



Differential growth responses to water flow and reduced pH in tropical marine macroalgae

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ABSTRACT

The physical environment plays a key role in facilitating the transfer of nutrients and dissolved gases to marine organisms and can alter the rate of delivery of dissolved inorganic carbon. For non-calcifying macroalgae, water motion can influence the physiological and ecological responses to various environmental changes such as ocean acidification (OA). We tested the effects of lowered pH under three different flow speeds on three dominant non-calcifying macroalgal species differing in their carbon-use and are commonly found in the back reefs of Moorea, French Polynesia. Relative growth rates (RGR) of two phaeophytes, *Dictyota bartayresiana* and *Lobophora variegata* (HCO_3^- users), and a rhodophyte, *Amansia rhodantha* (CO_2 user) were measured to examine how the combined effects of OA and flow can affect algal growth. Growth rates were affected independently by $p\text{CO}_2$ and flow treatments but there was no significant interactive effect. Additionally, growth rates among species varied within the different flow regimes. Of the three species, *L. variegata* had the overall greatest increase in RGR across all three flow speeds while *A. rhodantha* exhibited the greatest negative impact under elevated $p\text{CO}_2$ at $0.1 \text{ cm} \cdot \text{s}^{-1}$. These differential responses among algal species demonstrate the importance of flow when examining responses to a changing environment, and if the responses of macroalgae differ based on their carbon-use strategies, it may provide advantages to some macroalgal species in a future, more acidic ocean.

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1. Introduction

The shift in benthic coral reef communities has been linked to a number of local drivers contributing to the decline in calcifying marine organisms and an increase in fleshy macroalgae (McCook, 1999). Additional to overfishing, nutrient runoff, hurricanes and cyclones, and coral diseases (Hughes et al., 2003), the global stressor of ocean acidification (OA) due to increasing atmospheric CO_2 levels and the consequent reduction in seawater pH has negatively impacted calcifying organisms (Anthony et al., 2008; Comeau et al., 2016). Extensive research has focused on the responses of scleractinian corals and coralline algae to OA due to lowered carbonate saturation states and the reduction in calcification rates (Doney et al., 2009; Kleypas and Yates, 2009). Although these responses vary among species, calcifying organisms generally exhibit greater negative responses than non-calcifying organisms (i.e. fleshy macroalgae) (Kroeker et al., 2010). On the contrary, non-

calcifying macroalgae have exhibited either negligible (Israel and Hophy, 2002; Fernández et al., 2015) or positive responses to higher CO_2 levels (Connell and Russell, 2009; Diaz-Pulido et al., 2011; Porzio et al., 2011; Johnson et al., 2012), broadening interest to understand the varying responses of macroalgae to environmental changes.

The physical environment also plays a critical role influencing the physiological responses of benthic organisms. For marine macroalgae, water movement is a key factor influencing a number of physiological and biological processes: morphology (Hurd, 2000; Stewart and Carpenter, 2003), production and mass transfer (Adey and Steneck, 1985; Carpenter et al., 1991), photosynthesis and growth (Koch et al., 2013), some facilitating larval/spore dispersal (Lowe and Falter, 2015), light attenuation (Carpenter, 1985), and carbon acquisition (Hurd, 2000; Raven et al., 2005). The rate and mode of water motion (e.g. fast vs. slow; oscillatory vs. unidirectional) also contributes greatly to the variable effects of water motion on algal metabolism (Denny et al., 1985; Carpenter et al., 1991). An increase in water motion is beneficial for resource acquisition, ultimately increasing photosynthesis and growth, while a decrease in water motion (i.e. slow flow) can increase mass transfer limitation of gases and nutrients, potentially leading to negative effects on metabolic rates (Atkinson and Bilger, 1992; Hurd, 2000). However, decreased water motion also can ameliorate the negative effects of OA, particularly for calcifying organisms. This was

Abbreviations: CA, carbonic anhydrase; Ci, inorganic carbon; CCM, carbon-concentrating mechanism; DBL, diffusion boundary layer; DIC, dissolved inorganic carbon; OA, ocean acidification; RGR, relative growth rate.

