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Carbon economy of Mediterranean seagrasses in response to thermal stress



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ABSTRACT

Increased plant mortality in temperate seagrass populations has been recently observed after summer heatwaves, although the underlying causes of plant death are yet unknown. The potential energetic constrains resulting from anomalous thermal events could be the reason that triggered seagrass mortality, as demonstrated for benthic invertebrates. To test this hypothesis, the carbon balance of Posidonia oceanica and Cymodocea nodosa plants from contrasting thermal environments was investigated during a simulated heatwave, by analyzing their photosynthetic performance, carbon balance (ratio photosynthesis:respiration), carbohydrates content, growth and mortality. Both species were able to overcome and recover from the thermal stress produced by the six-week exposure to temperatures 4 °C above mean summer levels, albeit plants from cold waters were more sensitive to warming than plants from warm waters as reflected by their inability to maintain their P:R ratio unaltered. The strategies through which plants tend to preserve their energetic status varied depending on the biology of the species and the thermal origin of plants. These included respiratory homeostasis (P. oceanica warm-plants), carbon diversion from growth to respiration (C. nodosa cold-plants) or storage (P. oceanica warm-plants) and changes in biomass allocation (C. nodosa warm-plants). Findings suggest an important geographic heterogeneity in the overall response of Mediterranean seagrasses to warming with potential negative impacts on the functions and services offered by seagrass meadows including among others their capacity for carbon sequestration and carbon export to adjacent ecosystems.

1. Introduction

Global warming is increasing the average sea surface temperature at unprecedented rates, aside with an increase in the frequency of anomalous events of seawater warming (i.e. marine heatwaves; Hobday et al., 2016). During these heatwaves, the upper layers of the oceans can reach high temperatures intensifying water column thermal stratification (Schaeffer and Roughan, 2017) and exposing coastal marine ecosystems to anomalously warm conditions that are already altering the structure of coastal communities and increasing the mortality of habitat forming species (Hoegh-Guldberg and Bruno, 2010; Wernberg et al., 2012, 2016).

Habitat forming or foundation species, such as canopy-forming plants, gorgonians and reef-building corals, among others, are crucial for the functioning of the coastal ecosystems since they produce the resources and create stable conditions for the maintenance of highly diverse communities. Among them, seagrasses are marine clonal plants that form extensive meadows in most coastal areas of the world where

they perform numerous ecological functions and provide socio-economical services that render them one of the most valuable ecosystems on earth (Costanza et al., 2014). Seagrass habitats are globally declining as consequence of human activities (Waycott et al., 2009) and the situation is expected to worsen due to climate change (Short and Neckles, 1999; Koch et al., 2013). Indeed, catastrophic disasters (i.e. mortality rates up to 90%) have been reported in some temperate seagrass populations after recent summer heatwaves (Marbà and Duarte, 2010; Moore et al., 2014; Thomson et al., 2015). Post disaster recovery is still uncertain and can give rise to changes in species composition modifying the structural complexity of the ecosystem (Nowicki et al., 2017).

The effects of global warming and the incidence of summer heat-waves are expected to be particularly intense in the Mediterranean Sea (Meehl and Tebaldi, 2004), potentially aggravating the anthropogenically-induced decline of Mediterranean seagrass populations occurred during the last decades (Boudouresque et al., 2009). These periods of abnormally high temperatures occur from late spring/early summer to early autumn, with a duration ranging from few days to a

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whole month (Rebetez et al., 2009). One of the most dramatic heatwave in the Western Mediterranean has been recorded in 2003, when the average maximum temperature at 1 m depth across different locations was 27.4 °C (Garrabou et al., 2009). Posidonia oceanica and Cymodocea nodosa are the two main marine angiosperms in Mediterranean waters. The former is endemic and forms lush and extensive meadows from the surface down to 40 m depth, while the latter extends also in nearby subtropical Atlantic areas and dominates in shallow areas in confined or semi-confined waters, including coastal lagoon and estuaries (Green and Short, 2003; Borum, 2004). P. oceanica is perennial, slow colonizer and one of the longest living plants on Earth (Arnaud-Haond et al., 2012), whereas C. nodosa is a medium-size, high turnover and fast colonizer species (Mascaró et al., 2014). P. oceanica mortality has been reported at the Balearic Islands after the 2003 and 2006 summer heatwaves (Díaz-Almela et al., 2009; Marbà and Duarte, 2010) revealing the high vulnerability of the species to periods of intense warming, although the underlying causes of plant death are yet unknown. There is not such evidence available for C. nodosa, which seems reasonable at the light of its distribution reaching subtropical waters (Green and Short, 2003). Some authors have even suggested a positive reaction of C. nodosa to global warming (Boudouresque et al., 2009), although sensitivity to experimental warming has been documented (Olsen et al., 2012). So far, however, the vulnerability of Mediterranean seagrass species to seawater warming remains poorly understood as well as the response mechanisms they can eventually activate to cope with this climatic stressor.

