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Linking gene expression to productivity to unravel long- and short-term responses of seagrasses exposed to CO₂ in volcanic vents

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Ocean acidification is a major threat for marine life but seagrasses are expected to benefit from high CO₂. *In situ* (long-term) and transplanted (short-term) plant incubations of the seagrass *Cymodocea nodosa* were performed near and away the influence of volcanic CO₂ vents at Vulcano Island to test the hypothesis of beneficial effects of CO₂ on plant productivity. We relate, for the first time, the expression of photosynthetic, antioxidant and metal detoxification-related genes to net plant productivity (NPP). Results revealed a consistent pattern between gene expression and productivity indicating water origin as the main source of variability. However, the hypothesised beneficial effect of high CO₂ around vents was not supported. We observed a consistent long- and short-term pattern of gene down-regulation and 2.5-fold NPP decrease in plants incubated in water from the vents and a generalized up-regulation and NPP increase in plants from the vent site incubated with water from the Reference site. Contrastingly, NPP of specimens experimentally exposed to a CO₂ range significantly correlated with CO₂ availability. The down-regulation of metal-related genes in *C. nodosa* leaves exposed to water from the venting site suggests that other factors than heavy metals, may be at play at Vulcano confounding the CO₂ effects.

Rising atmospheric carbon dioxide (CO₂) is increasing the concentration of dissolved inorganic carbon (DIC) in the ocean causing ocean acidification. Projections forecast that ocean acidification will continue and that by the end of the century the mean global ocean surface pH will decrease up to 0.4 units¹, profoundly affecting marine systems^{1,2}. Biological responses associated with ocean acidification range from changes in organismal physiology and behaviour up to changes in population structure, with major global implications for the entire ecosystem functioning and the goods and services provided¹.

The increase in seawater DIC and CO₂ associated with ocean acidification may favour carbon-limited species, such as seagrasses, by increasing both the passive diffusion of CO₂ and the efficiency of RuBisCO carboxylation over photorespiration³, lowering the energetic photosynthetic requirements and consequently increasing photosynthetic production^{2,4}. Physiological acclimation to ocean acidification has been widely documented in seagrasses and includes changes in photosynthetic rates, metabolism, growth and survival (e.g. refs 5–7). However, experimental evidence for increased seagrass productivity as a response to elevated CO₂ levels and ocean acidification is inconclusive, and particularly scarce over long-time scale. Indeed, recent meta-analysis did not identify significant effects of ocean acidification on seagrass photosynthesis⁸.

The modulation of gene expression plays a central role in plant plasticity and adaptation to environmental changes⁹, since physiological machinery and metabolic pathways are coordinated at the genetic level by an array of regulatory genes, which are also affected by environmental stimuli¹⁰. In the last decade, molecular techniques for studying gene expression have been increasingly recognized as a powerful tool for physiological research to assess the acclimation responses and adaptive potential of marine organisms to ocean acidification (see ref. 11 for a review). Gene expression can be used to assess the role that plasticity and long-term adaptation to high CO₂ play in altering specific metabolic pathways related with the physiological response, but also the fast acclimation

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