

Seagrass photosynthesis controls rates of calcification and photosynthesis of calcareous macroalgae in a tropical seagrass meadow

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ABSTRACT: Diel fluctuations in seawater pH can be >1 pH unit (7.9 to >8.9) in the seagrass meadows of Chwaka Bay (Zanzibar, Tanzania). The high daily pH values are generated by the photosynthetic activity of the bay's submerged seagrasses and macroalgae, and maintained by the relatively low, tide-dominated, water exchange rate. Since pH in principle can affect rates of both calcification and photosynthesis, we investigated whether diel variations in pH caused by photosynthesis could affect rates of calcification and photosynthesis of the calcareous red (*Hydrolithon* sp. and *Mesophyllum* sp.) and green (*Halimeda renschii*) algae growing within these meadows. This was done by measuring rates of calcification and relative photosynthetic electron transport (rETR) of the algae *in situ* in open-bottom incubation cylinders either in the natural presence of the rooted seagrasses or after the leaves had been removed. The results showed that seagrass photosynthesis increased the seawater pH within the cylinders from 8.3–8.4 to 8.6–8.9 after 2.5 h (largely in conformity with that of the surrounding seawater), which, in turn, enhanced the rates of calcification 5.8-fold for *Hydrolithon* sp. and 1.6-fold for the other 2 species. The rETRs of all algae largely followed the irradiance throughout the day and were (in *Mesophyllum* sp.) significantly higher in the presence of seagrasses despite the higher pH values generated by the latter. We conclude that algal calcification within seagrass meadows such as those of Chwaka Bay is considerably enhanced by the photosynthetic activity of the seagrasses, which in turn increases the seawater pH.

KEY WORDS: Calcareous algae · Calcification · *Halimeda* sp. · *Hydrolithon* sp. · *Mesophyllum* sp. · Photosynthesis · *Halimeda renschii*

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INTRODUCTION

While the main environmental factors determining photosynthesis and growth of submerged marine macrophytes have been considered to be irradiance, temperature and nutrients, one of the outcomes of macrophyte photosynthetic activity is an increased pH of the seawater within the unstirred diffusion boundary layer (including the cell walls) of the plants. This is because CO₂ and, thus, its hydrated form carbonic acid are withdrawn from the water and/or because OH⁻ is excreted from the plant (Axelsson et al. 1995). When

biomass is high compared to the seawater volume surrounding the plants and/or the water exchange rate with the open ocean is low, the entire habitat where these plants grow can feature pH values of above (during the day) or below (during the night) that of normal seawater (~8.2). Some algae can cause drastic pH increases (Axelsson & Uusitalo 1988); in the case of *Ulva* spp., this may be because they release OH⁻ (Drechsler & Beer 1991). Only recently was it recognised that such high pH values could, in turn, affect the photosynthetic performance of other algae (see Björk et al. 2004 for *Ulva intestinalis* in isolated rockpools

and Middelboe & Hansen 2007 for shallow macro-algal habitats). Also, seagrasses can increase the pH of the surrounding seawater; Invers et al. (1997) showed a pH increase of up to 0.5 units in seagrass meadows, which negatively affected photosynthetic rates of 3 seagrasses (*Posidonia oceanica*, *Cymodocea nodosa* and *Zostera noltii*). Similarly, Beer et al. (2006) showed that dominant species from a tropical bay could raise the pH to 8.5–9.2 and suggested that certain species (in this case *Halophila ovalis*) were excluded from growing in mono-specific tidal pools with other species (e.g. *Thalassia hemprichii*) because they could not photosynthesise at the high pH values generated.

One effect of seawater pH that has been studied more than the effects of photosynthesis and growth is calcification (e.g. Yates & Halley 2006). However, most studies of macrophytes considered mainly the negative effects of decreasing pH as brought about by the projected future enrichment in atmospheric and, accordingly, dissolved CO₂ (Smith & Roth 1979, Borowitzka 1981, Gao et al. 1993, de Beer & Larkum 2001). While some higher pH values have also been tested (Smith & Roth 1979, Borowitzka 1981), the generally resulting increases in calcification rates were not considered as ecologically important. Only in 1 study was calcification at high pH values measured specifically: Semesi et al. (unpubl. data) showed increased calcification rates for the coralline alga *Hydrolithon* sp. in the laboratory at pH values of up to 9.8.

