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Nutrient Loading Fosters Seagrass Productivity Under Ocean Acidification

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The effects of climate change are likely to be dependent on local settings. Nonetheless, the compounded effects of global and regional stressors remain poorly understood. Here, we used CO_2 vents to assess how the effects of ocean acidification on the seagrass, *Posidonia oceanica*, and the associated epiphytic community can be modified by enhanced nutrient loading. *P. oceanica* at ambient and low pH sites was exposed to three nutrient levels for 16 months. The response of *P. oceanica* to experimental conditions was assessed by combining analyses of gene expression, plant growth, photosynthetic pigments and epiphyte loading. At low pH, nutrient addition fostered plant growth and the synthesis of photosynthetic pigments. Overexpression of nitrogen transporter genes following nutrient additions at low pH suggests enhanced nutrient uptake by the plant. In addition, enhanced nutrient levels reduced the expression of selected antioxidant genes in plants exposed to low pH and increased epiphyte cover at both ambient and low pH. Our results show that the effects of ocean acidification on *P. oceanica* depend upon local nutrient concentration. More generally, our findings suggest that taking into account local environmental settings will be crucial to advance our understanding of the effects of global stressors on marine systems.

Interactive and cumulative effects of global climate changes resulting from enhanced CO_2 emissions, such as seawater warming and ocean acidification (OA), have been extensively investigated in the last decade[1,2]. In contrast, despite the recognition that human stressors on natural systems build-up from global to local scales, less attention has been devoted to assess how the effects of global changes on marine systems can be modified by a regional or local stressor[3,4].

Anthropogenic ocean acidification is among the major climate-related stressors in marine coastal ecosystems (IPCC 2014). Increased partial pressure of CO_2 (pCO_2) in seawater can have both positive and negative impacts on marine primary producers[5,6]. Negative effects have been widely recorded for calcifying macroalgae[7,8]. Seagrasses are generally carbon-limited under current pCO_2, and may benefit from an increment in CO_2 and HCO_3[6], although their response can differ among species as a result of variation in carbon concentration mechanisms[9]. The increase in DIC and CO_2 associated to OA can enhance nitrogen demand for plants[10,11]. Previous studies on terrestrial plants have shown that the initial stimulation of photosynthesis and growth at elevated CO_2 levels were subsequently down-regulated as nitrogen content decreased[10,12]. Therefore, the net effect of OA on seagrasses may depend upon nitrogen availability.

Enhanced nutrient loading in coastal environments could be expected to generate[13] or amplify[14] positive effects of OA on the productivity of seagrasses. Mesocosm studies have found little evidence of positive effects of OA on seagrasses to be sustained by nutrient enhancement[9,15–17]. The duration of these studies (24 days to 6 weeks) could be too short for enhanced pCO_2 to induce nutrient limitation, although responses are likely species-specific, depending on the plant metabolism and growth dynamics. In addition, the effects of nutrients have been generally assessed by comparing the performance of seagrasses between nutrient ambient *versus* nutrient enhanced conditions, providing no information on how they can vary according to their concentration. Whether enhanced nutrient availability may alleviate N limitation at low pH, excessive loading could negatively

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