

NOTE

Growth response of the seagrass *Cymodocea nodosa* to experimental burial and erosion

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ABSTRACT: The response of *Cymodocea nodosa* (Ucria) Aschers. seedlings to experimental burial and erosion was examined to test the extent of coupling between fluctuations in sediment depth and seagrass growth. Shoot survivorship declined with erosion and with increasing burial depth, relative to the controls. Seagrass growth response, described by changes in internodal and leaf sheath length, the rate of appearance of new leaves, and shoot vertical growth showed a bell-shaped response to fluctuations in sediment depth. Shoot internodal and leaf sheath length, the rate of appearance of new leaves, and vertical growth all increased with sediment depth from minimal values under erosion to maximal values at burial of <7 cm. These results demonstrate that *C. nodosa* seedlings tolerate burial <7 cm, and that burial stimulates the growth of surviving seedlings. Examination of this growth response for *C. nodosa* and other seagrass species, which allows quantification of tolerable changes in sediment depth, may provide useful information for conservation of seagrass populations.

KEY WORDS: Seagrass growth · Sand burial · Sand erosion · *Cymodocea nodosa* · Seedlings

Seagrasses develop extensive meadows on sandy coastal areas around the world, where they often experience intense sediment dynamics. Seagrass species that develop vertical shoots (e.g. *Cymodocea*, *Thalassia*, *Thalassodendron*) may respond to fluctuations in sediment depth by modifying their vertical growth to relocate their leaf-producing meristems closer to the new sediment level, leading to a coupling between fluctuations in sediment depth and seagrass vertical growth (Patriquin 1973, Boudouresque et al. 1984, Marbà et al. 1994a, b). A coupling between fluctuations in sediment depth and plant growth, similar to that postulated here for seagrasses, has been demonstrated for rhizomatous coastal dune plants (e.g. Marshall 1965, Wallen 1980, Elderred & Maun 1982, Disraeli 1984, Maun & Lapierre 1984, Zhang & Maun 1990).

While the response of coastal dune plants to fluctuations in sediment depth has been well documented, this knowledge is mostly qualitative for seagrasses, and there are, as yet, few detailed quantitative reports on the response of seagrasses to burial and erosion (e.g. Patriquin 1975, Marbà et al. 1994a, b). This response must be, however, an important component of their adaptation to their sandy substrate, and may be important in forecasting seagrass dynamics in coastal areas subject to significant erosion or accretion rates, and to establish the limits to the siltation and erosion rates seagrasses tolerate.

We report here the response of seagrass *Cymodocea nodosa* (Ucria) Aschers. to fluctuations in sediment depth based on experimental manipulations.

Methods. We harvested about 200 *Cymodocea nodosa* seedlings and sediments from a shallow (–0.5 to –1.0 m) sandy littoral in Alfacs Bay (Ebro Delta, NE Spain) in July 1992. We preferred seedlings as experimental units because, unlike shoots from mature plants, they can be collected without damaging their rhizomes and are self-contained units, independent of each other. The seedlings collected had sprouted in 1992, and had produced between 5 and 10 leaves at the time of collection. The collected seedlings were transported to the laboratory where they were exposed to manipulations in sediment depth.

The experimental design included 8 levels of sediment depth relative to the leaf-producing meristem: erosion (sediment surface just below the rhizome); sediments maintained at the meristem level (the relative position they had in the field, i.e. 0 burial); and burial of 1, 2, 4, 7, 13, and 16 cm above the meristem. Each treatment consisted of 7 replicate seedlings to which the treatments were independently applied. The range of sediment depths tested were selected to encompass the range of burial and erosion observed in littoral