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demonstrated by Cornwall et al. (2014) on coralline algae grown under slow flows yet maintaining net calcification at a lowered pH, illustrating how algae respond physiologically to buffer against OA. Conversely, OA conditions may benefit some non-calcareous algae and the increase in water motion may further enhance metabolic and growth rates by promoting mass flux of materials (Hurd, 2000; Stewart and Carpenter, 2003). In a reef-lagoon system that is primarily wave-driven (as seen in Moorea, French Polynesia), reef organisms such as macroalgae can experience natural fluctuations of high and low circulation in water motion in the back reef that can differentially affect the physiological adaptations among algae (Hench et al., 2008). Thus, the responses of fleshy macroalgae are likely modulated by other abiotic factors such as water flow, yet few studies have examined the interactive effects of water motion and OA.

OA is altering the partitioning of dissolved inorganic carbon (DIC), increasing CO_2 and HCO_3^- while decreasing CO_3^{2-} concentrations (Andersson and Mackenzie, 2011; Veron, 2011). The alteration in DIC speciation can cause responses in calcifying and non-calcifying organisms to shift, thereby potentially affecting their metabolism, growth rates, and relative abundances. Macroalgae depend on the supply of inorganic carbon (Ci) for photosynthesis and growth, and their capability to assimilate Ci either via diffusion (for CO_2) or active uptake of HCO_3^- using carbon-concentrating mechanisms (CCMs) depends on the availability of CO_2 present (Beardall et al., 1998; Giordano et al., 2005). In many cases, CO_2 alone is insufficient for maximum photosynthesis (Giordano et al., 2005; Hurd et al., 2009), therefore the increase in concentrations of CO_2 is predicted to have various (positive) effects on carbon assimilation, photosynthesis, and growth for both CO_2 and HCO_3^- users. For obligate CO_2 users lacking CCMs, increase atmospheric CO_2 dissolution in seawater can alleviate carbon limitation and mitigate the potential disadvantages in their competitive ability with other non-calcareous algae. For HCO_3^- users, OA may not enhance photosynthetic rates as expected for CO_2 users (Zou, 2005; Hurd et al., 2009), but they may downregulate their CCM activity, thus reducing energetic investment for CO_2 active uptake (Raven and Hurd, 2012). Their ability to readily convert HCO_3^- to CO_2 is achieved by either using extracellular carbonic anhydrase (CA) or having CA acting intracellularly (Hurd et al., 2009; Fernández et al., 2014; Rautenberger et al., 2015). This evolutionary development has provided macroalgae with CCMs a more energetically costly, but beneficial advantage, eliminating the risk of carbon limitation under present $p\text{CO}_2$ in most environments (Giordano et al., 2005). These responses are species-specific (Kram et al., 2015), and the majority of studies have focused on OA effects in isolation (e.g. Cornwall et al., 2012; Fernández et al., 2015; Kim et al., 2016; Ober et al., 2016). Furthermore, the response and level of sensitivity to OA may vary across taxa due to the different carbon uptake strategies (i.e. CO_2 -only user or facultative HCO_3^- -user; Table 1) in fleshy macroalgae (Kroeker et al., 2010; Cornwall et al., 2012).

The present study focused on three dominant non-calcifying macroalgal species: *Lobophora variegata* (Phaeophyta), *Dictyota bartayresiana* (Phaeophyta), and *Amansia rhodantha* (Rhodophyta) commonly found in the back reef of Moorea, French Polynesia.

