Journal of Plant Physiology 173 (2015) 41–50

Contents lists available at ScienceDirect

Journal of Plant Physiology

journal homepage: www.elsevier.com/locate/jplph

Physiology

Ocean acidification modulates the response of two Arctic kelps to ultraviolet radiation

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ARTICLE INFO

Article history:
Received 6 May 2014
Received in revised form
19 September 2014
Accepted 20 September 2014
Available online 5 October 2014

Keywords:
Alaria esculenta
Arctic
Ocean acidification
Saccharina latissima
Ultraviolet radiation

ABSTRACT

The combined effects of ocean acidification and ultraviolet radiation (UVR) have been studied in the kelps *Alaria esculenta* and *Saccharina latissima* from Kongsfjorden (Svalbard), two major components of the Arctic macroalgal community, in order to assess their potential to thrive in a changing environment. Overall results revealed synergistic effects, however with a different amplitude in the respective species. Changes in growth, internal N, C:N ratio, pigments, optimum quantum yield (Fv/Fm) and electron transport rates (ETR) following CO_2 enrichment and/or UVR were generally more pronounced in *S. latissima* than in *A. esculenta*. The highest growth rates were recorded under simultaneous CO_2 enrichment and UVR in both species. UVR-mediated changes in pigment content were partially prevented under elevated CO_2 in both species. Similarly, UVR led to increased photosynthetic efficiency (α) and ETR only if CO_2 was not elevated in *A. esculenta* and even under high CO_2 in *S. latissima*. Increased CO_2 did not inhibit external carbonic anhydrase (eCA) activity in the short-term but in the mid-term, indicating a control through acclimation of photosynthesis rather than a direct inhibition of eCA by CO_2. The higher benefit of simultaneous CO_2 enrichment and UVR for *S. latissima* respect to *A. esculenta* seems to involve higher C and N assimilation efficiency, as well as higher ETR, despite a more sensitive Fv/Fm. The differential responses shown by these two species indicate that ongoing ocean acidification and UVR could potentially change the dominance at lower depths (4–6 m), which will eventually drive changes at the community level in the Arctic coastal ecosystem. These results support an existing consideration of *S. latissima* as a winner species in the global change scenario.

Introduction

Benthic primary producers in the intertidal and subtidal zones have to face a number of environmental changes related to the global change scenario. One of the most relevant changes in the polar coastal ecosystem is ocean acidification by increased dissolution of atmospheric CO_2, but it is still unknown how the interaction with other environmental factors such as the presence of solar ultraviolet radiation (UVR) will affect growth, photosynthetic performance and chemical composition of Arctic seaweeds. UVR penetration in coastal water imposes an upper depth limit for a given species, and as a result it might determine the vertical zonation pattern of benthic algal communities (Bischof et al., 2006) with far-reaching consequences for aquatic grazers and other members of these habitats.

Ocean acidification changes the water carbon chemistry, altering the form and amount of the available dissolved inorganic carbon (DIC), the major substrate for photosynthetic primary producers. The shift in DIC equilibria expected by the end of this century involves a decrease in pH to values around 7.7, a three-fold increase in dissolved free CO_2, only a small (about 10%) increase in bicarbonate and total DIC concentration, and a strong decrease in carbonate concentration to less than half, respect to preindustrial levels (Beardall et al., 2009a,b), bicarbonate remaining as the major form of inorganic C. Predictions about the ecological consequences of ocean acidification have mainly focused on the effects on calcifying organisms, particularly those critical to the formation of habitats such as coral reefs. This focus overlooks the direct effects of CO_2 on non-calcareous organisms, particularly those that

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Abbreviations: α, photosynthetic efficiency; A, thallus absorptance; CCM, carbon concentrating mechanisms; eCA, external carbonic anhydrase; ETR, electron transport rate; ETRm, maximum electron transport rate; Fv/Fm, optimum quantum yield; NRA, nitrate reductase activity; RGR, relative growth rate; UVR, ultraviolet radiation.

