



Ecophysiological strategies for growth under varying light and organic carbon supply in two species of green microalgae differing in their motility



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ABSTRACT

Mixing events in stratified lakes result in microalgae being exposed to varying conditions in light and organic carbon concentrations. Stratified lakes consist of an upper illuminated strata and a lower, darker strata where organic carbon accumulates. Therefore, in this contribution we explore the importance of dissolved organic carbon for growth under various light intensities by measuring some ecophysiological adaptations in two green microalgae. We compared the non-motile *Chlorella vulgaris* with the flagellated *Chlamydomonas acidophila* under auto-, mixo-, and heterotrophic growth conditions. In both algae the maximum photosynthetic and growth rates were highest under mixotrophy, and both algae appeared inhibited in their phosphorus acquisition under heterotrophy. Heterotrophic conditions provoked the largest differences as *C. vulgaris* produced chlorophyll *a* in darkness and grew as well as in autotrophic conditions, whereas *Chl. acidophila* bleached and could not grow heterotrophically. Although the fatty acid composition of both phytoplankton species differed, both species reacted in a similar way to changes in their growth conditions, mainly by a decrease of C18:3n-3 and an increase of C18:1n-9 from auto- to heterotrophic conditions. The two contrasting responses within the group of green microalgae suggest that dissolved organic carbon has a high deterministic potential to explain the survival and behaviour of green algae in the deeper strata of lakes.

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1. Introduction

Dimictic lakes stratify during the summer months resulting in an epi-, meta-, and hypolimnion, although the epilimnion can be repeatedly mixed during summer by changes in the air temperature and wind influence. Independent of such stratification, the light penetration into the water column depends, beside others, on the trophic state of the lake. The sunlit euphotic zone can be restricted to (part of) the epilimnion or extend into deeper layers. In oligotrophic -nutrient poor- lakes low, photosynthesis-limiting light intensities might reach the metalimnion and penetrate the hypolimnion. In contrast, in eutrophic -nutrient rich- lakes the euphotic zone is usually shallower than the mixing depth of the

epilimnion. During a mixing event phytoplankton species are mixed over the epilimnion and upper euphotic zone, facing photoinhibition at the surface and light limiting conditions for photosynthesis in the metalimnion (Kirk, 1994; Yoshiyama et al., 2009). Phytoplankton survival or dominance have been found to correlate with the ratio between the euphotic zone and the mixing zone of different eutrophic lakes in the Netherlands (Mur and Scheurs, 1995; Visser et al., 1996).

In oligo- and mesotrophic lakes light intensities reaching the metalimnion can be as low as 0.1 to a maximum of 10 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, which are high enough for specialized phytoplankton species to grow or thrive in a so-called deep chlorophyll maximum (DCM) (Clegg et al., 2012; Gervais et al., 2003; Klausmeier and Litchman, 2001), among which some appear to grow photoautotrophically (Dimier et al., 2009; Modenutti et al., 2004; Padisak et al., 1997). The classical hypothesis for the formation of a DCM considers opposing gradients of light and nutrients (Clegg et al., 2012; Huisman et al., 2006; Yoshiyama et al., 2009). Plankton tower experiments, in which opposing gradients of light and

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phosphorus, as a growth limiting nutrient, revealed that additional factors are important. Under high (eutrophic) nutrient conditions a surface bloom of *Chlamydomonas reinhardtii* occurred, while under low (oligotrophic) nutrient concentrations no DCM was observed (Mellard et al., 2012). Maxima in phytoplankton biomass occur where the growth rate exceeds the losses (respiration, sinking, vertical mixing and grazing), and therefore we suggest that the use of dissolved organic carbon (DOC) is a central factor with deterministic potential. DOC accumulates near or in the metalimnion as a result of an increasing density in the stratified water column (Pérez-Fuentetaja et al., 1999) and some phytoplankton species can utilize this DOC for heterotrophic growth (Droop, 1974). Even more species can use DOC simultaneously with photosynthesis in the light, which we define as mixotrophy. Mixotrophy, in its wider definition of a combined carbon acquisition from photosynthesis and organic carbon uptake, is now acknowledged as a widespread strategy for organisms living both on land (Selosse et al., 2017) and in water (Mitra et al., 2016; Worden et al., 2015). Inhabitants of the DCM are often mixotrophs, among which are a small selection of green algae (e.g. Sawatzky et al., 2006; Znachor and Nedoma, 2004). Although the green algae consist of species that have a wide variety of traits including mixotrophy. Therefore, we choose to study two species from within this group of phytoplankters, *Chlamydomonas acidophila* (Chlorophyceae) (Bissinger et al., 2000; Tittel and Kamjunke, 2004) and *Chlorella vulgaris* (Trebouxiophyceae) (Martinez and Orus, 1991; Villarejo et al., 1997) as they both can use DOC for mixotrophic growth but vary in their motility. *Chlamydomonas acidophila* inhabits the DCM of the acidic lake 111 (Clegg et al., 2012; Tittel et al., 2003), whereas the presence of *C. vulgaris* has not been shown yet because of the limited phenotypic characteristics to identify this species. As a genus, *Chlorella* sp. has been described in some DCMs dominated by chlorophytes (Sawatzky et al., 2006). In addition, the observation of coccal, green algae inhabiting a DCM could well suggest its presence (e.g. Descy et al., 2010; Zadereev and Tolomeyev, 2007), and its very low critical light intensity (Huisman et al., 1999) supports the probability that *C. vulgaris* could also be a DCM species. Although DOC consists of a large variety of complex molecules, occasional and localised spikes of glucose have been detected that stimulate growth of phytoplankters (Moore, 2013; Znachor and Nedoma, 2010). Therefore, glucose might be an important DOC compound.