Additionally, the three species have different carbon uptake strategies. *L. variegata* is known to be a HCO_3^- user (Koch et al., 2013) while a pH drift analysis (Maberly, 1990) was conducted prior to treatment to determine the Ci assimilation of *D. bartayresiana* and *A. rhodantha*. This technique measures the change in pH when carbon is assimilated through photosynthesis, and when the pH is raised above 9, generally indicates the alga utilizing HCO_3^- (Axelsson and Uusitalo, 1988; Maberly, 1990; Diaz-Pulido et al., 2016). The pH drift experiment revealed *D. bartayresiana* as a HCO_3^- user (raising pH > 9) and *A. rhodantha* as a CO_2 user (carbon saturated at a pH of 8.51) (R. Carpenter unpub. data). We examined the combined effects of unidirectional flow speeds and lowered pH on macroalgal growth rates and whether their responses varied based on their DIC use. We tested the following hypotheses: (i) algal growth rates would increase with increasing flow speed, (ii) *A. rhodantha* (CO_2 user) would benefit under elevated $p\text{CO}_2$ by having higher growth rates than *D. bartayresiana* and *L. variegata*, (iii) the growth rates of HCO_3^- users would not vary between current and elevated $p\text{CO}_2$ conditions, and (iv) the interactive effect of flow and OA would result in higher growth rates for *A. rhodantha* than the other two species. The relative growth rates were measured as a proxy of fitness to assess how the interaction of OA and flow can affect algal biomass.

2. Methods

2.1. Study site and collection

This study was conducted in Moorea, French Polynesia in June–July 2014. Three dominant non-calcifying species, *Lobophora variegata*, *Dictyota bartayresiana*, and *Amansia rhodantha* of similar biomass were collected on the back reef of the north shore at a depth < 3 m (Fig. 1). *L. variegata* exists in three morphologies, a ruffled form, a decumbent form, and an encrusting morph (Coen and Tanner, 1989). The decumbent and encrusting forms were commonly seen in Moorea and therefore, the decumbent morphology was used, as it was most similar to the other two fleshy macroalgal species. These species were chosen from preliminary field surveys on overall abundance of macroalgae on the back reef of the north shore in 2014 (unpub. data). Additionally, they represented some of the common species in the back reef of Moorea for benthic algal cover of 2014 (Carpenter, 2015), with majority of the algal cover being non-calcifying macroalgae. The most abundant non-calcifying species were: *Amansia rhodantha* (3%), *Dictyota bartayresiana* (8%), *Lobophora variegata* (~1%), *Chnoospora implexa* (~1%), *Sargassum pacificum* (~1%), *Turbinaria ornata* (10%), and algal turf (43%).

New algal samples were collected weekly ($n = 40$ per species), 2 days prior to each flow/ $p\text{CO}_2$ experiment and brought to the Richard B. Gump South Pacific Research Station located in Cook's Bay, Moorea. Algae were placed in a flow-through seawater table, cleaned of epiphytes, then each algal individual was placed into a nylon monofilament mesh bag with 1.3-cm openings (Fig. 2C and D). Mesh bags were used to retain as much algal biomass as possible and minimize the effects of

Table 1

The two general categories by which macroalgae assimilate carbon (adapted from Hepburn et al. (2011)) and some limitations in each strategy with the predictive responses to OA. CCM = CO_2 concentrating mechanism, OA = Ocean acidification.

Carbon use strategy	Disadvantages	Predictions to OA	Reference
CO_2 -only user (Non-CCM species)	<ul style="list-style-type: none"> CO_2 concentration in seawater is low. CO_2 diffusion rates are slow in seawater. Likely to be carbon-limited 	<ul style="list-style-type: none"> Enhance photosynthesis Increase growth Alter/improve competitive ability with other fleshy algae 	1, 3, 6, 8, 9
Facultative $\text{HCO}_3^-/\text{CO}_2$ user (CCM present)	<ul style="list-style-type: none"> CCMs are energetically costly. May be restricted to high light habitats 	<ul style="list-style-type: none"> Down-regulate active CO_2 uptake may lead to enhanced growth Expected to exhibit little (positive) or neutral responses in photosynthesis compared to CO_2 users 	2, 4, 5, 7, 8, 10, 11, 12

References: (1) Cornwall et al. (2012); (2) Cornwall et al. (2015); (3) Diaz-Pulido et al. (2016); (4) Fernández et al. (2015); (5) Giordano et al. (2005); (6) Hepburn et al. (2011); (7) Hurd et al. (2009); (8) Kübler et al. (1999); (9) Rautenberger et al. (2015); (10) Raven (1991); (11) Raven et al. (2014); (12) Zou (2005).

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