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Short communication

Evidence for vertical growth in *Zostera noltii* Hornem.

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Abstract

We report first evidence for rhizome vertical growth (driven by sediment burial) in the temperate seagrass *Zostera noltii*. The study was carried out in a population of *Z. noltii* occurring on the intertidal sandflats of Cádiz Bay Natural Park (Spain), an area subjected to episodic events of a high sediment transport driven by wind. In surveyed plants of *Z. noltii,* rhizomatic vertical growth was observed (9 cm maximum, 6.1±0.31 cm average) with shorter internodes and longer leaf-sheaths (0.74±0.05 cm and 10.1±0.5 cm, respectively) than those recorded for horizontal rhizomes (2.2±0.05 cm and 3.3±0.18 cm, respectively). Mean vertical rhizome growth rate, calculated from reconstructive techniques (0.083±0.003 cm d^{-1}), is half than that estimated for horizontal rhizome growth (0.15±0.008 cm d^{-1}) using the punching method. Vertical nodes lacked shoots, and resumed horizontal growth and shoot recruitment once the meristem reached the sediment surface. Plasticity in this trait allowed *Z. noltii* populations to withstand moderate burial in this highly dynamic environment.

Keywords: burial; phenotypic plasticity; seagrass; vertical growth; *Zostera noltii*.

Coastal zones are highly dynamic areas, where different driving forces (e.g., storms, currents, waves, tides, etc.) acting at several temporal (minutes to years) and spatial (centimetres to kilometres) scales reshape the sea bottom (Woodroffe 2002, Peralta et al. 2005). Sediment erosion and/or accretion of marine soft bottoms are recurrent, and follow seasonal cycles as well as unpredictable events (storms, hurricanes, etc.). Species living on these substrata, such as seagrasses, may counteract these phenomena through a variety of adaptive mechanisms. In seagrasses, these mechanisms are 1) the possession of a well developed belowground network of rhizomes and roots, providing an enhanced anchoring and storage capacity (den Hartog 1970, Tomlinson 1974), and 2) the protection of the basal meristems (by leaf sheath) against most chemical and physical damage (Kuo 1978, Tyerman 1989, Brun et al. in press). In addition, vertical rhizome growth of most seagrass species avoids sediment burial. Vertical growth depends on size of the species and the magnitude and frequency of the burial event relative to the seagrass life-history (Duarte et al. 1997).

Vertical growth of rhizomes (i.e., orthotropism) has been described in many seagrass species (see den Hartog 1970 and Tomlinson 1974), and is interpreted as a counteracting mechanism directed to avoid or, at least, to reduce sediment burial (Patriquin 1973, Marbà et al. 1994a,b, Marbà and Duarte 1994, Duarte et al. 1997, Vermaat et al. 1997). This process also prevents overcrowding in dense stands by allowing shoots to access a more favourable light climate (Hemminga and Duarte 2000). It seems that seagrass response to burial is triggered by darkness (Terrados 1997), and involves the elongation of vertical internodes until the apical meristem (enfolded by the leaf sheath) is repositioned at the sediment surface. Once the surface is reached, the orthotropic rhizome can resume its regular average growth rate and/or branch, yielding a horizontal (plagiotropic) rhizome and developing a horizontal ramet (Marbà et al. 1994a, Duarte et al. 1997, Kenworthy and Schwarzschild 1998).

Dimorphic rhizomes (i.e., horizontal and vertical rhizomes) have been described in most seagrasses inhabiting tropical and temperate habitats. Of the four species occurring on the Iberian Peninsula [*Posidonia oceanica* (Linnaeus) Delile, *Cymodocea nodosa* (Ucria) Ascherson*,* *Zostera marina* Linnaeus and *Z. noltii* Hornem.] only *P. oceanica* and *C. nodosa* are known to develop vertical shoots (short shoots) and orthotropic growth (den Hartog 1970, Tomlinson 1974, Marbà and Duarte 1998, Duarte and Hemminga 2000). However, in contrast to previous data and considerations, this study shows that *Z. noltii* can grow vertically and that this response seems to be triggered by sediment burial.