Chwaka Bay (Zanzibar, Tanzania) is dominated by those same seagrasses previously found capable of increasing the pH of their surrounding seawater up to 9.2 (Beer et al. 2006), and it also contains large amounts of calcifying algae such as *Hydrolithon* sp. (Semesi et al. 2009). Since Semesi et al. (2009) showed that calcification rates of *Hydrolithon* sp. increased with pH in the laboratory, since photosynthetic rates of algae may also be sensitive to high pH values (Axelsson et al. 2000) and since pH may be modulated by future ocean acidification as CO₂ levels rise, we set out to investigate the extent to which variations in pH caused by seagrasses could affect the rates of calcification and photosynthesis of *Hydrolithon* sp. and 2 other common calcifying algae within their natural environment.

MATERIALS AND METHODS

Field measurements were carried out in the mixed seagrass and calcifying algae beds of Chwaka Bay, a ~50 km² shallow estuary in Zanzibar (Cederlöf et al. 1995), Tanzania (6° 10' S, 39° 26' E), during February to July 2008. The timing of these experiments relied on spring low tides that occurred from late morning to mid-day; such conditions were usually available dur-

ing at least 1 wk mo⁻¹. On some days however, data could not be obtained due to bad weather (too cloudy or rainy). In all, field measurements were conducted for 26 independent days within seagrass beds in the upper sub-tidal zone, dominated by *Thalassia hemprichii* but also containing small patches of *Halophila ovalis*, *Cymodocea rotundata* and *C. serrulata*.

Natural fluctuations in seawater alkalinity and carbon concentration within these beds during daily tidal cycles were determined by sampling 4 ml of water and directly measuring the pH (using a Radiometer, Denmark, Multi 340i portable pH meter) before (pH_b) and after (pH_a) the addition of 1 ml 0.01 M HCl. Alkalinity was then calculated from pH_a according to the 'rapid electrometric determinations of the alkalinity' sensu Anderson & Robinson (1946) as described in Parsons et al. (1984). Even though it is not as precise as an endpoint titration, this is a commonly used, quick, simple and accurate enough method for its purpose that allows for a large amount of samples to be analysed in the field. The total carbon concentration of the seawater was calculated from pH_b and pH_a according to the formula of Riley & Skirrow (1965) using constants from Smith & Kinsey (1978).

In order to measure calcification rates of the calcifying algae *Hydrolithon* sp., *Mesophyllum* sp. and *Halimeda renschii*, transparent open cylinders (24 cm diameter) were set along the upper sub-tidal area inhabited by seagrass beds and each of the calcareous macroalgae by pushing them some 10 cm into the sediment just at the lowest water level so that a volume of water (~4 l) was trapped within the cylinders, leaving the plants covered. In the surrounding seagrass meadow, water levels were slightly lower, but still covered the plants even at the lowest tide level. A total of 9 cylinders were used for each repetition of the experiment such that 3 cylinders contained macroalgae only (the seagrasses were manually removed), 3 contained the mixture of seagrasses and macroalgae, and 3 contained the rooted seagrasses only (algae removed). When the cylinders were set, a bucket of seawater was used as a blank for monitoring possible pH changes within cylinders due to causes other than the plants within them. However, pH values within these blanks did not significantly fluctuate throughout the experiments, with an average pH of 8.19.

Seawater pH and temperature within the cylinders were recorded at intervals of 45 min. Together with this, water samples were drawn from the cylinders (4 samples per cylinder) and placed in test tubes for immediate alkalinity measurements as described above. The replicate cylinders were sampled 6 to 8 times for each species. At the end of each experiment, algae and seagrasses within the cylinders were taken to the laboratory for wet weight measurements.

The amount of carbon used in calcification was estimated as the change in total alkalinity (TA) divided by 2. This is commonly used and was explained by Smith & Key (1975, p. 494) as

TA is lowered by 2 equivalents for each mole of CaCO_3 precipitated. Thus, there is a clear and simple stoichiometric relationship between TA and calcification: calcification lowers the total CO_2 content of seawater one mole for each mole of CaCO_3 precipitated, and the total CO_2 content of seawater is therefore lowered by 0.5 moles for each equivalent of TA reduction.

