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Photosynthetic activity and productivity of intertidal macroalgae: *In situ* measurements, from thallus to community scale

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ABSTRACT

The photosynthetic activity and productivity of four dominant canopy intertidal macroalgae were measured under emersion and immersion, at saturating light levels (PAR > 300 μmol photons m^{-2} s^{-1}), and compared at two sites (eastern and western English Channel) in spring and summer. The photosynthetic activity of thalli was measured by the electron transport rate (ETR) using pulse-amplitude modulated (PAM) fluorescence and the productivity of individuals and of communities was measured by carbon fluxes in closed chambers. Under emersion, when thalli were still hydrated, the uppermost species *Pelvetia canaliculata* had higher photosynthetic activity (mean ETR between 327 and 460 μmol e^- m^{-2} s^{-1}) and individual gross productivity (between 60 and 212 μmol C $g_{DW}{}^{-1}$ h^{-1}) than the lowermost species *Laminaria digitata* (mean ETR between 24 and 53 μmol e^- m^{-2} s^{-1} and gross productivity between 2 and 38 μmol C $g_{DW}{}^{-1}$ h^{-1}), whatever the site and season. *P. canaliculata* had higher ETR in air than underwater (averaged 146 μmol e^- m^{-2} s^{-1}) and *L. digitata* had lower ETR in air than underwater (averaged 112 μmol e^- m^{-2} s^{-1}), while they exhibited, respectively, 3 and 5 times higher gross productivity underwater. At the community scale, the low mid-shore zone of *Fucus serratus* had the highest mean gross productivity under emersion (47 mmol C m^{-2} h^{-1}) while rates were higher for the uppermost than lowermost zone at the eastern site (average 20 and 6 mmol C m^{-2} h^{-1}, respectively) and of the same order of magnitude for both zones at the western site (about 30 mmol C m^{-2} h^{-1}). Finally, the variability of under emersion primary productivity among sites and seasons was reduced when the measurements were performed on entire communities compared to isolated individuals of the dominant species.

1. Introduction

Rocky shores are frequently dominated by dense populations of macroalgae that exhibit distinct patterns of vertical zonation. On northern hemisphere temperate coasts, this pattern typically consists of the succession of fucoid algae from the high to the low mid shore and of laminarians (or kelps) in the lower shore. The productivity of such seaweed populations has long been shown to be important, ranging from 1 to several kg C m^{-2} y^{-1} (Mann, 1973). However, these estimations were rather raw and still need to be specified. In particular, the ecological performance of macroalgae

Abbreviations: A, absorption coefficient; DIC, dissolved inorganic carbon; DW, dry weight; Em, emersion; ETR, electron transport rate; $F_m{}'$, maximal fluorescence level; Fse, *Fucus serratus*; Fsp, *Fucus spiralis*; F_t, fluorescence steady-state level; FW, fresh weight; GCP, gross community productivity; GP, gross productivity; Im, immersion; Ld, *Laminaria digitata*; NCP, net community productivity; NP, net productivity; PAM, pulse-amplitude modulated; PAR, photosynthetically available radiation; Pc, *Pelvetia canaliculata*; R, respiration; Ro, Roscoff; Sp, spring; Su, summer; TA, total alkalinity; Wx, Wimereux; Φ_{PSII}, effective quantum yield of photosystem II.

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has to be measured *in situ* and at the multi-species community scale to take into account not only the dominating species but all the species as well as their interactions in relevant conditions. Intertidal macroalgae experience two very different environments for photosynthesis, aerial and aquatic. The capacity of species from different shore levels to maintain photosynthesis during emersion periods has long been investigated based on measurements performed on isolated thalli under controlled laboratory conditions (*e.g.* Johnson et al., 1974; Quadir et al., 1979; Dring and Brown, 1982). Since then, differences between some shallow-water macroalgae species have been shown to be smaller at the communities scale than experiments on single thallus pieces suggested (Binzer and Middelboe, 2005) and an increasing productivity of fucoid assemblages down a shore-height gradient has been shown (Tait and Schiel, 2011). These community-scale measurements were limited, however, to immerged conditions and trends might be different under peculiar conditions of the emersion periods. The present study compares the photosynthetic activity and productivity of thalli of the dominant canopy macroalgae (*i.e.* the zone-forming species typical of the northern hemisphere temperate shores) and the productivity of the communities, based on *in situ* measurements performed either during emersion or immersion periods. First, the photosynthetic activity of adult thalli was examined using pulse-amplitude modulated (PAM) fluorescence. This technique, which relies on the variable fluorescence of chlorophyll *a*, is not a direct measurement of photosynthesis but allows an examination of the dynamic properties of photosynthesis in response to environmental changes (Enriquez and Borowitzka, 2010) during the whole tidal cycle (emersion and immersion). Second, the productivity of single individual, or several individuals of a single species, was assessed using a closed chamber system. This monospecific approach aimed at understanding the productivity dynamic of each species in response to the environment variation (aerial *versus* aquatic). Third, the productivity of multi-species communities was assessed using closed chamber systems under emersion. This assemblage-based approach integrated the resource partitioning among canopy-forming macroalgae and their sub-canopy assemblages. The aim of the study was to test two hypotheses: (1) the in air *versus* underwater ratio of photosynthetic performance decreases down a shore-height gradient; (2) the variation in photosynthetic performance among dominant canopy species of the shore is reduced when the measurements are scaled up from thallus to community.

