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Ecophysiological plasticity of shallow and deep populations of the Mediterranean seagrasses *Posidonia oceanica* and *Cymodocea nodosa* in response to hypersaline stress

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A B S T R A C T

The differential expression of the plant phenotypic plasticity due to inter- and intraspecific divergences can determine the plant physiological tolerance under stress. In this work, we examined the interspecific ecophysiological plasticity that the main Mediterranean seagrass species with distinct marine environmental distribution (*Posidonia oceanica* and *Cymodocea nodosa*) can exhibit in response to hypersaline stress. We also tested the potential implication of ecotypic intraspecific divergences in the development of such plasticities. To this end, plants from shallow (5–7 m) and deep (18–20 m) meadows of both were maintained under two salinity treatments (natural salinity level of 37, and hypersaline treatment of 43; Practical Salinity Scale) during a long-term experiment (i.e. 62 days) developed in a highly controlled mesocosm system. Hypersaline stress caused notable plastic physiological alterations in *P. oceanica* and *C. nodosa*, with appreciable inter- and intraspecific differences. Although both species were similarly able to osmoregulate by means of organic solute accumulation (proline and sugars) in response to hypersalinity stress, higher carbon balance reductions were detected in *P. oceanica* plants from the deep meadow and in shallower *C. nodosa* plants, due to both photosynthetic inhibition and enhancement of respiration. None of these deleterious effects were found in *C. nodosa* plants form the deeper meadow. Leaf photosynthetic pigments generally increased in *P. oceanica* from both depths, but light absorbance capacities by leaves and photosynthetic efficiency followed contrasting patterns, increasing and decreasing in plants from the deep and the shallow meadows, respectively, indicating distinct strategies to cope with photosynthetic dysfunctions. Despite the significant reduction of pigments in the shallower *C. nodosa* plants, their leaves were able to increase their light capture capacities under hypersaline stress, by means of particular leaf optics adjustments (pigment packaging reduction). The metabolic costs as a consequence of the physiological plasticity integration seemed to compromise the vitality of *P. oceanica*, but not in the case of *C. nodosa*. These results confirm that both the inter- and intraspecific divergences play a key role in the responses which both Mediterranean seagrasses could develop under hypersaline stress conditions, and that these were consistent with their distinct ecological strategies and salinity tolerance ranges.

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1. Introduction

Seagrasses must exhibit specific plant phenotypic plasticity to be able to acclimate to the changing environment (Dudley, 2004; Nicotra et al., 2010). Within their particular distribution ranges, seagrasses undergo natural changes of environmental factors (e.g. light, salinity or temperature), repeated at different temporal and spatial scales (e.g. light daily cycles, currents, water turbidity or pluviosity). Under such conditions, seagrasses can develop rapid and reversible metabolic adjustments that allow for an efficient plant acclimation (Lichtenthaler, 1996; Dudley, 2004). However, these acclimative strategies (i.e. expression of plasticity) must be more drastic (i.e. strain responses) if plants are exposed to much more extreme environmental alterations that exceed the natural plant tolerance thresholds (Levitt, 1980). These stress events are closely related to the higher persistence and/or intensity of the

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environmental change, and can lead to the stress syndrome responses of plants (Lichtenthaler, 1996). Seagrass habitats provide valuable functions and services to coastal ecosystems and hence, knowledge of their tolerance to environmental stress is today an issue of major concern in forecasting its consequences on these coastal sentinels (Orth et al., 2006; Boudouresque et al., 2009)

Some alterations of the environment can play as potential stressors affecting seagrass growth and performance, most of all related to human coastal impacts (Ruiz et al., 2001, 2009; Ruiz and Romero, 2003; Burkholder et al., 2007; Boudouresque et al., 2009). Among them, the alteration of salinity regimes caused by water-use management practices (e.g. seawater desalination, control of freshwater inflow; Ruiz et al., 2009, Rudnick et al., 2005; Herbert et al., 2011) is considered a primary factor with demonstrated harmful consequences on seagrass beds (Gacia et al., 2007; Ruiz et al., 2009). Changes in salinity and particularly salinity increments above specific natural ranges (i.e. hypersalinity stress) comprise osmotic and ionic stress factors that can lead to variable plastic ecophysiological and morphological responses of seagrasses (see Touchette, 2007 for a review). These have been documented, for instance, as changes in leaf-water relations, dysfunctions of the photosynthetic/respiratory machinery, structural changes, as well as leaf optics and pigment alterations (Beer et al., 1980a; Ralph, 1998, 1999; Tyerman, 1989; Kahn and Durako, 2006; Koch et al., 2007; Marín-Guirao et al., 2013a). In terms of phenotypic plasticity, these strain responses can reflect acclimatative strategies enabling plant resistance but also, and more generally, non-adaptive (or maladaptive) physiological responses resulting in deleterious effects on plant fitness and survival (Lichtenthaler, 1996; Dudley, 2004; Ghalambor et al., 2007). Hence, seagrass tolerance to hypersaline stress must be conditioned by the physiological integration among these adaptive and non-adaptive plastic responses and their related metabolic costs. Contrary to land plants subjected to environmental stress (DeWitt et al., 1998; Dudley, 2004; Valladares et al., 2007), there are no seagrass-related works describing these complex phenotypic plasticity interactions. Moreover, these are closely associated with the ecological strategies of species in response to environmental heterogeneity (generalist *vs.* specialists; Van Tyenderen, 1991; Baquedano et al., 2008), also poorly studied in the framework of plasticity of seagrasses under stress (Sandoval-Gil, 2012).