By assuming that calcification and photosynthetic inorganic carbon uptake were the only significant cause for carbon removal from seawater, the photosynthetic inorganic carbon uptake could then be deduced from the changes in total inorganic carbon less calcification.

Relative electron transport rates (rETR) of the calcareous algae were measured by pulse-amplitude modulated (PAM) fluorometry using a Diving-PAM (Walz). The rates were relative since the thallus absorption of incident photosynthetically active radiation (PAR) of these algae could not be measured. Thus, rETR was calculated as the effective quantum yield multiplied by the PAR irradiance reaching the thallus—measured under water at the thallus surface with the Diving-PAM's PAR sensor calibrated against a Model IL 1400A photometer (International Light). The rETRs were measured when water was withdrawn for the alkalinity measurements (every 45 min).

Data were pooled so that the average values from the 4 samples collected from each cylinder made up 1 replicate for each time. Paired sample *t*-tests were performed to test for differences in calcification as a function of time on cylinders with either algae only or with combinations of algae and sea grasses using the SPSS programme for Windows; differences between treatments were considered as significant at the level of $p \leq 0.05$.

RESULTS

Natural diurnal fluctuations in pH, total alkalinity and dissolved inorganic carbon within the seagrass-dominated bay are illustrated in Fig. 1. The highest pH values (around 8.9) were recorded during low tide, when the water depth was <10 cm in the seagrass bed and the flow was relatively low, coinciding with low values of total alkalinity and dissolved inorganic carbon. Conversely, pH was low, and total alkalinity and dissolved inorganic carbon were high during high tide. The drop in total alkalinity during low tide is likely a result of high calcification rates of the calcareous algae and other calcifiers (cf. Yates & Halley 2006), probably

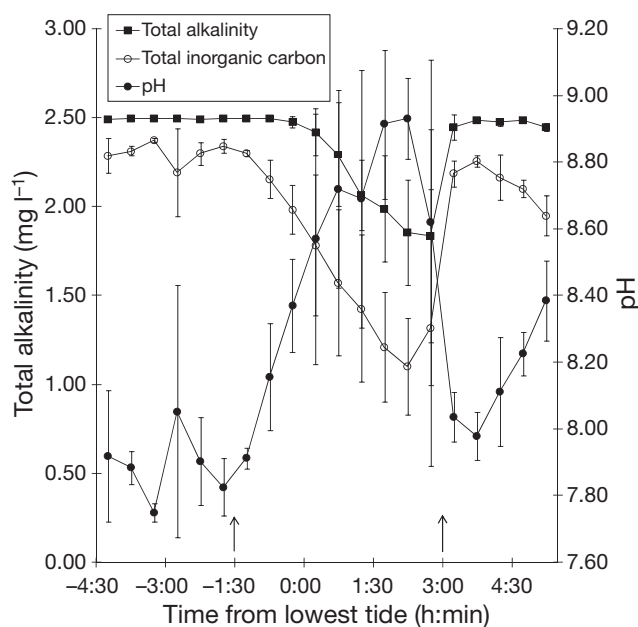


Fig. 1. Diurnal changes in physico-chemical characteristics (total alkalinity and inorganic carbon, pH) of seawater during a tidal cycle at Chwaka Bay in the intertidal area dominated by seagrasses and calcareous algae. Arrows indicate the beginning of incoming tide (left arrow) and the beginning of outgoing tide (right arrow). Data are means \pm SD, $n = 3$ (sampling on 3 independent days)

favoured by the high pH values. During low tide, the temperature increased from ~ 27 to $\sim 33^\circ\text{C}$.

The calcification rates of *Hydrolithon* sp. increased with incubation time and became significantly higher ($p \leq 0.05$) in the presence of seagrasses than in their absence after 55 min (Fig. 2a). At the end of the incubation, calcification rates were 5 to 6 times higher in the presence of seagrasses. During this time, the pH in the incubation cylinders containing both algae and seagrasses had increased to 8.7 while the pH in the cylinders without seagrasses remained 8.3. The rETR of *Hydrolithon* sp. followed the PAR during the incubations, so that the photosynthetic rates dropped at the end of the incubation period, while calcification increased. There was no significant difference ($p \geq 0.05$) in rates whether seagrasses were present or absent (Fig. 2b).