2. Materials and methods

2.1. Target species and study sites

The target species were the three fucoids *Pelvetia canaliculata* (the uppermost zone-forming species), *Fucus spiralis* (the immediately contiguous zone-forming species) and *Fucus serratus* (the lowermost zone-forming fucoid) and the kelp *Laminaria digitata* (the lowermost zone-forming species). Two seasons (spring and summer) and two sites, differing for the timing of the tide and for turbidity, were investigated. Measurements were performed at the rocky shore of Wimereux (50°44′48″N–1°35′54″E, eastern English Channel, France) during spring tides in September 2009 (summer) on the four seaweed communities (*P. canaliculata*, *F. spiralis*, *F. serratus* and *L. digitata*) and in April 2010 (spring) on three seaweed communities (*P. canaliculata*, *F. spiralis* and *L. digitata*) and at the rocky shore of Roscoff (48°43′53″N–3°59′16″W, western English Channel, France) during spring tides in August 2010 (summer) and in May 2011 (spring) on the uppermost and the lowermost seaweed communities (*P. canaliculata* and *L. digitata*). At Wimereux, water turbidity is high and low tides of spring tide occur in the early morning (low tides occurred between 7:30am and 10:00am, UT + 2 h, for summer measurements and between 7:00am and 8:30am, UT + 2 h, for spring measurements). At Roscoff, water turbidity is low and low tides of spring tide occur in the early afternoon (low tides occurred between 2:00pm and 3:30pm, UT + 2 h, for summer measurements and between 1:30pm and 2:30pm, UT + 2 h, for spring measurements).

2.2. Light and temperature

Photosynthetically available radiation (PAR in μmol photons m^{-2} s^{-1}) was measured in air and underwater and recorded every minute using a WinCQ flat sensor (Alec Electronics). Temperature was measured in air and underwater and recorded every minute using a MDS MkV-T sensor (Alec Electronics). Average temperature during the periods of selected measurements was 18 °C underwater and 20 °C in the air in summer and 11 °C underwater and 14 °C in the air in spring, at Wimereux. It was 17 °C underwater and 27 °C in the air in summer and 14 °C underwater and 22 °C in the air in spring, at Roscoff.

2.3. Fluorescence

In vivo chlorophyll fluorescence properties were measured *in situ* using a submersible PAM fluorometer (Diving PAM, Walz). The fluorescence signal was always taken from the middle of the frond in the same place for three haphazardly-selected and marked individuals of the target species. The effective quantum yield of photosystem II (Φ_{PSII}) was measured under ambient light at different stages of the tidal cycle. The fiber optic was mounted in a home-made transparent Plexiglas holder applied to one side of the thallus in such a way that the distance between the fiber optic and the algal tissue was constant and standard. The fiber optic forms a 60° angle with the sample, avoiding shading or darkening. Φ_{PSII} was calculated as $(F_m' - F_t)/F_m'$ (Genty et al., 1989), where F_m' is the maximal fluorescence level measured during a single saturating light pulse (0.8 s) for light-adapted samples, and F_t is the fluorescence steady-state level immediately prior to the flash. Then, the electron transport rate (ETR in μmol electrons m^{-2} s^{-1}, here after referred to as μmol e^- m^{-2} s^{-1}) was estimated using the following equation:

$$\text{ETR} = \Phi_{PSII} \times \text{PAR} \times 0.5 \times A \quad (1)$$

where PAR is the photosynthetically available radiation (in μmol photons m^{-2} s^{-1}), 0.5 is a correction factor based on the assumption that the incident photons are absorbed equally by the pigments of the two photosystems, and *A* is the absorption coefficient determined in the laboratory using an integrating sphere (ISR-240A, Shimadzu). The absorption coefficient varied between 0.93 and 0.97 according to the species and season.

2.4. Carbon fluxes

Productivity of single or several individuals (depending on the size of the species) was measured using a benthic chamber placed on the shore at the target species level. The system was made of a transparent closed perspex dome tightly sealed on the polyvinylchloride (PVC) base of the chamber and enclosed a volume of 35.3 l. During immersion periods, an electronic management system controlled three external pumps; two pumps ensured the rapid and constant homogenization of the media while the third one ensured the renewal of the media by flushing ambient seawater between two consecutive incubations (Gévaert et al., 2011). pH was measured with a WTW sentix 41 probe (Multi 350i, WTW) and monitored every minute during 10 min incubations. Seawater was collected from inside the benthic chamber using a 100 ml