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Morphometric variations as acclimation mechanisms in *Zostera noltii* beds

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Abstract

The use of morphometric variations as acclimation mechanisms was tested in natural populations of the intertidal seagrass *Zostera noltii* in Ria Formosa (Algarve, southern Portugal). To achieve the objective, two populations of *Z. noltii* were studied; a bed exposed and physically impacted by the artificial opening of a new inlet, and a second bed protected from dynamic impacts. At each meadow, morphometry and other plant-key variables such as tissue composition, photosynthetic parameters and dynamic properties (i.e. modules and whole plant growth rates) were monitored. After severe physical impacts in winter 1998, the newly appeared plants in the exposed meadow showed permanent morphometric changes. This new morphotype (small-leaved morphotype, SLM) had shorter (65%) and narrower leaves (25%) with longer internodes (4 times), than the large-leaved morphotype (LLM) found in the protected meadow or in the exposed meadow prior to the large disturbance. The SLM also had a larger non-photosynthetic biomass fraction, but increased photosynthetic capacity compared with the LLM. The morphometric and physiological changes were related to the fast recovery (<6 months) exhibited in the exposed meadow. In the protected meadow, morphometric changes (minor and short term) were associated with seasonal patterns. After the recovery, exposed and protected meadows gave similar production estimates supporting the hypothesis that a new stable state had been established in the exposed meadow. From these results, it can be concluded that *Z. noltii* has a remarkable phenotypic plasticity supported by coordinated changes in dynamic variables (i.e. leaf and internodal elongation rates and plastochrone index). Phenotypic plasticity seems to be the main mechanism by which this species is able to cope with short and long term environmental changes.

Keywords: growth; hydrodynamics; morphometry; phenotypic plasticity; Ria Formosa; seagrass

1. Introduction

Acclimation and adaptation are different processes, but both are important for the understanding and predicting the short and large-scale effects of environmental changes on biota. For plants, acclimation refers to reversible physiological or structural changes in response to extreme values of environmental variables causing stress, while the term adaptation includes all irreversible genetic changes that enhance the performance of the plant in a specific environment (Lambers et al., 1998; Sultan, 2000). For seagrasses, examples of acclimation are mostly physiological changes in response to light availability (i.e. photoacclimation, Evans et al., 1986; Major and Dunton, 2002), temperature (Zimmerman et al., 1989), or salinity (Benjamin et al., 1999). Only a few studies have shown that acclimation may also involve ultrastructural changes in seagrass modules (i.e. leaves, rhizome and roots) (Iyer and Barnabas, 1993; Benjamin et al., 1999). However, none of these structural changes have been related to

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morphometric responses at the whole plant level, since such morphometric responses are commonly interpreted as irreversible genetic adaptations to the local environmental constraints (Yabe et al., 1995; Hemminga and Duarte, 2000; van Katwijk, 2000).

Inter- and intraspecific divergences in seagrass morphometry have been associated with the high capacity of seagrasses to colonize different environments, explaining also differences in productivity and ecological strategies (Duarte, 1991). Currently, morphotypes are considered as genetic adaptations to local environmental conditions (Pérez-Lloréns and Niell, 1993; Masini and Manning, 1997; van Katwijk, 2000). However, such thought disagrees with the seasonal patterns in module morphometry described for numerous seagrass species (Marbà et al., 1996). The existence of seasonal patterns in morphometry and physiological rates, together with references on physiological divergences between seagrass morphotypes (Drew, 1979; McMillan, 1984; Pérez-Lloréns and Niell, 1993; Peralta et al., 2000), supports the hypothesis that morphometric and physiological characteristics may be linked and act as reversible and dynamic acclimation mechanisms.