Mesophyllum sp. also showed a significantly higher rate of calcification ($p \leq 0.05$) in the presence of seagrasses after 55 min of incubation (Fig. 3a). At the end of the incubation, the calcification rate was 1.6-fold higher in the presence than in the absence of seagrasses. This coincided with a higher pH in the cylinders with algae and seagrasses (8.9 at the end of the incubation) than in those with algae alone (8.4). The rETRs of the algae in these cylinders followed the PAR during the day, but

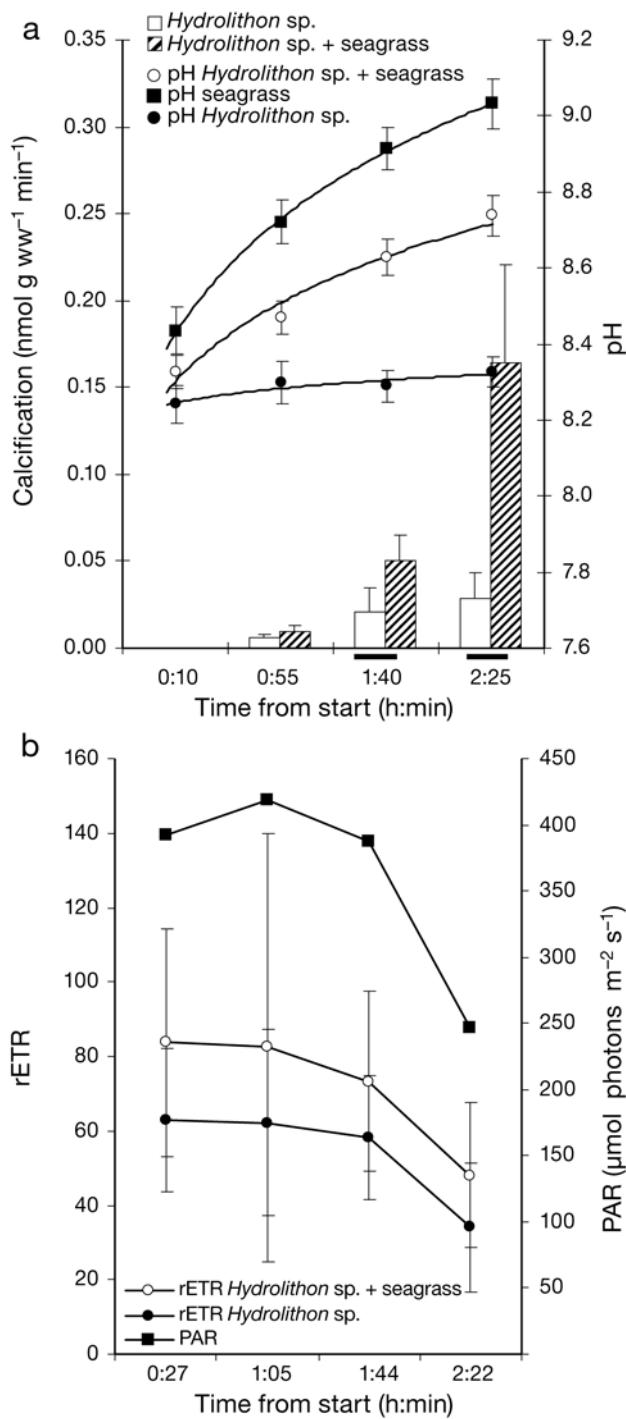


Fig. 2. *Hydrolithon* sp. Irradiance, pH, rates of calcification, and relative electron transport rate (rETR) as a function of incubation time with and without seagrasses. (a) Calcification rates with algae only (open bar) and algae together with seagrasses (hatched bar), and the pH generated in each treatment: seagrasses only (■), algae only (●) and algae together with seagrasses (○); lines below bars indicate a significant difference between treatments ($p \leq 0.05$); ww: wet weight. (b) rETR values of algae alone (●) and algae together with seagrasses (○), and PAR (■). Data are means \pm SD, $n = 7$