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http://dx.doi.org/10.1016/j.jplph.2014.09.008

also play critical roles in ecosystem structure such as kelps (Connell and Russell, 2010; Russell et al., 2011; Krause-Jensen et al., 2012). Marine macroalgae in the Arctic occur commonly in the intertidal and subtidal zones of the coastal waters, and play a major role in the coastal carbon cycle, as well as serving as habitat and reproduction and nursing sites for many species. The kelps *Alaria esculenta* and *Saccharina latissima* are habitat-forming key species of the mid sublittoral zone of Kongsfjord (Svalbard), although they can also be observed in the low intertidal, and are major contributors to the coastal carbon cycle. *A. esculenta* dominates in the depth range 5.5–10.5 m and *S. latissima* in 7.5–12.5 m (Hop et al., 2012), but there is evidence that depth ranges and dominance of kelp species may change due to climatic forcings (Weslawski et al., 2010; Krause-Jensen et al., 2012), although little is known on the underlying metabolic processes involved.

Macroalgal growth, photosynthetic performance, chemical composition, and nutrient assimilation, have been shown to respond to increased levels of CO_2, as well as to increased UVR by separate; but simultaneous and interactive effects are poorly understood (Swanson and Fox, 2007; Gao and Zheng, 2009). CO_2 can increase growth in some species despite their photosynthesis being C-saturated by means of a carbon concentrating mechanism (CCM) (*e.g.* Gordillo et al., 2001, 2003). Attempts to relate the effects of increased CO_2 to the operation of CCMs have been generally unsuccessful (Giordano et al., 2005) and the extension and direction of changes are species-specific. Some macroalgal species have shown enhanced growth (*e.g.* Gordillo et al., 2001) while some rhodophytes, both calcifying (Gao and Zheng, 2009) and non-calcifying (Mercado et al., 1999; Israel et al., 1999) showed negative effects in response to elevated CO_2. There are also many species with varying CCM showing no significant changes (Israel and Hophy, 2002). The variety in the response pattern of the different species in a community is a clear indication that, in an acidifying ocean, there will be changes in competition, settlement and dominance that will propagate to other trophic levels and affect the entire ecosystem (Connell and Russell, 2010).

UVR is well known to cause deleterious effects on the physiological performance and growth of marine photosynthetic organisms (reviewed by Vincent and Roy, 1993; Helbling and Zagarese, 2003; Häder et al., 2011). Potential UVR targets include mainly nucleic acids and proteins (Vass, 1997). In plants, pigments of the photosynthetic apparatus can also be degraded by UVR exposure; but differences in the sensitivity between pigment types depend on species (Teramura, 1983; Häder and Häder, 1989; Figueroa et al., 2010). Regarding the metabolism of seaweeds these UVR effects result in the inhibition of nutrient assimilation (Gómez et al., 1998) damage to DNA (Van de Poll et al., 2002; Roleda et al., 2007) and damage to carbon assimilation mechanisms (Bischof et al., 2000), but there is still no clear insight on how these responses are to be modified in an acidified ocean scenario.

In the Arctic coastal environment, potentially harmful UVR penetrates down to 6 m in the water column (Hanelt et al., 2001). The overall effect of UVR on photosynthesis and physiological performance is a balance between damage and repair (*e.g.* Heraud and Beardall, 2000) that can be largely modulated by interactions with other environmental factors such as PAR light, nutrient limitation and levels of dissolved CO_2 (Beardall et al., 2009a,b; Häder et al., 2011). Some multifactorial analyses exist dealing with the interactions between CO_2 and nutrients (Gordillo et al., 2001, 2003; Russell et al., 2009), and UVR and nutrients (Figueroa et al., 2010). However, only few have focused on the interactions between CO_2 and UVR (Swanson and Fox, 2007; Gao and Zheng, 2009). Gao and Zheng showed that enhanced CO_2 decreases calcification of *Corallina sessilis*, making it prone to UVR damage. Conversely, Swanson and Fox evidenced that, in the long term, enhanced CO_2 and UVR might benefit the two non-calcifying kelp species examined, *S. latissima* and *Nereocystis luetkeana* but with species-specific differences in growth an phlorotanins production.