The objective of this work was to show that natural beds of *Zostera noltii* use morphometric changes (i.e. phenotypic variation) as an acclimation mechanism. To achieve this objective, changes in a natural population affected by dynamic disturbances (i.e. coastal engineering works and storms) were monitored. To discriminate seasonal changes from acclimation to episodic impacts, a second meadow close to the first station that was naturally protected from the dynamic disturbances was simultaneously monitored.

2. Materials and methods

2.1. Sampling site

The Natural Park of Ria Formosa is a tidal lagoon sited in the South coast of Portugal with an extensive intertidal area ($>50\ \mathrm{km}^2$; Machás and Santos, 1999). The lagoon is a complex system of creeks and channels protected by a set of barrier islands (Morris et al., 2001). The inlets between these islands allow a high water exchange with the coastal waters (50–75%) at every tidal cycle. This ecosystem is mainly dominated by perennial beds of *Cymodocea nodosa*, *Zostera marina* and *Zostera noltii* (Machás and Santos, 1999). However, the intertidal flats, which are highly exposed to the hydrodynamic forces, are mainly occupied by *Z. noltii*.

In 1997, an artificial inlet was opened in the western most sand island (Williams et al., 2003). The opening affected a nearby meadow of *Zostera noltii*. This situation offered an excellent opportunity to study the capacity of this species to cope with anthropogenic-induced environmental changes. Therefore, the present study was focused on a *Z. noltii* meadow sited in the major tidal channel, close to the opening of the new inlet (exposed meadow, Fig. 1). To discern between seasonal variations and effects caused by the environmental impact, a second *Z. noltii* population, sited in a more protected area, not far from the first studied meadow was also monitored (protected meadow, Fig. 1).

2.2. Plant analysis

Every 3 months, from November 1997 to September 1999, three random samples of biomass ($400\ \mathrm{cm}^2$), including shoots and root/rhizome systems, were carefully harvested at low tide and transported in ice chests. In the laboratory, plants were separated into above and belowground parts. Subsequently, biomass ($\mathrm{g\ DW\ m}^{-2}$), shoot density ($\mathrm{no.\ shoots\ m}^{-2}$) and tissue composition (% DW) were estimated.

Additionally, architectural and dynamic properties of *Zostera noltii* (Figs. 3, 5 and 6) were studied using a modification of the method described by Zieman (1974) (more details in Peralta et al. (2000)). Except for November 1997, when only leaves were studied, this method was used to estimate growth and morphometry of leaves, internodes and roots. At each sampling site, 19–21 terminal shoots (i.e. those showing apical

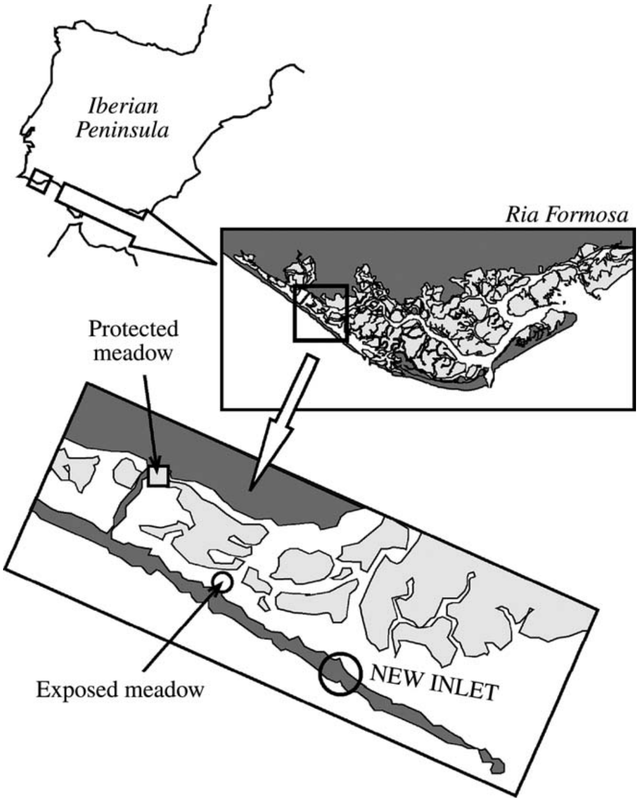

Fig. 1. Geographical location of Ria Formosa, the new inlet and the two studied *Zostera noltii* meadows.