In mesocosms experiments, P. oceanica has not evidenced signs of lethal or permanent injury after growing for several days under a temperature of 32 °C, which is however well above the maximum levels registered during recent heatwaves (Marín-Guirao et al., 2017a). Minor plant mortality was observed under this extreme temperature only after exposures of several weeks, whereas lower temperatures (27-30 °C) although reducing plant productivity, did not affect their survival (Olsen et al., 2012). These findings suggest that, rather than the instant effect produced by a lethal heat level, the declines reported in natural P. oceanica populations after intense warming events could be the consequence of prolonged heat-induced physiological alterations affecting plant productivity and/or of indirect effects of warming (Heckathorn et al., 2013). Increased temperatures tend to unbalance the seagrass carbon budget, since leaf respiration is usually more stimulated than photosynthesis (Drew, 1978, 1979; Pérez and Romero, 1992; Lee et al., 2007). However, this effect is highly variable among species and among populations of the same species, depending on the temperature regime that is characteristic of the environment in which plants grow (e.g. Collier et al., 2011; Winters et al., 2011). For instance, P. oceanica plants from shallow depths showed the capability to re-balance photosynthetic carbon gains and leaf respiratory carbon losses (as indicated by the P:R ratio) after a few days of increased temperatures exposure. Contrarily, deep plants from colder and more stable thermal environments experienced a progressive P:R ratio reduction likely jeopardizing their fitness and survival (Marín-Guirao et al., 2016). Notwithstanding the potential physiological acclimation of the species, heated plants are prone to experience severe whole-plant carbon imbalance if warming persists for a long period, since belowground tissues also increase their respiratory carbon demand under increased temperatures (Collier et al., 2011).

Carbon metabolism of Mediterranean seagrasses has a strong seasonality and follows the annual cycle of light and temperature (Touchette and Burkholder, 2000; Mateo et al., 2006). The plant carbon balance, which is determined by the offset between carbon assimilating (i.e. photosynthesis) and carbon consuming processes (e.g. respiration and growth), is negative during winter when photosynthetic performance of plants is reduced (Pérez and Romero, 1992; Terrados and Ros, 1995; Alcoverro et al., 1999, 2001). As a strategy for winter survival, plants rely on carbon reserves to cover their metabolic and growth

requirements until the following growing season (Drew, 1978; Alcoverro et al., 2001; Brun et al., 2008; Mascaró et al., 2014). These reserves for long-term use are stored in rhizomes by the accumulation of the photosynthetic carbon assimilated in excess during the summer period (Pirc, 1989; Terrados and Ros, 1995; Olivé et al., 2007). The optimal season for plant productivity is, therefore, critical for completing the annual growth cycle, and any alteration on the plant carbon metabolism during this period may represent a threat to their survival. Yet, heatwaves mainly occur in summer, curtailing carbon storage in rhizomes and potentially causing delayed decline, such as that registered in natural populations. Similarly, the recorded mass mortality of Mediterranean benthic macroinvertebrates after summer heatwaves was induced by the energetic constraints caused by sustained heat-enhanced respiratory activities (Coma et al., 2009; Garrabou et al., 2009). The real consequences of the metabolic imbalances experienced by temperate seagrasses during prolonged periods of warming, as those occurring during summer heatwaves, remain largely unexplored.

The primary objective of the present study is to test the hypothesis that long-lasting warming events during the summer season impact the carbon economy of Mediterranean seagrasses, undermining their energetic status and eventually causing the death of plants or endangering their ability for overwintering due to carbohydrate shortage. To increase the generality of our findings, we also intend to assess the variability of plant-responses, either interspecific (based on the different ecological strategies and biological traits) or intraspecific (based on the different thermal regimes under which different populations inhabit). For this purpose, P. oceanica and C. nodosa plants, collected from two distant regions and growing under contrasting thermal regimes, were exposed to a six-week simulated heatwave in mesocosms, and subsequently allowed to recover during another six weeks. Plant photochemistry was followed during the experiment to detect warming effects on the integrity and function of the photosynthetic apparatus at the photosystem II level. At the end of the heatwave exposure and recovery periods, the photosynthetic (P) and respiratory (R) activity rates of plants were determined to characterise the response of the metabolic carbon balance (as indicated by the P:R ratio) to warming. To evaluate the consequences of potential shifts in the carbon economy due to warming, we analysed carbohydrate content in both leaves and rhizomes and plant growth and mortality.

2. Methods

2.1. Collection sites and experimental setup

Two distant regions (ca. 700 km) of the western Mediterranean with contrasting thermal regimes were selected. In these regions, dense and healthy shallow *P. oceanica* (5–7 m) and *C. nodosa* (1–2 m) meadows were chosen to sample plants from contrasting thermal environments (see Beca-Carretero et al., 2018). *P. oceanica* plants were collected in extensive meadows in Cala Montgó (Catalonia: 42° 6.38′ N, 3° 10.27′ E) and in Isla Grosa (Murcia: 37° 43.7′ N, 0° 42.75 W) for cold-adapted (C-plants) and warm-adapted (W-plants) respectively. Mean summer temperature (\pm SD), from July to September (i.e. the period in which the experiment was conducted), naturally experienced by *P. oceanica* C-plants and W-plants is 22.78 \pm 0.89 °C and 25.17 \pm 0.88 °C respectively (Supplementary Fig. S1), according to the temperature time series available from the network of oceanographic buoys of the Spanish Ministry of Development (http://www.puertos.es/es-es/oceanografia/Paginas/portus.aspx).

C. nodosa plants were collected in Isla Grosa and in a locality at the Ebro Delta (Catalonia: 40° 35.23′ N, 0° 37.38′ E), where summer water temperatures can reach up to 30 °C due to the shallow and semi-enclosed geomorphological nature of the site. Consequently, plants from the Ebro Delta are considered W-plants (warm-adapted) while those from Isla Grosa are considered C-plants (Beca-Carretero et al., 2018).

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