We hypothesise that expected ocean acidification may modify the mechanisms of acclimation to UVR, so changing the ability of a given species to thrive in a CO_2 enriched environment with a significant presence of solar UVR. The aim of this work is to elucidate to what extent the synergistic or antagonist effects of simultaneous CO_2 enrichment and UVR can alter growth, photosynthetic performance and chemical composition of two common Arctic species, and shed light on the potential shifts in the community.

Materials and methods

Plant material and cultivation

Around 30–45 young specimens of the kelp species *Alaria esculenta* (L) Greville and *Saccharina latissima* (L) Lane et al. (formerly *Laminaria saccharina* (L) Lamouroux) were collected by SCUBA diving from the Kongsfjorden, Spitsbergen (78°55′ N 11°56′ E) at approximately 6 m depth in the Arctic summer (July). The blades of the sampled thalli were about 15–30 cm long. Healthy thalli free of macroscopic epibiota were selected. Between 10 and 15 discs 12 mm in diameter were cut from the meristematic part of each blade for cultivation. A number of discs up to 3.3 g in fresh weight (FW) of *A. esculenta* or 4.8 g FW of *S. latissima* were placed in 1.5 L aquaria and kept in culture for 12 days. The difference in weight accounts for the different thickness of the two species so that exposure area was kept the same for both. Every second day seawater was changed and enriched with 10 $\mu M\ NO_3{}^-$ and 1 $\mu M\ PO_4{}^{3-}$.

The aquaria were aerated at 0.5 $L\,min^{-1}$ either with non-manipulated ambient air (C−, *ca.* 380 ppm CO_2) or with air enriched with CO_2 to 1000 ppm (C+) allowing all discs to circulate without settling. The required level of CO_2 was achieved by mixing air with pure CO_2 from a gas tank. Final CO_2 level in the mixture was continuously recorded by a CO_2 sensor (Airsense, DCS, USA) prior to bubbling the cultures. Initial pH values were 8.13 ± 0.02 and 7.71 ± 0.03 for seawater from the fjord and CO_2-enriched seawater, respectively. Total alkalinity was measured by titration resulting in 2530 ± 90 mequiv. kg^{-1} SW, so that calculated values for pCO_2 in equilibrium seawater were 359 and 1028 μatm for non-enriched (C−) and CO_2-enriched (C+) seawater, respectively, at 4 °C and 31.8 psu salinity. Final pH of *S. latissima* cultures before water change averaged 8.32 ± 0.02 and 7.79 ± 0.02 for C− and C+, respectively, corresponding to pCO_2 values of 217 μatm for C− and 846 μatm for C+. Final pH for *A. esculenta* before water change averaged 8.14 ± 0.03 and 7.71 ± 0.01 for C− and C+, respectively, corresponding to pCO_2 values of 351 μatm for C− and 1028 μatm for C+ Calculations were made using the CO2Calc software (Robbins et al., 2010).

Cultures run at 4–5 °C in continuous light. Temperature was regulated by submersing the aquaria in a temperature-controlled recirculating water bath. For the PAR-only treatment (UV−), light was supplied from the top by fluorescent lamps (OSRAM L58/W19) at 30 $\mu mol\,m^{-2}\,s^{-1}$ and no further lamp or filter was applied. For UV+ treatment, the above-mentioned white light was proportionally supplemented with ultraviolet radiation (UVR) supplied by Q-Panel 340 lamps (Q-Lab, Dusseldorf, Germany) rendering 2 $W\,m^{-2}$ of UVA and 0.2 $W\,m^{-2}$ of UVB as measured by a Gröbel RM11 radiometer (Gröbel UV-elektronik, Ettlingen, Germany), which was intercalibrated with a Macam spectroradiometer double monocromator SR22791 (Tranent, Scotland) using the same lamp setting. The contribution of the Q-panel lamps to PAR was only 1.2 $\mu mol\,m^{-2}\,s^{-1}$, so no additional cut-off filter was required. Both PAR and UV irradiance were chosen according to the average daily solar irradiance recorded at 4–6 m depth in the Kongsfjord for this