After two weeks of wind-driven strong currents, the seaward edges of the *Zostera noltii* meadows underwent pronounced erosion (10–20 cm) (Figure 1; Figure 2A). The sediment from the central parts of the meadow was also washed out, revealing the vertical rhizomes of the exposed *Z. noltii* plants turning into creeping horizontal rhizomes (Figure 2B). Mean values for age (77±4.1 days), number of internodes (9.7±0.5 nodes $plant^{-1}$), length (6.1±0.31 cm) and rhizomatic growth (0.083±0.003 cm d^{-1}) for vertical rhizomes were recorded (n=52; Table 1). Figure 2C, D, E, F and G show the *Z. noltii* plants with vertical rhizomes after washing out the adjacent sediment experimentally. Three different types of plants were found: 1) plants bearing vertical rhizomes with many short-length internodes positioned close to the buried horizontal rhizome, while internodes close to the sediment surface were longer (Figure 2C and Figure 3); 2) plants with thin and highly flexible vertical rhizomes (Fig-

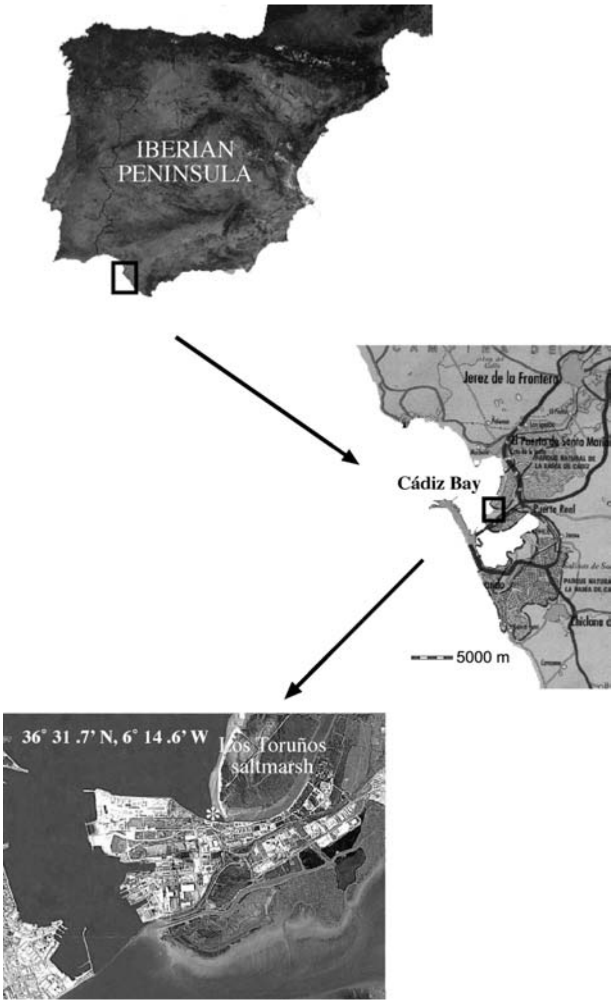

Figure 1 *Zostera noltii*: geographical location of the study site. The study was carried out in a meadow occurring on the intertidal sandflat in Los Toruños (el Bajo de la Cabezuela), a salt marsh ecosystem of 773 ha situated in Cadiz Bay Natural Park (36°31.7′ N, 6°14.6′ W). This sandflat, colonized by patches and meadows of *Z. noltii* in the intertidal zone, is located at the mouth of a sea arm and subjected to high currents powered by tide, waves and winds (Cadiz Bay is a very windy area) with recurrent episodes of erosion and accretion. Asterisk indicates the precise sampling location.

ure 2E and Figure 3E); 3) plants with vertical rhizomes that developed plagiotropic rhizomes once the meristem reached the sediment surface (Figure 2C–G and Figure 3A, C, D). Regardless of the kind of vertical rhizome, they shared two characteristics: firstly, buried vertical nodes lack shoots; secondly, vertical internodes were shorter than horizontal internodes (0.74 cm±0.05 and 2.2±0.05 cm, respectively, df=584, $p<0.0001$, t-test; Table 1). Furthermore, longer leaf-sheaths (10.1±0.5 cm) were observed in plants with vertical rhizomes that did not reach the sediment surface (3.3±0.18 cm for plants without vertical growth) (df=271, $p<0.0001$, t-test; Table 1), allowing the leaf blade to reach the sediment surface (Figure 3E).

