



Combined effect of high light and high salinity on the regulation of photosynthesis in three diatom species belonging to the main growth forms of intertidal flat inhabiting microphytobenthos



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ABSTRACT

The strong biological production of estuarine intertidal flats is mainly supported by benthic diatoms in temperate areas. Their photosynthetic productivity is largely driven by changes in light intensity and temperature at the surface of sediment flats during emersion. The impact of an increase in salinity of the upper-layer sediment pore-water during emersion, which is often coupled with high light (HL), has been less studied. Furthermore, benthic diatoms show several growth forms which inhabit specific sediment types where the pore-water salinity can differentially vary due to the degree of cohesion of sediment grains. So far, no study explored if the main growth forms of benthic diatoms (i.e. epipelon, epipsammon and tycho plankton) show different photophysiological response to a combine high salinity-HL stress. Based on field monitoring, we compared the photophysiology (photosynthetic efficiency and photoprotection) of three representatives of the main growth forms during a short high salinity coupled with a moderate HL stress and stable optimal temperature, i.e. experimental conditions reproducing Spring environmental conditions in intertidal flats by the Atlantic French coast. Our results show that all growth forms reacted to HL exposure alone, as expected. While the epipelon representative was relatively insensitive to high salinity alone and combined with HL, the tycho plankton representative was highly sensitive to both, and the epipsammon representative was sensitive mainly to the stress combination. These specific responses fitted well with i) their natural habitat (i.e. more or less cohesive sediment) for which light climate and changes in salinity are different, ii) their growth form (i.e. motile, immotile or amphibious) which determines their probability to be confronted to a combined high salinity-HL stress. Hence, the negative effect of high salinity on photosynthetic efficiency of benthic diatoms appears to be mostly restricted to epipsammon and tycho plankton, and in field conditions, its effect probably remains negligible compared to HL stress.

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1. Introduction

Estuarine intertidal flats belong to the most productive ecosystems on Earth (MacIntyre et al., 1996; Underwood and Kromkamp, 1999) and they have a central role in structuring the food-web of coastal areas (Kromkamp et al., 2006). A large part of the strong productivity of intertidal flats is due to the microphytobenthos (MPB) (Admiraal, 1984; MacIntyre et al., 1996; Underwood and Kromkamp, 1999) which in temperate seas is mainly dominated by benthic diatoms

(Méléder et al., 2007; Ribeiro et al., 2013). Benthic and planktonic diatoms are essential primary producers which contribute to about 40% of the marine primary production; they also play a major role in the silica and nitrogen biogeochemical cycles (Armbrust, 2009). The MPB diatoms constitute the bulk of the diatom diversity (Kooistra et al., 2007). They can be divided in three main growth forms which mainly differ in their life in the sediment (Kooistra et al., 2007; Ribeiro et al., 2013): i) the epipelon comprises motile species free-living in between sediment particles (Herlory et al., 2004), ii) the epipsammon which lives attached to sediment particles, and iii) the tycho plankton which presumably have an amphibious life style (i.e. both sediment and water column) (e.g. Sabbe et al., 2010). Epipelon and epipsammon growth forms show distinct distribution among intertidal habitats characterised by different types of sediment (Méléder et al., 2007; Ribeiro et al., 2013; Sabbe, 1993). Epipelon dominates cohesive muddy sediments (>90% of MPB; Haubois et al., 2005), while epipsammon dominates less cohesive sandy

Abbreviations: Chl *a*, chlorophyll *a*; DD, diadinoxanthin; DES, de-epoxidation state of diadinoxanthin to diatoxanthin; DT, diatoxanthin; E, light intensity; ETR, electron transport rate; HL, high light; LL, low light; MPB, microphytobenthos; NPQ, non-photochemical quenching of chlorophyll fluorescence; PSII, photosystem II; RLC, rapid light curve; XC, xanthophyll cycle.