The most abundant seagrass species growing in the Mediterranean Sea (i.e. *Posidonia oceanica* and *Cymodocea nodosa*) notably differ in biological attributes and ecological strategies (Drew, 1978b; Van Tyenderen, 1991; Cancemi et al., 2002; Olesen et al., 2002), which has been observed to match with differential specific physiological capacities to cope with human-induced hypersalinity stress (i.e. brine discharges from desalination plants; Fernández-Torquemada and Sánchez-Lizaso, 2005; Ruiz et al., 2009; Marín-Guirao et al., 2011; Sandoval-Gil et al., 2012a,b). In effect, *P. oceanica* L. (Delile) is a large slow-growing and stenohaline species generally adapted to narrow salinity ranges throughout the Mediterranean Sea (e.g. 36.5–38, Practical Salinity Scale, in oceanic waters of the southeast of Spain; Ruiz et al., 2009) and usually not present in hypersaline coastal waters (but see Pergent et al., 2002; Tomasello et al., 2009); on the other hand, the smaller *C. nodosa* (Ucria) Ascherson is considered a pioneer and more euryhaline species able to form dense and productive meadows in oceanic, estuarine and hypersaline coastal waters (Terrados and Ros, 1991; Pérez and Romero, 1994; Olesen et al., 2002). Such interspecific differences are consistent with the differential tolerance to hypersalinity shown by both seagrass species in recent studies, mainly in terms of plant growth and survival (Fernández-Torquemada and Sánchez-Lizaso, 2005, 2006; Gacia et al., 2007; Ruiz et al., 2009; Pagés et al., 2012; Fernández-Torquemada and Sánchez-Lizaso, 2011) but also at the ecophysiological level (Ruiz et al., 2009; Marín-Guirao et al., 2011, 2013b; Sandoval-Gil et al., 2012a,b). The bulk of evidence indicates that *C. nodosa* is more tolerant than *P. oceanica* to salinity increments, probably due to some inherent ecophysiological properties of the former conferring the species certain adaptive advantages (e.g. highly negative water potential, accumulations of certain protective solutes and mild inhibition of photosynthetic activity; Marín-Guirao et al., 2011; Sandoval-Gil et al., 2012a,b).

Further to interspecific variation, intraspecific physiological plasticity between plants from separated populations (in space and/or time) could operate as another source of variation in the mechanisms to cope with stress conditions (Dudley, 2004; Ghalambor et al., 2007; Baquedano et al., 2008). These ecotypic/genotypic divergences can reflect particular adaptive features to contrasting environmental regimes (e.g. latitudinal clines, saline regimes; Koch and Dawes, 1991; Van Katwijk et al., 1999; Peralta et al., 2000; Santamaría et al., 2003; Winters et al., 2011) and local gradients (e.g. light availability depending on depth, estuarine gradients, distribution within the intertidal; Dunton, 1996; Kamermans et al., 1999; Mercado et al., 2003; Collier et al., 2008). In this sense Mediterranean populations of both *P. oceanica* and *C. nodosa* span contrasting environmental conditions throughout their respective distribution areas (e.g. depth and geographical gradients) and annual production cycles (e.g. seasonal variations), which seems to drive structural and physiological plant variations related to that intraspecific differentiation (Dennison, 1987; Duarte, 1991; Dalla Via et al., 1998; Olesen et al., 2002; Migliaccio et al., 2005). Thus, for instance, depth-associated variation in photosynthetic-related traits has been described in both species (Drew, 1978b; Olesen et al., 2002). However, it is unknown at which point the plasticity of these and other relevant ecophysiological aspects could lead to intraspecific differences in the capacity of the species to tolerate hypersaline stress.

In the present study, we analysed species-specific ecophysiological responses of the Mediterranean seagrasses *P. oceanica* and *C. nodosa* to hypersaline stress, taking into consideration i) the distinct acclimation plasticity among species, and more specifically, ii) the potential intraspecific divergences in such plasticity among plants adapted to different depths. We particularly hypothesize that the capacity of each seagrass species to cope with hypersaline stress may be a function of the differential plastic expression of ecophysiological and vegetative traits among plants from shallow and deep meadows. To this end, several physiological (i.e. photosynthesis, leaf pigmentation, leaf-water relations, and leaf optical properties) and vegetative descriptors were examined in both seagrass species and experimental populations exposed to chronic hypersaline stress, simulated in a highly controlled mesocosm system.

2. Materials and methods

2.1. Plant collection

In April (spring) 2010, large fragments of rooted *P. oceanica* and *C. nodosa* rhizomes bearing apical growth meristems and 7–10 connected shoots (i.e. maintaining clonal plant integrity) were collected by scuba divers in dense and healthy shallow (5–7 m) and deep (18–20 m) meadows of the Murcia Region on the south-eastern coast of Spain. Shallow and deep *P. oceanica* meadows had, respectively, a shoot density of 687 ± 16.5 and 321 ± 20.7 shoots m^{-2} and were located in Isla Plana (Mazarrón Bay, 37° 33′14.4″N 1° 10′35.5″SO); the shallow meadow of *C. nodosa* was adjacent to the shallow *P. oceanica* meadow and had a shoot density of 347.8 ± 9.4 shoots m^{-2}, while the deep *C. nodosa* meadow

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