As far as we are aware this is the first evidence of vertical growth in the seagrass *Zostera noltii*. There are two possible reasons for the lack of previous records. Firstly, the rhizomes of *Z. noltii* have a shorter life span, and are smaller than those of most seagrass species (den Hartog 1970, Duarte 1991) making them highly breakable during sampling. Thus, once in the laboratory it is difficult to associate this form of growth with vertical growth if the plant network has not been sampled with extreme care. Secondly, *Z. noltii* populations can be annuals (northern Europe) or perennials (southern areas). A certain degree of plasticity in vertical growth would be important in perennial populations subjected to frequent burial and erosion episodes, where predictability or frequency of these phenomena allows adaptive responses in the plants (DeWitt et al. 1998, Alpert and Simms 2002). Such plasticity would not have adaptive value in annual populations where, for example, adaptation to ice disturbance or waterfowl grazing would be more important in relation to life-history (Jacobs et al. 1981, Robertson and Mann 1984) than adaptation to sediment burial. As well, expression of vertical growth in this species seems to require moderate burial. Severe burial (>9 cm; the highest vertical rhizome length recorded in this study) appears to exceed the vertical growth of this species. However, modest burial results in minimal vertical growth (millimetres) and, thus, it might not be recognized as such. In any case, further investigation is required to determine if this severe burial refers to sudden burial or a gradual accumulation of sediment. By using reconstructive techniques, the estimated vertical growth (0.083 cm d^{-1}) is half than that estimated for horizontal growth (0.15±0.008, n=581; Brun et al. 2003 and unpublished data) calculated by punching (see Peralta et al. 2000). However, the large variability recorded in the plastochrone interval (range 1–29 days; Brun et al. 2003, Peralta et al. 2005) makes this growth estimation uncertain, and direct measurements of this dynamic parameter are required to fully explore the extent of the vertical growth in this species.

Table 1 *Zostera noltii*: morphometric and dynamic properties of the vertical and horizontal rhizomes in the sampling zone.

Morphometric properties	Vertical	Horizontal	F/t values	df	p
Age (days)	77±4.1	–	–	–	–
Number of internodes (internodes rhizome^{-1})	9.7±0.5	–	–	–	–
Rhizome length (cm)	6.1±0.31	–	–	–	–
Rhizome growth (cm d^{-1})	0.083±0.003	0.15±0.008*	–	–	–
Internode length (cm)	0.74±0.05	2.2±0.05	17.3/20.9	584	<0.0001
Leaf-sheath length (cm)	10.1±0.5	3.3±0.18	30.2/13.0	271	<0.0001

Morphometric differences between horizontal and vertical rhizomes were checked by using a Student t-test with unequal number of replicates. Data are presented as means±1 SE. Level of significance was set at 5% (Zar 1984).

* Data from Brun et al. 2003 and unpublished, obtained by direct measurements using the punching method.

