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Effects of a submarine eruption on the performance of two brown seaweeds

Séfora Betancor [a,*], Fernando Tuya [a], Teba Gil-Díaz [a], Félix L. Figueroa [b], Ricardo Haroun [a]

[a] Centro en Biodiversidad y Gestión Ambiental, Marine Sciences Faculty, Universidad de Las Palmas de Gran Canaria, Las Palmas, Canary Islands, Spain
[b] Departamento de Ecología, Facultad de Ciencias, Universidad de Málaga, Campus Universitario de Teatinos s/n, 29071 Málaga, Spain

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ABSTRACT

World oceans are becoming more acidic as a consequence of CO_2 anthropogenic emissions, with multiple physiological and ecological implications. So far, our understanding is mainly limited to some species through in vitro experimentation. In this study, we took advantage of a recent submarine eruption (from October 2011 to March 2012) at ~1 nautical mile offshore El Hierro Island (Canary Islands, central east Atlantic) to determine whether altered physical–chemical conditions, mainly sudden natural ocean acidification, affected the morphology, photosynthesis (in situ Chl-a fluorescence) and physiological performance (photo-protective mechanisms and oxidative stress) of the conspicuous brown seaweeds *Padina pavonica*—a species with carbonate deposition – and *Lobophora variegata*—a species without carbonate on thallus surfaces – , both with similar morphology. Seaweeds were sampled twice: November 2011 (eruptive phase with a pH drop of *ca.* 1.22 units relative to standard conditions) and March 2012 (post-eruptive phase with a pH of ca. 8.23), on two intertidal locations adjacent to the eruption and at a control location. *P. pavonica* showed decalcification and loss of photo-protective compounds and antioxidant activity at locations affected by the eruption, behaving as a sun-adapted species during lowered pH conditions. At the same time, *L. variegata* suffered a decrease in photo-protective compounds and antioxidant activity during the volcanic event, but its photosynthetic performance remained unaltered. These results reinforce the idea that calcareous seaweeds, as a whole, are more sensitive than non-calcareous seaweeds to alter their performance under scenarios of reduced pH.

1. Introduction

World oceans are becoming more acidic as a consequence of anthropogenic CO_2 emissions, a phenomenon known as ocean acidification' (OA) (Caldeira and Wickett, 2003; Orr et al., 2005; Dupont et al., 2010; Dupont et al., 2012). These emissions are likely to have severe impacts on the part of the marine life, since organisms will encounter conditions that their ancestors never had to face (Ruttimann, 2006). Benthic photoautotrophs have exhibited various responses to ocean acidification (Connell and Russell, 2010). Some marine algae benefit from higher CO_2 levels, which enhances their growth (Gao et al., 1999; Kübler et al., 1999; Riebesell et al., 2007), Coralline algae, however, appear to be amongst the most sensitive photoautotrophs, as they have a skeletal mineralogy that dissolves easily at predicted levels of calcium carbonate saturation (Gao et al., 1993; Martin and Gattuso, 2009).

Nowadays, our knowledge on the way OA may affect marine biota come from a range of confined, short-term experiments, i.e. in vitro approaches, which are usually single-species oriented (Widdicombe et al., 2010; Wernberg et al., 2012). These laboratory-based approaches have shown that many calcareous species may be incapable to create their skeletons as oceans acidify over the next century. A recent meta-analysis on the vulnerability of marine biota to OA concluded, however, that most experimental assessments overestimate the negative effects on the concerned organisms, and proposed that marine species are more resistant to OA than expected (Hendriks et al., 2010). Few studies, however, have analyzed the effects of sea water acidification over marine organisms through direct observations; e.g. fluxes of hydrothermal fluids drastically change sea water conditions as temperature rises and pH, visibility and dissolved oxygen are notably reduced (Staudigel et al., 2006). In situ observations on macroalgal communities affected by volcanic carbon dioxide vents have been conducted (Porzio et al., 2011). These 'natural' phenomena, therefore, provide useful pH gradients to find out physiological and ecological responses of a range of organisms under different acidification scenarios (Hall-Spencer et al., 2008; Arnold et al., 2012). Typically, these dramatic changes in seawater quality often lead to a rapid decline in the abundance and physiological performance of a variety of organisms in the area immediately affected by the volcanic activity, particularly those with no possibility of escape (Hall-Spencer et al., 2008). Thus, organisms experience then physiological and morphological changes to acclimate their metabolism to the new environmental scenario.