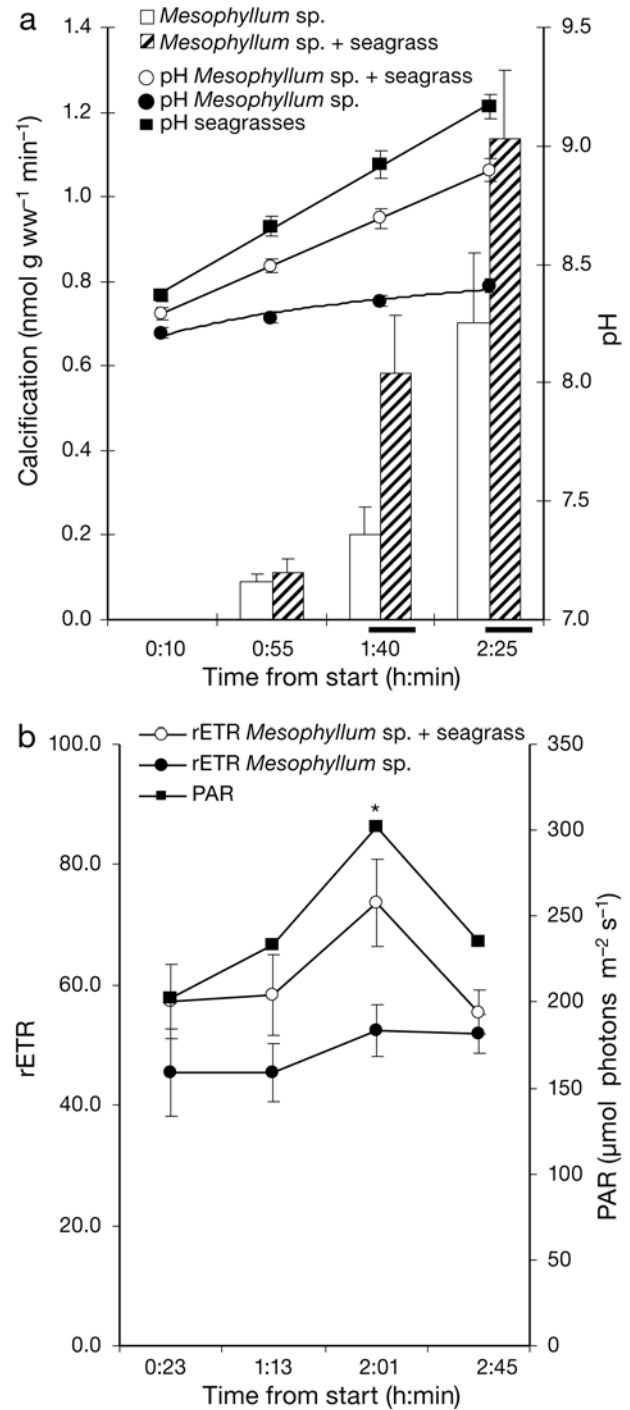


Fig. 3. *Mesophyllum* sp. Irradiance, pH, rates of calcification, and relative electron transport rate (rETR) as a function of incubation time with and without seagrasses. (a) Calcification rates with algae only (open bar) and algae together with seagrasses (hatched bar), and the pH generated in each treatment: seagrasses only (■), algae only (●) and algae together with seagrasses (○); lines below bars indicate a significant difference between treatments ($p \leq 0.05$); ww: wet weight. (b) rETR values of algae alone (●) and algae together with seagrasses (○), and PAR (■); stars above the graphs indicate a significant difference between treatments ($p \leq 0.05$). Data are means \pm SD, $n = 5$

were significantly higher ($p \leq 0.05$) when the algae were in the presence of the seagrasses than alone at 1:13 h and 2:01 h (Fig. 3b). The drop in ETR at the end of the experiment was marked only when seagrasses were present, indicating an effect of the high pH values in those incubations.

Similar to the 2 coralline red algae, *Halimeda renschii* also showed significantly higher rates of calcification ($p \leq 0.05$) when in the presence of seagrasses (Fig. 4a). This was already clear at the 55 min observation, when the pH values were 8.5 in the cylinders containing seagrasses and 8.2 in those with the algae only. After this timepoint, calcification rates (together with pH) increased further. At the end of the incubation, the calcification rate was 1.6-fold higher in the presence of seagrasses than in their absence; at this time, the pH was 8.8 and 8.3 for the 2 incubation conditions, respectively. This alga also showed rETRs that followed the PAR, and the drop in rates was higher when the seagrasses were present, but there was no significant difference ($p \geq 0.05$) in rETRs between the algae in the presence or absence of seagrasses (Fig. 4b).