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sediments (>95% of MPB; Méléder et al., 2007). Because of different habitats, epipelon and epipsammon have evolved different ways of coping with their intertidal environment. Epipelon displays vertical 'migration' following endogenous tidal/dial rhythms and environmental stimuli (Coelho et al., 2011; Consalvey et al., 2004; Saburova and Polikarpov, 2003): typically, during daylight emersion, epipellic diatoms move to the sediment surface and form a dense biofilm, while before immersion they migrate downward. Epipsammon lives more or less firmly attached (stalked or adnate forms) to individual sand grain including some species able to exert micro-movements within the sphere of grains. Tychoplankton (which is sometimes considered as resuspended epipelon and/or epipsammon during immersion; MacIntyre et al., 1996) can live either as part of MPB or of phytoplankton, depending on the hydrodynamics (Koh et al., 2006); it can contribute to up to one third of phytoplankton (Brito et al., 2012; Guarini et al., 2004).

Environmental cues can rapidly vary to an extreme in intertidal flats (Admiraal, 1984; Paterson and Hagerthey, 2001) and impair the photosynthetic productivity of MPB diatoms (i.e. photoinhibition) (Blanchard et al., 2004; Serôdio et al., 2008). In order to prevent such situation, benthic diatoms have evolved diverse responses that can be distinguished in two main types: behaviour and physiology. Only epipelon can escape from a combination of sometimes harsh environmental conditions at the sediment surface by 'migrating' downward to the most optimal conditions (i.e. the so-called 'behavioural photoprotection'; Admiraal, 1984; Kromkamp et al., 1998; Consalvey et al., 2004; Serôdio et al., 2006), especially as regards to salinity (Sauer et al., 2002). In contrast, all growth forms use physiological processes for the fast regulation of photochemistry (i.e. 'physiological photoprotection'; Lavaud, 2007; Goss and Jakob, 2010; Depauw et al., 2012; Lepetit et al., 2012). In diatoms, two physiological processes are important in field situation (Brunet and Lavaud, 2010; Lavaud and Goss, 2014): i) the non-photochemical quenching of chlorophyll (Chl) fluorescence (NPQ) (Depauw et al., 2012; Lavaud and Goss, 2014; Lepetit et al., 2012), and ii) the partly related light-dependent conversion of diadinoxanthin (DD) to diatoxanthin (DT) by the DD de-epoxidase (i.e. the 'xanthophyll cycle', XC) (Brunet and Lavaud, 2010; Goss and Jakob, 2010). In benthic diatoms, NPQ and XC have been scarcely studied *in situ*: it varies with the diurnal and tidal cycles, season, latitude (Chevalier et al., 2010; Serôdio et al., 2005, 2012; van Leeuwe et al., 2009), and with the position of diatom cells within the sediment and along the intertidal elevation gradient (Cartaxana et al., 2011; Jesus et al., 2009). The respective importance of behavioural and physiological responses in epipelon has received a major interest (Cartaxana et al., 2011; Mouget et al., 2008; Perkins et al., 2010b; Serôdio et al., 2012; van Leeuwe et al., 2009). These studies have shown that although motility is essential for an optimal response to the changes in environmental conditions, NPQ and XC remain important features, and even compensate for migration under conditions where motility is limited, to finely tune photosynthetic efficiency. Also, a recent analysis of NPQ and XC abilities among the growth forms of MPB diatoms has revealed a clear relationship between growth form and capacity for physiological photoprotection (Barnett et al., *in press*), i.e. while epipsammon shows the highest NPQ and XC capacity, epipelon and tychoplankton shows the lowest ones, reflecting their respective motility and adaptation to a low light (LL) environment (i.e. tychoplankton is either buried in sediment or resuspended in a turbid water column; Roncarati et al., 2008).

