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Preservation of seagrass clonal integration buffers against burial stress

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ABSTRACT

The survivorship and performance of seagrasses are affected by environmental stressors, yet clonal integration of seagrasses can ameliorate these adverse environmental changes. We experimentally assessed the response of the seagrass *Cymodocea nodosa* (Ucria) Ascherson off Gran Canaria to changes in the intensity of burial, determining whether responses could be modulated by the clonal integration of the plant. Plants were buried in situ to 0 ('ambient'), 8 ('moderate') and 24 cm ('high') within PVC cylinders, which were left untouched or isolated from adjacent shoots by sawing their clonal connection. The number of living shoots under 'moderate' and 'high' burial scenarios declined with time when the clonal integration was severed. After 15 weeks, cores were harvested. The effect of burial over *C. nodosa* depended on whether the clonal integration was maintained or severed. When the clonal integration was maintained, the shoot density, the number of leaves, the above-ground biomass and the leaf length did not change significantly with burial levels. When the clonal integration was severed, the shoot density and the number of leaves were larger in cores under 'ambient' and 'moderate' than 'high' burial levels, the above-ground biomass was larger under 'ambient' than 'moderate' and 'high' burial levels, and the leaf length was larger in 'ambient' than in cores under 'high' burial. The below-ground biomass was not affected by burial and clonal integration. The internodal length of vertical rhizomes increased with burial; this increase was larger when the clonal integration was severed. In conclusion, preservation of the clonal integration of the seagrass *C. nodosa* buffered seagrass performance against small-scale burial events.

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1. Introduction

Seagrass meadows are one of the most productive marine habitats, providing high-value ecosystem good and services, which has caused their inclusion within different international conservation legislative frameworks, e.g. EU 92/43/CEE Habitats Directive (Hemminga and Duarte, 2000). Conservation of these habitats is therefore important, since seagrass meadows are declining worldwide, particularly in areas of intense human-mediated disturbances, such as large urban and industrial coastal zones (Hughes et al., 2009; Waycott et al., 2009).

Seagrasses typically occur on shallow-water soft substrates where they are naturally subjected to physical mechanisms that redistribute sediments, causing events of burial and erosion over seagrasses (Cabaço and Santos, 2007; Marbà et al., 1994). In addition, coastal run-off, construction of infrastructures (e.g. ports, marinas, dikes) and associated activities, particularly dredging, may cause a redistribution of sediments and so abrupt sedimentation (burial) events (Cabaço and Santos, 2007; Ruiz and Romero, 2003). These episodes can partially, or totally, bury seagrasses (reviewed by Cabaço et al., 2008). Seagrasses experience then physiological and morphological responses, mainly as a result of a decrease in the amount of actively photosynthetic parts of seagrass shoots and an elevation of the sediment anoxic level towards the photosynthetic parts of seagrass shoots. In particular, the growth of vertical rhizomes is enhanced under burial to promote photosynthetic compartments to reach light and subsequently stimulate seagrass survivorship and performance (e.g. Manzanera et al., 2011; Marbà and Duarte, 1994; Terrados, 1997). Seagrass responses, however, can vary among species (Cabaço et al., 2008; Duarte et al., 1997; Sim Ooi et al., 2011; Terrados et al., 1998). Seagrasses are clonal plants and, therefore, nutrients and resources are translocated between adjacent shoots to cope with adverse environmental conditions; a relevant factor that can facilitate seagrass performance and survivorship during periods of high stress (Marbà et al., 2002; Terrados et al., 1997a; Tomasko and Dawes, 1989), including short-term burial events (Sim Ooi et al., 2011).

Small-scale in situ manipulations of burial have been performed on a suite of seagrasses, according to different burial levels and durations (reviewed by Cabaço et al., 2008). These studies have provided a wealth of knowledge to assess those limits of sediment burial that can be tolerated by different seagrasses to avoid an irreversible deterioration. Except for a recent study (Sim Ooi et al., 2011), these studies have, however, maintained the clonal (connection) integration of shoots under experimentation with adjacent shoots. This could potentially ameliorate the negative effects of burial on seagrass performance, as a

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result of the transfer of nutrients and resources from neighboring, undisturbed, shoots (Sim Ooi et al., 2011; Tomasko and Dawes, 1989).

The marine phanerogam *Cymodocea nodosa* (Ucria) Ascherson is distributed across the Mediterranean Sea and the adjacent eastern Atlantic, including the archipelagos of Madeira and the Canaries. Meadows constituted by *C. nodosa* are the dominant vegetated communities on shallow soft substrates across the Canaries (Barberá et al., 2006), providing food and shelter for diverse invertebrate and fish assemblages (Tuya et al., 2001; Espino et al., 2011). These meadows are generally located along the eastern and southern coasts of the islands, forming extensive, but fragmented, subtidal meadows. Oceanic swells and large wind-driven seas cause severe movements of sediments that routinely alter the local cover and density of *C. nodosa* (Marbà et al., 1994), including seagrass meadows in the Canaries (Portillo, 2007). The horizontal rhizomes of *C. nodosa* do connect shoots a few meters apart, so resources can be translocated among neighboring shoots; in fact, this plant has been considered as an appropriate candidate to study the effects of clonal integration on the physiology and ecology of seagrasses (Terrados et al., 1997b). When subjected to experimental burial, the survivorship of *C. nodosa* seedlings has declined with the level of experimental burial, though *C. nodosa* seedlings have tolerated a burial<7 cm (Marbà and Duarte, 1994). Burial promoted the growth of *C. nodosa* seedlings under a moderate burial; in turn, *C. nodosa* seedling growth has showed a bell-shaped response to experimental burial (Marbà and Duarte, 1994). The response of *C. nodosa* adult shoots to in situ experimental burial, however, has not been tested.