Phototrophs have shown a superior growth and undiminished rates of photosynthesis at elevated CO_2 concentrations (Levitan et al., 2007;

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* Corresponding author. Tel.: +34 928457456; fax: +34 928452900.
E-mail address: sefora.betancor@gmail.com (S. Betancor).

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Riebesell et al., 2007). For example, the photosynthesis and content of soluble carbohydrates of seagrasses can be enhanced under a scenario of reduced pH (Palacios and Zimmerman, 2007). At the same time, increasing atmospheric CO_2 typically triggers the production of phenolic compounds that may help as herbivore deterrents, digestion reducers, antimicrobials and UV protectors; this is particularly pertinent in models linking excess CO_2 and carbohydrates to an increased production of carbon-based defenses (Mattson et al., 2005). However, protective phenolic substances can be severely reduced under an acidic scenario (Arnold et al., 2012); hence, such a discrepancy requires new data. Despite most seaweeds may tolerate pH levels predicted for the end of this century, the richness and coverage of coralline algae has been observed to decrease as a result of sea water acidification, while the abundance, growth and fitness of non-calcareous algae and seagrasses may increase as a result of a larger $[CO_2]$ availability (Gao et al., 1999; Kübler et al., 1999; Riebesell et al., 2007; Fabricius et al., 2011; Porzio et al., 2011). In addition, changes in pH may occur in conjunction with changes in other environmental variables. For example, a decrease in pH may interact with an increase in UV radiation to synergistically reduce the photosynthesis, calcification, pigment contents, and so the growth, of the red seaweed *Corallina sessilis*, while the concentration of photo-protective compounds is enhanced (Gao and Zheng, 2010).

The Canary Islands are a chain of volcanic islands located in the eastern central Atlantic, offshore the western African coast. In the past, volcanic activity responsible for island formation varied among islands and volcanic episodes, including several historical eruptions that have been reported since the islands' colonization. On the 10th of October 2011, at about 1 nautical mile south offshore the small village of *La Restinga* (El Hierro Island, Fig. 1A), a submarine eruption began to release volcanic material, including intense bubbling at the surface, foam rings and floating rock fragment ('restingolites') reaching the sea surface (Carracedo et al., 2012). The water column over the volcanic area suffered dramatic physical and chemical alterations, including warming, acidification and deoxygenation; the release of CO_2 produced total inorganic carbon concentrations ranging from 4000 to 7500 μmol kg^{-1}, causing water acidification of up to 2.8 units within the first 100 m of the water column (Fraile-Nuez et al., 2012). At the same time, the volcanic activity released nutrients into the seawater, principally Fe, Si, P and N; increased nutrients concentrations caused a fertilization of the offshore waters during the eruptive event (Santana-Casiano et al., 2013). The release of this volcanic material produced large greenish seawater plumes that intermittently extended onshore, according to meso-scale oceanographic activity (Fraile-Nuez et al., 2012; Nolasco et al., 2012) and affected a range of organisms in the coast (Santana-Casiano et al., 2013). The volcanic activity officially