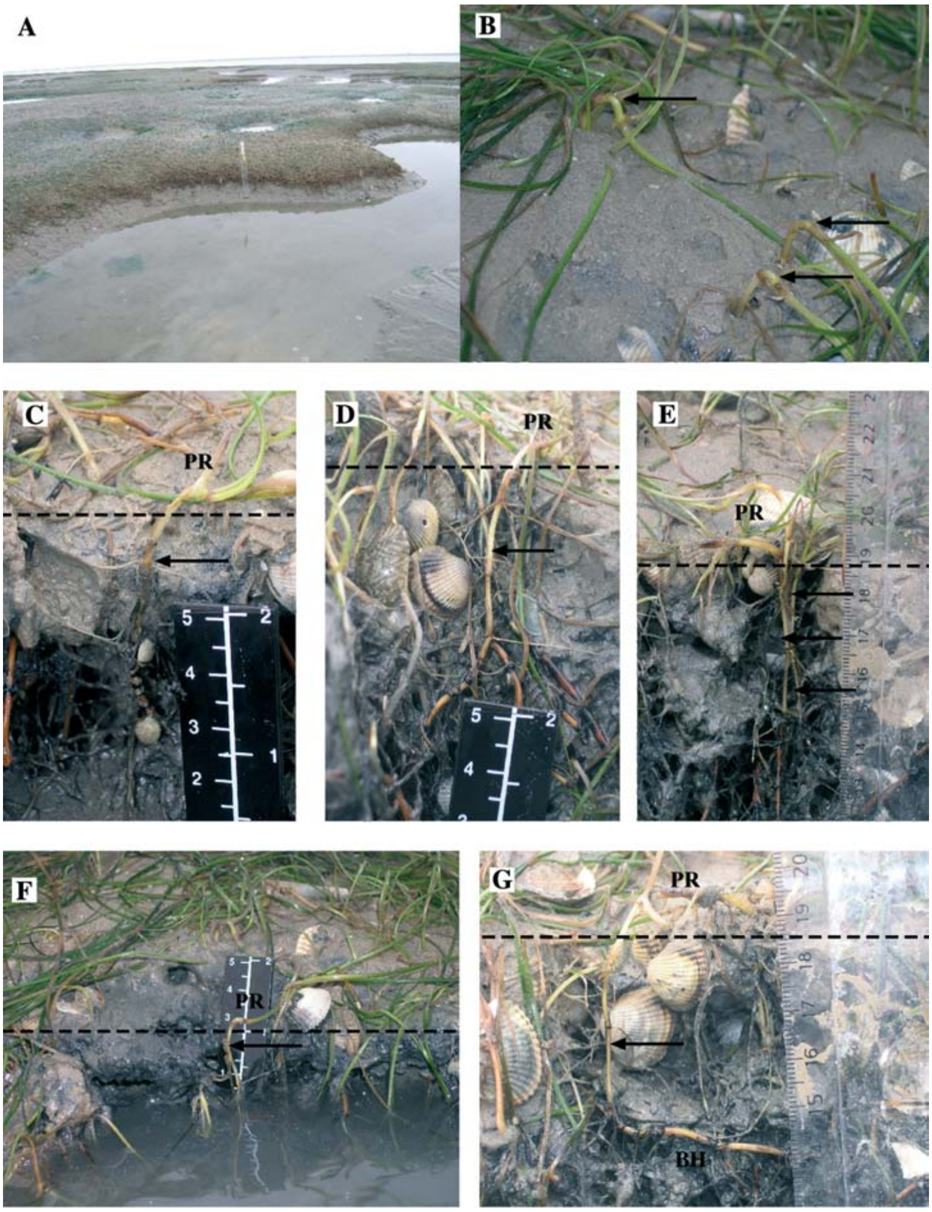

Figure 2 *Zostera noltii* meadows at Cádiz Bay Natural Park (Spain).
(A) A meadow was surveyed in March 2005 after two successive weeks of high wind, which eroded large areas inhabited by this species. Plants at the meadow edge were selected, where an erosion cliff was created (rule is 40 cm long). (B) *Z. noltii* plants with vertical rhizomes turning into creeping horizontal rhizomes from the central parts of the meadow where the sediment was naturally washed out. For photographs, the sediment wrapping the plants (including the rhizome network) was washed away with natural seawater using a small sprayer, while keeping plant structure and position within the sediment intact. In addition, 50 plants with orthotropic rhizomes and 50 with plagiotropic rhizomes were sampled to measure internode number and length, and sheath length. To convert rhizome length to rhizome age, the number of internodes per plant was multiplied by an annual averaged leaf plastochrone interval (8.3±0.67 days, n=959; Brun et al. 2003 and unpublished data). Rhizomatic vertical growth (cm d^{-1}) was estimated using the vertical rhizome length and the estimated age as was previously calculated by other authors (see Hemminga and Duarte 2000). (C) Plants with vertical rhizomes bearing many short internodes situated close to the buried horizontal rhizome, and longer rhizomes close to the sediment surface. (D) Plants with vertical rhizome converting into horizontal rhizome once the meristem reached the sediment surface. (E) Plants with thin and highly flexible vertical rhizomes converting into horizontal rhizome. (F) Plants from Figure B after washing out the sediment experimentally. (G) Plants with vertical rhizomes coming from a buried apical shoot that started to develop plagiotropic rhizomes once the meristem reached the sediment surface. Arrows denote vertical rhizomes while dashed lines represent the original sediment level. Abbreviations: BH, buried horizontal rhizome; PR, plagiotropic rhizome. Scale units are cm.

The vertical growth observed in this population of *Zostera noltii* seems to be triggered by recurrent sediment burial and erosion episodes. In other species, the cycles in the internodal length of vertical rhizomes have been associated with seasonality and with different burial or erosion rates (Marbà et al. 1994a). Short internodes are associated with low sediment accretion rates, whereas longer internodes are found under severe burial conditions (Marbà et al. 1994a, Duarte et al. 1997). Orthotropic rhizomes of *Z. noltii* possessed numerous short internodes near the insertion point with the horizontal rhizome, whereas above this point, internodes were longer

