (Larkum et al. 2003).

The make-up of the photosynthetic apparatus and consequently to the capacity of photoacclimation depends on the availability of iron. Previously it has been found that iron-limited cells contain less chlorophyll *a*, but relatively more photoprotective pigments (Geider et al. 1993; van Leeuwe and Stefels 1998; van Leeuwe and De Baar 2000). In addition, various protein-pigment complexes that constitute the photosystems require iron for synthesis (cytochromes and FeS proteins). Under iron limitation, impairment of those protein complexes results in a decrease in the efficiency of electron transport (Greene et al. 1991). Experiments that were carried out under low, stable light conditions showed that while iron limitation resulted in a reduction in photosynthetic efficiency, the absorption efficiency had increased due to a reduction in the package effect (Greene et al. 1991; van Leeuwe and De Baar 2000). Accordingly, iron-limited cells were acclimated to low irradiance to a large extent. However, nothing is known about the effects of iron limitation on the photosynthetic response towards variable light conditions. A disorder in the architecture of the photosynthetic membranes may have negative consequences for the flexibility of the photosystems through constraining effects on the coupling and decoupling of pigment-protein complexes that are involved in xanthophyll cycling (Muller et al. 2001). Even so, alternative quenching processes that depend on conformational changes of membrane proteins are likely to be disturbed.

So far, few studies addressed photoacclimation to rapidly changing light conditions. The data that are available show that diatoms acclimate to the average irradiance levels they encounter. Under variable light conditions, this strategy has negative consequences for their growth success as it makes the algae more susceptible to photoinhibition when exposed to high irradiance levels (Flameling and Kromkamp 1995; Flameling 1998, van Leeuwe et al 2005). No studies are currently available on the effects of iron limitation on photoacclimation towards a variable light regime. Here, we present the first data on photosynthetic responses by the marine microalga *Phaeocystis antarctica* towards varying conditions of light and iron availability. *P. antarctica* is abundant in the Southern Ocean, and it plays a prominent role in various biogeochemical cycles (Smith et al. 1998; Arrigo et al. 1999; Vaillancourt et al. 2003). The alga may form massive