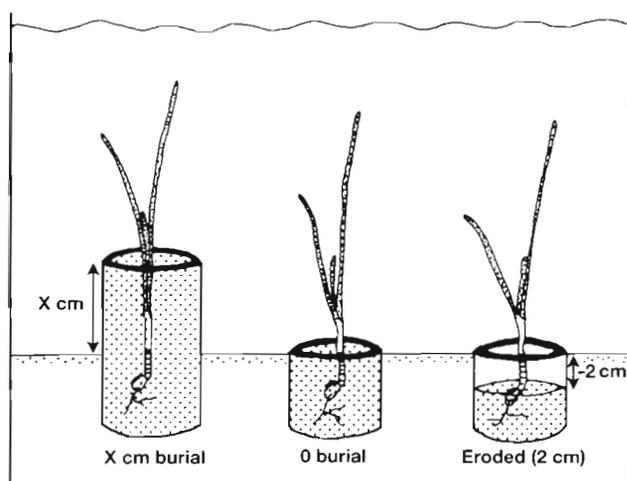


Fig. 1. Schematic representation of the experimental design used to examine the response of seagrass seedlings to altered sediment depth

zones supporting *Cymodocea nodosa* (Marbà et al. 1994a). Because most seedlings had 2 vertical shoots, the 7 replicate treatments involved a total of 103, rather than 56, shoots.

Since seagrasses have been shown to be nutrient limited in Alfacs Bay (Pérez et al. 1991), we avoided confounding nutrient effects in the experiment by amending the sediments with nutrients. This was done by inserting 7 slow-release mixed fertilizer sticks in the sediments, representing a loading of about 7.6 g N m^{-2} and 1.04 g P m^{-2} , prior to sowing the seedlings in 2 aquaria (50 cm long \times 32 cm width \times 35 cm height). This nutrient loading has been shown to prevent nutrient limitation in this seagrass population (Pérez et al. 1991). Seedlings were randomly assigned to the treatments and to either of the 2 experimental aquaria, so that seedlings subject to all of the treatments were represented in both aquaria. By applying the treatments independently to each replicate seedling and assigning them randomly to each of the 2 aquaria we ensured a proper design and replication. Seedlings were

maintained in running sea water (about 3 d renewal time) at 20°C and an irradiance of $500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in a 12 h day: 12 h night photoperiod. The seedlings were planted so that the leaf-producing meristem was just at the sediment surface, the position they adopt after seedling sprouting (Marbà unpubl. data). We allowed the seedlings to acclimate to experimental conditions for 5 d before marking the shoots by punching a hole through the leaves just above the leaf sheath with a needle (cf. Pérez et al. 1991). Leaves were punched in order to measure the rate of appearance of new leaves on the shoots, which is closely related to leaf growth (Brouns 1985).

Treatments were then imposed by enclosing the roots and rhizomes of each individual seedling within a 5 cm diameter opaque PVC cylinder. The cylinders extended from just below the roots to a height above the sediment equivalent to the corresponding treatment and were filled with sediments (Fig. 1). The control seedlings (i.e. 0 burial) were also enclosed within PVC cylinders. The seedlings were then allowed to grow for 35 d, slightly longer than the annual average time in between production of 2 consecutive leaves in a *Cymodocea nodosa* shoot in this area (26 d; Duarte & Sand-Jensen 1990), before harvesting. We then counted the number of surviving shoots (i.e. those with standing green leaves) and the number of new leaves they produced. We also measured the length of the leaf sheath and the youngest vertical internode on each surviving shoot, which is the one showing the greatest response to changes in sediment depth (Marbà et al. 1994a). The youngest vertical internodes appeared prior to the experiment, but elongated during the study. Shoot survivorship was recorded as a binomial variable, taking the values of 0 and 1 for dead and surviving shoots respectively.

Seedling response to experimental burial and erosion was evaluated using analysis of variance (ANOVA). Some of the variables were square-root transformed prior to the analysis, which was found to be necessary to homogenise their variance (Sokal & Rohlf 1981). The significance of pairwise compari-

Table 1. *Cymodocea nodosa*. Analyses of variance of the parameters measured on seagrass seedlings after treatments. Similar treatment responses (Tukey's HSD analysis) share a common underline. No. of observations for all variables = 102