Within the controls (cylinders with seagrasses only), some calcification was detected, even though those rates were only 1 to 3% of the ones observed when calcareous algae were present. At the same time, pH in these cylinders increased more than in any of the other incubation cylinders, eventually reaching values above 9 (Figs. 2 to 4). Microphytobenthic photosynthesis stimulates calcification within coral reef sediment by increasing the pH of the pore waters and thereby the saturation state of CaCO_3 (Werner et al. 2008), so the observed calcification within the seagrass controls might be due both to the activity of microphytobenthos within the sediments or the superimposed pH shift from the seagrass photosynthesis, or a combination of both. Furthermore, even though the seagrasses used in the present study did not harbour any substantial amount of epiphytes, especially not calcareous crusts that are common on many tropical species (Uku & Björk 2005), we cannot exclude the possibility that small amounts of epiphytic calcareous algae were present on the leaves and thus contributed to the minute rates of calcification in the seagrass control cylinders, where the rates were probably also enhanced by the observed pH increase.

DISCUSSION

In the present study, we show for the first time that the high pH values caused naturally by seagrass photosynthesis can enhance calcification rates of calcifying macroalgae growing within a seagrass bed. For some algae (i.e. *Mesophyllum* sp. and *Halimeda ren-*

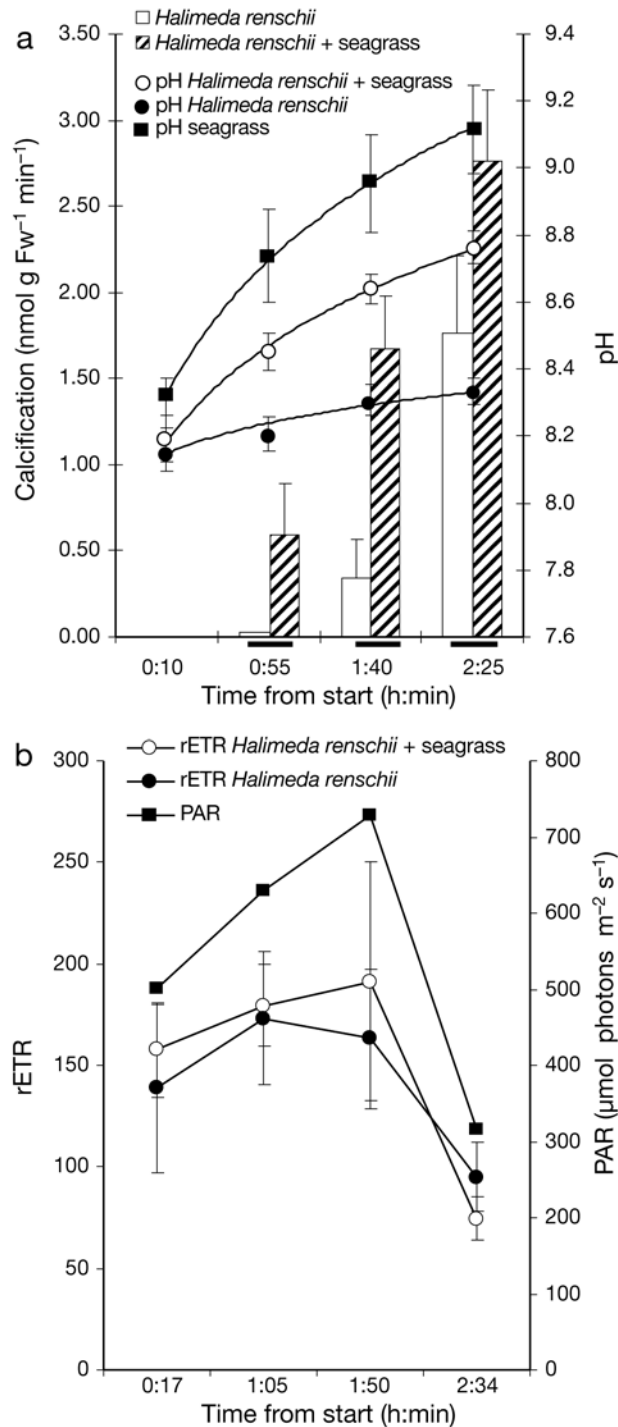


Fig. 4. *Halimeda renschii*. Irradiance, pH, rates of calcification, and relative electron transport rate (rETR) as a function of incubation time with and without seagrasses. (a) Calcification rates with algae only (open bar) and algae together with seagrasses (hatched bar), and the pH generated in each treatment: seagrasses only (■), algae only (●) and algae together with seagrasses (○); lines below bars indicate a significant difference between treatments ($p \leq 0.05$); ww: wet weight; (b) rETR values of algae only (●) and algae together with seagrasses (○), and PAR (■). Data are means \pm SD, $n = 5$

schii), the high pH also tends to lower photosynthetic rate, but this finding needs further verification.