In this study, we aimed to experimentally assess the response of the seagrass *C. nodosa* to changes in the intensity of burial, determining whether responses could be modulated by the clonal integration of the plant. We hypothesized that preservation of the seagrass clonal integration would ameliorate the stress induced by burial on seagrass vitality.

2. Materials and methods

2.1. Experimental design

This study was carried out on a *C. nodosa* meadow located at 8–9 m depth off the south coast of Gran Canaria (N 27° 44.923′, W 15° 33.855′). A previous study (Barberá et al., 2006) indicated that the mean height of *C. nodosa* leaves was ca. 32 cm off the south of Gran Canaria. Three burial treatments were then established, on the basis of this value, corresponding to 0 cm (0% of burial), 8 cm (25%) and 24 cm (75%) of the mean height, respectively, following a previous study that used a parallel approach (Mills and Fonseca, 2003). Thereafter, these treatments will be considered as: 'ambient', 'moderate' and 'high' burial, respectively. Treatments were established within 20 cm-inner diameter PVC opaque cylinders; adjacent cylinders were, at least, 0.5 m apart. Two 50 cm metal stakes were attached to each cylinder on its outer side through cable ties, and hammered into the bottom to assure cylinders were not moved away by waves and currents. In all cases, cylinders were filled with sand from an adjacent sandy unvegetated patch. Twelve cylinders (i.e. 4 per treatment) were randomly allocated on each of two seagrass patches. On one patch, all plots were left untouched, while all plots on the second patch were isolated from adjacent shoots by halting their clonal connection, i.e. sawing horizontal rhizomes, around each plot down to 30 cm inside the seabed. Both patches were separated by ca. 100 m, so no treatment (clonal integration) confounding was expected. The experiment was set up on the 5th of May-2011, and re-visited every 5 weeks to ensure burial levels were appropriately maintained. On each occasion, we also counted the number of living shoots in each cylinder. After 15 weeks, all 24 cylinders were harvested, including above and below-ground compartments. To provide a baseline to compare against seagrass responses, four replicate natural samples were also collected haphazardly from a seagrass patch about 100 m away from the experimental set up. All material was transferred to labeled bags and frozen (−20 °C) until processed in the lab.

2.2. Seagrass responses

For each sample (cylinder), we counted the number of living shoots and the total number of leaves. The length of 10 leaves without apparent necrosis and the length of the youngest vertical internode (for 5 shoots) were also measured. This internode has been shown to elongate during a similar experiment (Marbà and Duarte, 1994). The seagrass biomass was separated into above (leaves) and below-ground sections (horizontal rhizomes and roots) and subsequently oven-dried (24 h at 70 °C) to obtain dry-weight biomass measurements.

2.3. Statistical analyses

Since the number of living shoots within cores was followed through time, a repeated-measures ANOVA (RM-ANOVA) tested whether shoot survivorship differed between burial (sedimentation) levels and the presence/absence of clonal integration through time. Permutation-based ANOVAs (Anderson, 2001) were used to test whether burial levels and the presence/absence of clonal integration affected seagrass responses; both factors were treated as fixed. Analyses were based on Euclidean distances and P-values calculated from 4999 unrestricted permutations of the raw data. Despite all data were $\ln(x+1)$ transformed to stabilize heterogeneous variances, homogeneous variances were only obtained for the ANOVA performed on the below-ground biomass (Cochran test's; $P>0.05$). As a result, we reduced an increase in a type I error rate by taking a more conservative alpha at the 0.01 level (Underwood, 1997). Because in almost all cases we detected a significant interaction term between burial (sedimentation) treatments and the presence/absence of clonal integration, pairwise comparisons (using 4999 permutations) were used to resolve differences among burial levels separately when the clonal integration was maintained or severed.

3. Results

The number of living shoots through time was dependent on both sedimentation treatments and maintenance (or not) of the clonal integration of the seagrass (Fig. 1A and B; Table 1, R-M ANOVA: 'Times × Sed' and 'Times × CI', $P<0.0001$). The number of living shoots under 'moderate' and 'high' burial scenarios particularly declined with time when the clonal integration was severed (Fig. 1B; Table 1, R-M ANOVA: 'Sed × CI', $P=0.002$). At the end of the experiment, the effect of sedimentation treatments over *C. nodosa* depended, except for the below-ground biomass, on whether the clonal integration of the plant was maintained or severed (Fig. 2; Table 2, ANOVAs: 'Sed × CI', $P<0.05$ for all responses, except the below-ground biomass). When the clonal integration was preserved, the shoot density, the number of leaves, the above-ground biomass and the leaf length of *C. nodosa* did not significantly change among burial levels (Fig. 2A, B, C and F, respectively, pairwise tests), although a slight decrease in the number of leaves and the above-ground biomass under a 'high' burial scenario was observed (Fig. 2B and C). When the clonal integration was severed, however, the shoot density and the number of leaves were significantly larger in cores subjected to 'ambient' and 'moderate' than 'high' burial levels (Fig. 2A and B, respectively, pairwise tests), the above-ground biomass was significantly larger in cores under 'ambient' than 'moderate' and 'high' burial levels (Fig. 2C, pairwise tests), and the leaf length was larger in 'ambient' than cores under 'high' burial (Fig. 2F, pairwise tests). The below-ground biomass did not change with either sedimentation levels or preservation/destruction of the clonal integration (Fig. 2D; Table 2, ANOVA: all terms, $P>0.05$). The internodal length of vertical rhizomes increased with sedimentation (Fig. 2E; Table 2, ANOVA: 'Sed', $P=0.0008$, pairwise tests indicated a larger internodal length

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