Variable	r	F ratio	p	Treatment (cm)
Shoot survival	0.76	18.62	<0.00001	<u>-2 0 1 2 4 7 13 16</u>
Internodal length ^a	0.53	5.35	<0.00001	<u>-2 0 1 2 4 7 13 16</u>
Leaf appearance rate	0.49	4.28	<0.0005	<u>-2 0 1 2 7 13 16</u> 4
Vertical rhizome growth rate ^a	0.48	3.97	<0.001	<u>-2 0 1 2 7 13 16</u> 4
Leaf sheath length	0.66	10.42	<0.00001	<u>-2 0 1 2 4 7 13 16</u>

^a Values were square-root transformed to homogenise the variance prior to the analysis

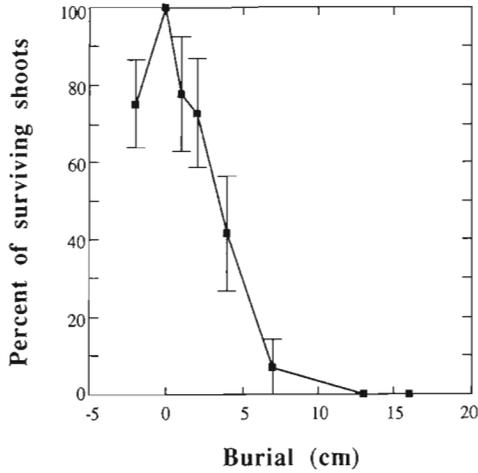


Fig. 2. *Cymodocea nodosa*. Relationship between shoot survivorship and experimental changes in sediment depth. Values are means \pm 1 SD

sons between treatments were tested for using Tukey's HSD multiple comparisons test (Sokal & Rohlf 1981).

Results. The proportion of surviving shoots varied significantly among treatments (Table 1). All shoots survived when the sediment level was not altered (i.e. 0 burial), however, the proportion of surviving shoots decreased significantly as burial depth increased, with no shoots surviving burial > 7 cm (Table 1, Fig. 2). Survival was also significantly reduced when shoots were exposed to experimental erosion (Table 1, Fig. 2). Although both burial and erosion induced shoot mortality, some *Cymodocea nodosa* shoots were able to survive burial < 7 cm. The length of the youngest vertical internode produced differed significantly among treatments (Table 1). The average length of the youngest vertical internode ranged between 0.35 and 4.17 mm, and increased as burial increased up to 7 cm (Fig. 3a). The appearance of new leaves on the shoots also differed significantly among treatments, increasing with burial up to 2 cm (Table 1, Fig. 3b).