Shifts in seawater pH may be significant in shallow areas with high plant densities when water movement is restricted (e.g. in pools or lagoons) but, except in a few cases (Björk et al. 2004, Beer et al. 2006, Middelboe & Hansen 2007), such shifts have not been ascribed any importance as a controlling factor for photosynthesis and growth of species featuring e.g. inorganic carbon limitations in nature. On the other hand, high pH values generated by adding a base to seawater have been shown to accelerate calcification rates in calcifying algae (Borowitzka & Larkum 1976, de Beer & Larkum 2001, Semesi et al. 2009), but the relevance of this occurrence in natural settings was not investigated hitherto.

While the increased calcification rates of the algae due to increasing pH values during the incubations was expected, an unexpected finding in this work was the significantly higher (by ~15%) photosynthetic rates in *Mesophyllum* sp. when incubated together with seagrasses (thus experiencing higher pH values). Even if we cannot pinpoint the reason(s) behind this, it seems that either the increased calcification rate promoted photosynthesis or that there was some type of allelopathy between the seagrasses and the algae. In the case of calcification, it could be that because the process releases CO₂, this additional carbon source was utilised efficiently from the diffusion boundary layer of the algae. Another unexpected finding was the lower pH values obtained when the seagrasses were photosynthesising together with the algae than when alone (despite similar seagrass biomasses in all incubations). This, again, could be due to a contribution of CO₂ from the algae's calcification process that moderated the pH increase caused by the seagrasses.

The basic reason that submerged photosynthesising organisms raise the pH of the surrounding water is that CO₂ is removed by the photosynthetic process. This is true also for the many macroalgae and seagrasses that utilise HCO₃⁻, which is in equilibrium with the dissolved CO₂. In some cases, macroalgae of the genus *Ulva* can also transport OH⁻ to the medium while taking up HCO₃⁻ (Beer 1998), but this is rather an exception and has not been noted for seagrasses (at least not those featuring other means of inorganic carbon acquisition, Beer et al. 2002). These high pH values may, in turn, reduce photosynthetic rates by lowering both the surrounding CO₂ concentration (in areas where dissolved and atmospheric CO₂ are not in equilibrium) and, at pH values above ~8.2, the HCO₃⁻ concentration as well (in favour of CO₃²⁻ formation).

The pH variations caused by the photosynthetic activity in marine systems such as Chwaka Bay have only rarely been found to affect other biological func-

tions. In one case, it was shown that the high pH generated by *Ulva intestinalis* in temperate rockpools could hinder the photosynthetic activity of other algae, thus restricting them from growing there (Björk et al. 2004). In another case, similar effects were found in shallow temperate waters with restricted water flow (Middelboe & Hansen 2007). Regarding seagrasses, it was shown that some tropical species in intertidal pools of Chwaka Bay could increase the pH to such high values that photosynthesis of others was hindered (Beer et al. 2006). The growing understanding of the ecological importance of biogenic generation of pH variations is strengthened by our demonstration of its significant effect on rates of calcification by calcifying algae.

The algae investigated here are major calcifiers in Chwaka Bay and may be in other tropical areas as well. For example, much of the inorganic sandy substrate of the bay is made up of the remainders of *Hali-medea* spp. thalli, which are gradually broken down to finer particles (Muzuka et al 2001). Also, seawards in the bay area, calcifying red algae are an important component building reef-like structures. Considering this, the highly significant influence of biologically generated pH changes on processes such as calcification may be of great importance in other shallow marine systems too. Even though the number of reports on its significance is small, pH should be looked upon as an important ecological factor in many marine environments, the fluctuations of which can control several biological processes including calcification, rates of photosynthesis and, thus, growth rates.

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