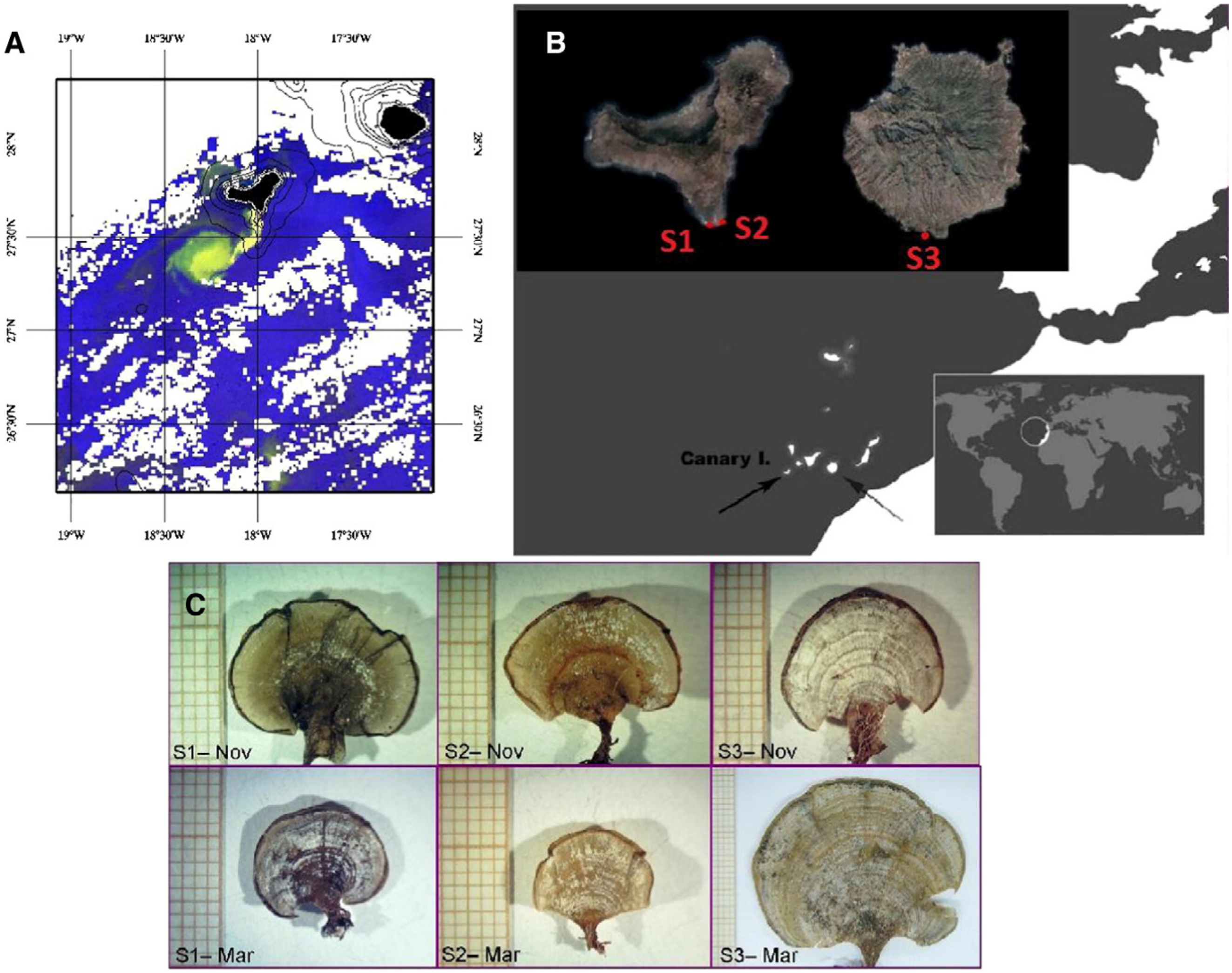

Fig. 1. (A) RGB composition of reflectancies for 6671, 531 and 412 nm from MODIS sensor in AQUA satellite on the 2nd November-2012 showing the island of El Hierro and the offshore, green discolored, plume created by the submarine eruption. (B) Geographical situation of study locations. Top-left panel shows El Hierro and Gran Canaria islands, denoting sampled locations. (C) *P. pavonica* thallus highlights calcification changes.