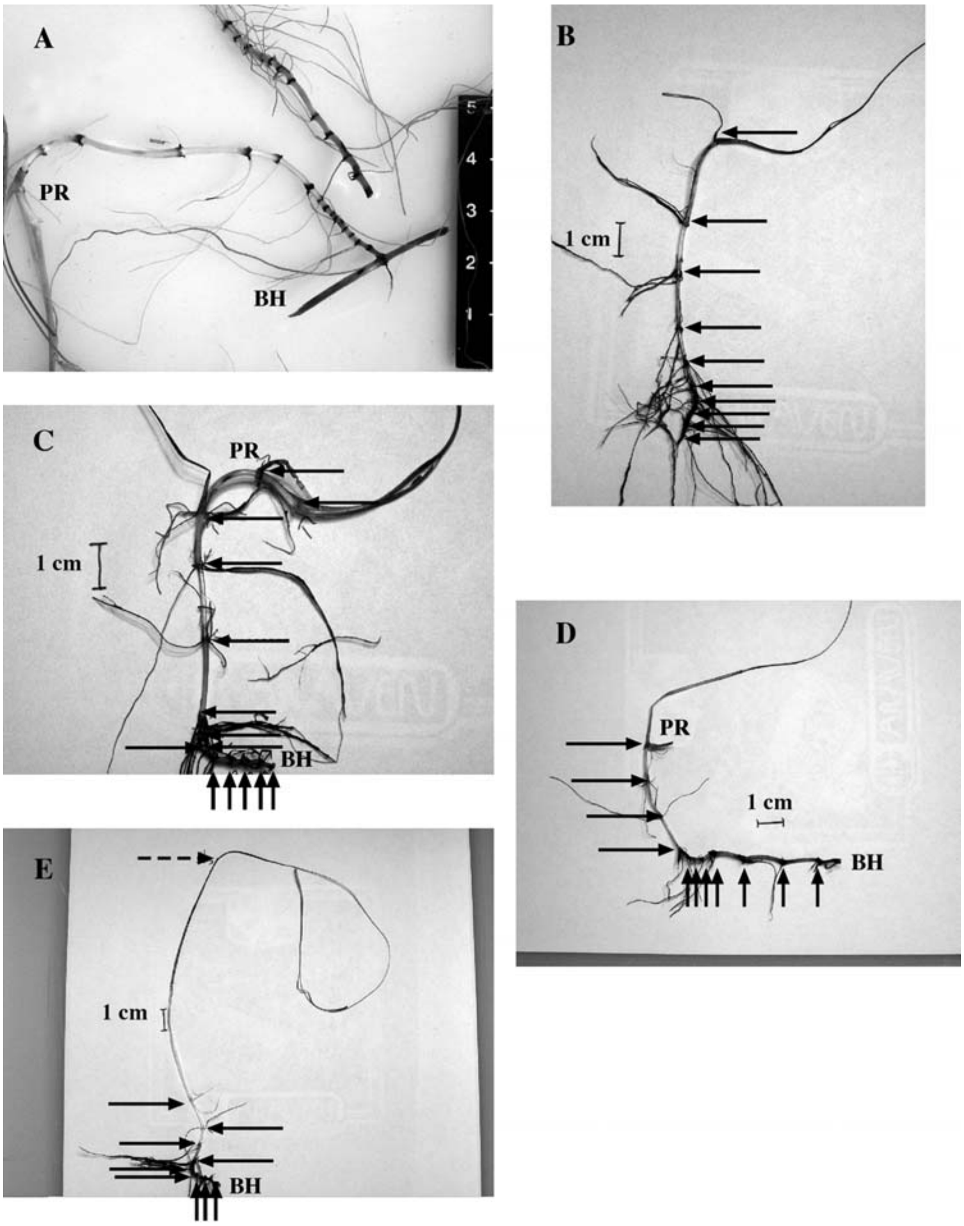

Figure 3 *Zostera noltii* plants.
(A) Vertical rhizome with many short internodes coming from a short-shoot in the buried horizontal rhizome. The vertical rhizome developed a plagiotropic rhizome once it reached the sediment surface. (B) Vertical rhizomes with many short internodes, increasing its length toward the sediment surface. (C) and (D) Vertical rhizomes coming from a buried apical shoot, growing finally in a plagiotropic manner once the meristem reached the sediment surface. (E) Thin and highly flexible vertical rhizomes with long leaf-sheaths. Continuous arrows indicate nodes, while broken arrows show the sheath height. Asterisks denote apical shoots. Abbreviations: BH, buried horizontal rhizome; PR, plagiotropic rhizome. Scale is set in the photographs, otherwise scale units are in cm.

until starting to grow horizontally at the sediment surface. It might indicate different sediment accretion rates, but dynamic studies are required to check this hypothesis. Lack of shoots in the buried nodes is also found in other species with orthotropic growth, and may be considered as a reallocation of available resources to vertical shoot growth, and away from the production of new heterotrophic (shaded) shoots that would drain plant resources (Hemminga and Duarte 2000). Moreover, a failure in the recruitment of shoots in the buried nodes could result from physical and/or chemical damage, as described in short-shoots of this species using photomicrographs (Brun et al. in press).

In conclusion, perennial *Zostera noltii* plants from a highly dynamic intertidal sandflat displayed orthotropic growth that seemed to be triggered by burial. Vertical rhizomes were shorter than horizontal rhizomes and lacked shoots in the nodes. Plagiotropic growth and shoot recruitment was re-established once the meristem reached the sediment surface.

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