Changes in light intensity and temperature are often considered as the two major forcings of the photosynthetic productivity of MPB diatoms (Guarini et al., 2006). Surprisingly, changes in salinity have been less studied in benthic diatoms, while in planktonic diatoms it is known to induce modification of community species diversity (Dijkman and Kromkamp, 2006; Muylaert et al., 2009; Petrou et al., 2011; Thessen et al., 2005), and of growth and photosynthesis (Dijkman and Kromkamp, 2006; Petrou et al., 2011; Thessen et al., 2005). Salinity often co-varies with other environmental gradients like light and temperature in the case of high salinities (due to pore-water evaporation in the upper-layer of the

sediment) and with nutrient concentrations in the case of low salinities (due to the discharge of estuarine rivers) (Admiraal and Peletier, 1980; Thornton et al., 2002; Underwood and Provot, 2000). Although early works stated that MPB diatoms are highly tolerant to a wide range of salinity changes (Admiraal, 1977; Admiraal and Peletier, 1980; Williams, 1964), further studies have shown that salinity changes, often combined with high light (HL), impairs the growth from a salinity of 40 and above (Natana Murugaraj and Jeyachandran, 2007; Scholz and Liebezeit, 2012), it reduces the photosynthetic performance (Le Rouzic, 2012; Roncarati et al., 2008) via (photo-)oxidative stress (Rijstenbil, 2003, 2005; Roncarati et al., 2008), and it can modify the motility of epipellic diatoms in the sediment (Sauer et al., 2002) via changes in the excretion of exopolysaccharides (Apoya-Horton et al., 2006). Furthermore, although the different growth forms of MPB diatoms pertain to habitats in which the salinity can differentially vary due to the degree of cohesion of sediment (Paterson and Hagerthey, 2001), to our knowledge, no study explored if they show different photophysiological response to a combine high salinity-HL stress and if it correlates to their habitat-associated growth form. The objectives of the present study were therefore to determine i) if a higher salinity can increase the negative effect of HL on the photosynthetic efficiency, ii) if three representatives belonging to each of the growth forms of MPB diatoms react differently to a combined high salinity-HL stress.

2. Materials and methods

2.1. Sediment grain size, pore-water salinity, temperature and MPB biomass of sediment

Parameters were measured at different seasons and for two sites of the Atlantic French coast: the bay of Brouage and the bay of Bourgneuf; see Haubois et al. (2005) and Méléder et al. (2007) for a respective characterization of the two sampling sites (see Table 1 and Fig. 1 for all details). Sediment grain size was determined with a laser granulometer (Mastersizer 2000, Malvern Instruments, UK) as previously described (Méléder et al., 2007). The mud fraction (grain size < 63 μm) of each sample was determined using the software Gradistat (Blott and Pye, 2001). Sediment samples were centrifuged for 10 min at 3500 $\times g$ and salinity was measured on the supernatant with a sensor TetraCon325 (WTW, Weilheim, Germany). The temperature at the sediment surface was measured every 30 s with a universal data logger (ULM-500, Walz Effeltrich Germany) equipped with a plane temperature sensor (accessory of the ULM-500). The sediment content of chlorophyll *a* ($\mu\text{g Chl } a \text{ g dry sediment}^{-1}$) was used as a proxy for MPB biomass. Chl *a* was extracted and measured as previously described (Herlory et al., 2004): spectrofluorimetric measurement (Turner TD-700 fluorometer) was performed on supernatant of sediment samples after lyophilisation, extraction (90% acetone, 12 h, 4 °C, in the dark, continuous shaking) and centrifugation 10 min at 4000 $\times g$.

2.2. Diatom culture conditions

Three species belonging to the three main growth forms of MPB diatoms were used: 1) Epipelon, *Navicula phyllepta* (Culture Collection Yerseke-The Netherlands CCY9804, isolated in the Westerschelde estuary, North sea, The Netherlands); 2) Epipsammon, *Biremis lucens* (Nantes Culture Collection-France NCC360, isolated in the bay of Bourgneuf, Atlantic, France); 3) Tychoplankton, *Plagiogrammopsis vanheurckii* (NCC186-2, isolated in the bay of Bourgneuf). Cultures were grown in batch sterile artificial seawater F/2 medium completed with Tropic Marin artificial sea salt (Dr. Biener GmbH, Germany) at a salinity of 33, and enriched with NaHCO_3 (80 mg L^{-1} final concentration). Temperature was 20 °C and light was 60 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (white fluorescent tubes L58W/840, OSRAM, Germany) with a 16 h:8 h light:dark photoperiod. When cultures reached exponential phase, cells were harvested by gentle centrifugation (5 min, 4000 $\times g$), resuspended to a

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