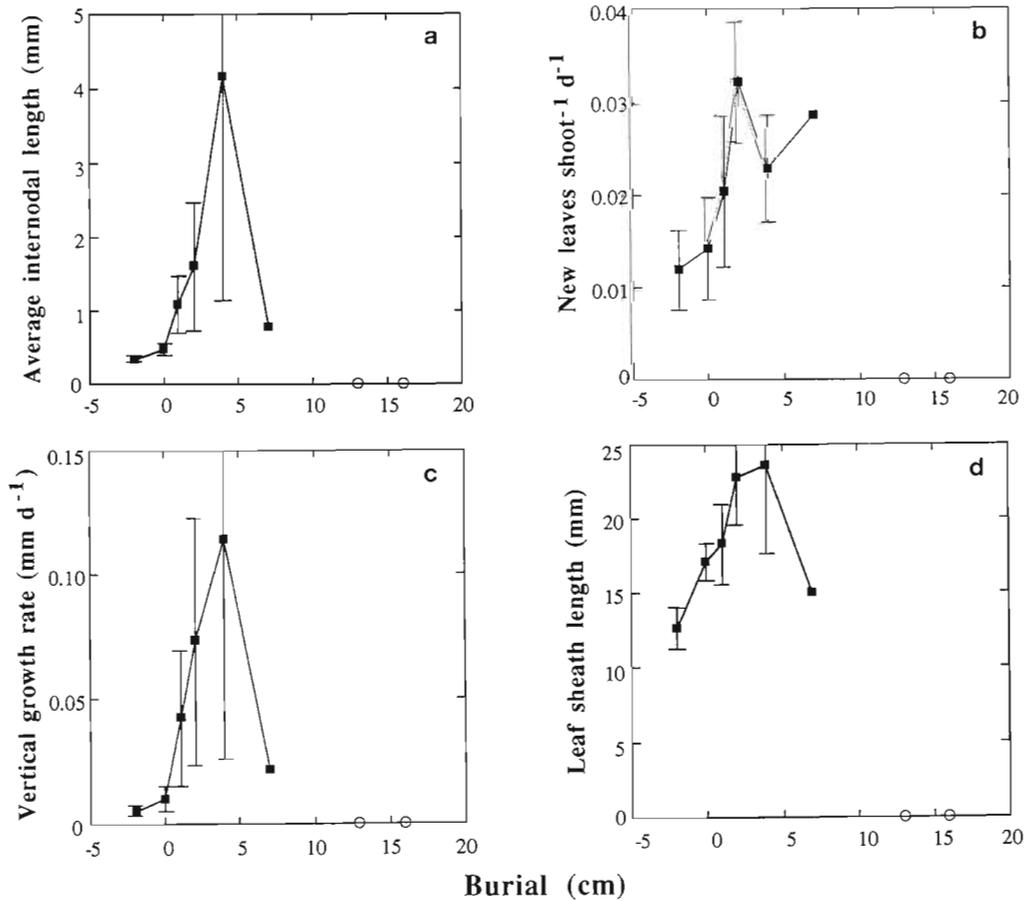


Fig. 3. Relationship between (a) internodal length, (b) the rate of appearance of new leaves, (c) shoot vertical growth, and (d) leaf sheath length of surviving shoots and experimental changes in sediment depth. Values are means \pm 1 SD. Absence of error bar indicates that only 1 shoot survived. (O) No shoots survived the treatments

Because shoot vertical growth is the product of internodal length and the rate of appearance of new internodes (i.e. $\text{mm internode}^{-1} \times \text{internodes d}^{-1} = \text{mm d}^{-1}$), which equals the rate of appearance of leaves, these results indicate that the vertical growth of shoots exposed to burial < 7 cm should also increase significantly, as confirmed by our data (Table 1, Fig. 3c). Shoot vertical growth also showed a bell-shaped response to burial, increasing significantly with increasing burial to reach a maximum rate, about 5-fold greater than that of the control, when shoots were buried 4 cm. Burial > 7 cm and erosion lead to reduced vertical growth (Fig. 3c). The increased vertical growth of shoots in response to burial < 7 cm allowed them to relocate their apical meristems to the sediment surface (Fig. 3c). This relocation should improve the carbon balance of the plants by increasing the leaf surface exposed to light. The response needed to expose the entire leaf surface to light following burial was also made possible by the faster elongation of these short shoots (Table 1). The length of the leaf sheaths increased from the short leaf sheaths of shoots exposed to erosion, to maximal lengths with burial of 4 cm; leaf sheath length declined at greater burial depths (Fig. 3d, Table 1).

Discussion. The results obtained reveal a consistent bell-shaped relationship between sediment depth fluctuations and the performance of *Cymodocea nodosa* seedlings. This response involved reduced leaf production rate, leaf sheath length and internodal length as a result of erosion and burial greater than 4 cm. Maximal shoot vertical growth and leaf production rate were achieved at intermediate (4 cm) burial. Hence, intermediate burial (about 4 cm) stimulates *C. nodosa* vertical growth, supporting the notion that seagrass vertical growth should be closely coupled to changes in sediment depth (Patriquin 1973, Boudouresque et al. 1984, Marbà et al. 1994a, b). Moderate burial also stimulated leaf growth of the surviving shoots, as reflected in a faster rate of appearance of new leaves (Fig. 3b). This finding is consistent with suggestions that moderate burial stimulates growth of *Thalassia testudinum* in the Mexican Caribbean (Gallegos et al. 1993). Similar to the results observed here, the increased vertical growth of *T. testudinum* in response to burial involved both a faster rate of appearance of new leaves and the production of longer internodes in the surviving shoots (Marbà et al. 1994b).