To advance our understanding of adaptations to live in a DCM based on the use of DOC in varying light conditions, we explored the necessity of photosynthesis for our two microalgae. The concept of an organism being a mixotroph lies in the required photosynthesis (Flynn and Mitra, 2009). It has been acknowledged in earlier studies that although DOC is taken up in the dark it does not automatically mean that heterotrophic growth can be realised (Bennet and Hobbie, 1972). Based on this ecophysiological difference, different strategies for phytoplankton can be considered. The first strategy consists of “Avoidance” or “Bridge-over” behaviour as photosynthesis is essential for the algae. Based on phytoplankton behaviour, species either avoid heterotrophy or light limiting conditions via migration to strata enabling photoautotrophy (Clegg et al., 2004), or the metabolism is slowed down to await mixing events and transport to the euphotic zone. In case of the latter, exposure to the lower temperatures in the metalimnion supports this strategy to survive and linger during the unfavourable conditions. Avoidance behaviour requires some sort of motility. For example, depth regulation can be realised by gas vesicles, that supported diel migration in the colony forming, non-flagellated cyanobacterium *Microcystis* sp. (Visser et al., 2016). Although floating by spines or sinking might appear to be an inefficient strategy, some large species of centric diatoms rapidly regulated their sinking speed in response to nutrient concentrations

(Gemmell et al., 2016). Furthermore the presence of flagella, e.g. in *Chl. acidophila* indicates a good motility, but the species only realised small diel vertical migrations within the DCM of Lake 111 (Clegg et al., 2012) suggesting that the avoidance strategy might be not satisfactory. A comparison between the photosynthetic responses in phytoplankton species with or without flagella (Striebel et al., 2009) pointed at different photosynthetic acclimation strategies related to motility. Therefore, we assume that the acclimation response in photosynthesis might relate to the avoidance strategy, which is likely also reflected in a decreased cellular polyunsaturated fatty acid (PUFA) content in heterotrophic conditions (Poerschmann et al., 2004; Wacker and Weithoff, 2009). The second strategy considered is defined as “Acclimation”, where algae acclimate to ‘dark time intervals’ by quick changes in their metabolism (as suggested by Striebel et al., 2009). This strategy will be advantageous for planktonic organisms in which photosynthesis can be quickly regulated and to which photosynthesis is not essential for growth. The possibility to acclimate does not exclude an avoidance strategy, because photosynthesis often stimulates growth of mixotrophs under heterotrophy (Raven, 2009) and triggers movement of cells towards the light (Clegg et al., 2004).

Here we tested these strategies for growth in *Chlamydomonas acidophila* and *Chlorella vulgaris* by growing them under auto-, mixo-, and heterotrophic conditions. In an attempt to link physiological and biochemical characteristics with growth characteristics under the various conditions, we conducted laboratory experiments with both species that vary in their motility.

2. Results

Growth rates of both algal species differed between different growth conditions (ANOVA, $F_{2,6} = 69.5$ for *C. vulgaris*, $F_{2,6} = 4029$ for *Chl. acidophila*, both $p < 0.001$), and both species realised their highest growth rates under mixotrophic growth conditions compared to auto- or heterotrophic growth conditions (Fig. 1A). Growth rates of *C. vulgaris* were the same when cultured autotrophically or heterotrophically. In contrast, heterotrophic growth rates of *Chl. acidophila* were very low. Both algal species had a different chlorophyll *a* (Chl *a*) content per carbon under different culture conditions (ANOVA, $F_{2,6} = 76.5$ for *C. vulgaris*, $F_{2,6} = 648$ for *Chl. acidophila*, both $p < 0.001$) with the highest Chl *a* content in autotrophically growing species (Fig. 1B). The latter indicates that the higher growth rates in the mixotrophic algae were not related to a high Chl *a* content per se. Interestingly, the Chl *a* content did not differ between mixotrophic and heterotrophic growth conditions in *C. vulgaris*, whereas *Chl. acidophila* hardly contained any Chl *a* when cultured heterotrophically (see also Table 1 for Chl *a* per cell values).

The culturing conditions influenced the cellular carbon (C) content of both species (ANOVA, $F_{2,6} = 7.5$, $p < 0.05$ for *C. vulgaris*, $F_{2,6} = 53.2$, $p < 0.001$ for *Chl. acidophila*; Table 1) in that the C contents were higher under mixotrophic compared to autotrophic conditions. Besides the impact on C content, algal C to phosphorus ratios (C:P) differed between growth conditions (ANOVA, $F_{2,6} = 28.6$ for *C. vulgaris*, $F_{2,6} = 128.6$ for *Chl. acidophila*, both $p < 0.001$; Fig. 1C). In both species the C:P ratio was higher when algae were grown heterotrophically, which resulted from the lowest P contents under heterotrophic conditions than in the other treatments (ANOVA, $F_{2,6} = 45.8$ for *C. vulgaris*, $F_{2,6} = 27.8$ for *Chl. acidophila*, both $p < 0.001$; Table 1). The cellular nitrogen (N) content was little influenced between the treatments and replicates of molar C:N ratios varied between 5.5 (in *Chl. acidophila* under autotrophy) and 9.6 (in *C. vulgaris* under autotrophy; see mean C:N ratios in Table 1).

The growth condition also impacted the maximum

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