However, both erosion and burial resulted in increased shoot mortality relative to the controls; no seedlings survived burial greater than 7 cm. Hence, even though burial up to 4 cm stimulated leaf growth of the surviving shoots, this may not suffice to compensate for the reduction in production due to parallel increase in shoot mortality. Calculation of the net effect

of burial or erosion on seagrass production must, therefore, consider the balance between increased mortality and production. There is evidence, however, that our results may underestimate the response capacity of established *Cymodocea nodosa* meadows. The reason for this is that seedlings are less vigorous than established plants, as reflected by their thinner leaves (1 to 2 mm compared to 2 to 4 mm of plants in established meadows) and slower growth rates (plastochrone interval, PI, = 70 d compared to 26.9 d of plants in established meadows). Hence established meadows may be able to survive greater burial depth than seedlings, and burial may continue to stimulate *C. nodosa* vertical growth at depths greater than the 4 cm threshold observed here for seedlings. Indeed, *C. nodosa* shoots within patches are able to survive burial as great as 6 cm, and their vertical growth continues to increase up to those burial depths (Marbà & Duarte unpubl.). Hence, established meadows are expected to show a similar bell-shaped growth response to fluctuations in sediment level, but with the maxima displaced towards larger burial depths than that (4 cm) observed here. The reason for this may be that while the resources contained within *C. nodosa* seedlings are lost upon their death, these may be transferred to surviving neighbour shoots along the rhizomes in established meadows, thereby enhancing the growth response of survivors. However, seagrass growth response to fluctuations in sediment depth should depend on the timing of these fluctuations in relation to the seasonal pattern of seagrass growth. Shoot growth response and survivorship to burial or erosion should be lower in winter, when *C. nodosa* grows very slowly (Pérez 1989).

The increased growth of *Cymodocea nodosa* seedlings in response to experimental burial closely resembles the results observed for plants growing over emerged coastal dunes (e.g. *Ammophila breviligulata*: Disraeli 1984, Maun & Lapierre 1984; *Cakile edentula*: Zhang & Maun 1992). Plants growing over emerged coastal dunes also respond to burial by increasing their vertical growth (Disraeli 1984, Zhang & Maun 1992), and their productivity (Eldered & Maun 1982, Disraeli 1984, Zhang & Maun 1990, Yuan et al. 1993). The mechanism for increased plant growth in response to burial is, however, uncertain. It was originally attributed to the increased nutrient load associated with the sediment mass deposited over the plants (Disraeli 1984). This hypothesis was, however, rejected by Zhang & Maun (1992), who observed no difference in the growth response of plants buried by washed and amended sediments. Increased nutrient supply is also unlikely to account for the response observed here, for nutrient concentrations in the enriched sediments were sufficient to fulfil the nutritional requirements of

C. nodosa seedlings (Pérez et al. 1991), independent of the extent of burial. Similarly, the alternative hypothesis that the growth response observed is a response to the dark conditions experienced by plants after burial has been experimentally rejected for *Cakile edentula* (Zhang & Maun 1992).

Whatever the causal mechanisms, the coupling between vertical growth and sediment accretion in *Cymodocea nodosa* provides support for the usefulness of this species (Marbà et al. 1994a) and other seagrass species with vertical shoots (e.g. *Thalassia testudinum*: Patriquin 1973, 1975, Marbà et al. 1994b) as tracers of sediment dynamics. The height of the bell-shaped response curve to fluctuations in sediment depth must be, however, dependent on the rate of vertical growth of the plants, and, therefore, must be species specific. Elucidating these response curves for key seagrass species is important to establish critical levels of erosion and burial the plants may tolerate and, therefore, to define conservation policies.

Acknowledgements. This work was funded by a projects of the Ramón Areces Foundation and project MAR-91-0503 of the CICYT (Spanish Government). We thank Guiomar Duarte for assistance in the field.

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This note was presented by G. W. Thayer (Senior Editorial Advisor), Beaufort, N. Carolina, USA

Manuscript first received: March 30, 1993
Revised version accepted: February 8, 1994