dominance) were marked and collected after 8–14 days, depending on the season. Plant dynamic properties were estimated according to the following equations:

$$\mathrm{LER}=\frac{\sum_{i=1}^{n}\left[\left(\mathrm{LL}_{i,f}-\mathrm{LL}_{i,o}\right)>0\right]}{t_f-t_o} \tag{1}$$

$$\mathrm{LAR}=\frac{\sum \mathrm{NL}}{t_f-t_o} \tag{2}$$

$$\mathrm{PI}=\frac{t_f-t_o}{\sum \mathrm{NL}_\mathrm{a}} \tag{3}$$

$$\mathrm{LLR}=\frac{\sum_{i=1}^{n}\left[\left(\mathrm{LL}_{i,f}-\mathrm{LL}_{i,o}\right)<0\right]-\sum_{i=1}^{m}\mathrm{LL}_{i,o}}{t_f-t_o} \tag{4}$$

$$\mathrm{IER}=\frac{\sum_{i=1}^{n}\left(\mathrm{IL}_{i,f}-\mathrm{IL}_{i,o}\right)}{t_f-t_o} \tag{5}$$

$$\mathrm{IAR}=\frac{\sum \mathrm{NI}}{t_f-t_o} \tag{6}$$

$$\mathrm{RER}=\frac{\sum_{i=1}^{n}\left(\mathrm{RL}_{i,f}-\mathrm{RL}_{i,o}\right)}{t_f-t_o} \tag{7}$$

$$\mathrm{RAR}=\frac{\sum \mathrm{NR}}{t_f-t_o} \tag{8}$$

where:

LER: leaf elongation rate (cm plant^{-1} d^{-1}), LL is the leaf length (cm) and n the number of leaves at end of the studied period ($t_f - t_o$).

LAR: leaf appearance rate, (leaves plant^{-1} d^{-1}), NL is every new leaf appeared during the studied period.

PI: plastochrone index (d), calculated as the number of days elapsed between the appearance of two consecutive leaves from the apical meristem (NL$_\mathrm{a}$).

LLR: leaf loss rate (cm plant^{-1} d^{-1}), where m is the number of leaves lost during the studied period.

IER: internodal elongation rate (mm plant^{-1} d^{-1}), where IL is the internodal length and n the number of internodes between the punched leaf and the apical meristem.

IAR: internodal appearance rate (internodes plant^{-1} d^{-1}), where NI is every new internode appeared during the period of study.

RER: root elongation rate (mm plant^{-1} d^{-1}), where RL is the root length resulting from the sum of all roots presents at the node i, and n the number of nodes between the punched leaf and the apical meristem.

RAR: root appearance rate (roots plant^{-1} d^{-1}), where NR is each new root appeared during the studied period.

Elongation rates of leaves, rhizome and roots (LER, IER, and RER) were transformed in biomass growth rate (GR, mg DW plant^{-1} d^{-1}, Eq. (9)), using the length/dry weight ratio of each marked plant.

$$\mathrm{GR}=\left(\mathrm{LER}\frac{\mathrm{DW}}{\mathrm{LL}}\right)+\left(\mathrm{IER}\frac{\mathrm{DW}}{\mathrm{IL}}\right)+\left(\mathrm{RER}\frac{\mathrm{DW}}{\mathrm{RL}}\right) \tag{9}$$

where DW/LL, DW/IL and DW/RL are the dry weight/length ratio for leaves, internodes and roots, respectively.

Finally, the production of the meadow (g DW m^{-2} d^{-1}) was estimated for each sampling date according to Eq. (10).

$$\mathrm{Production}=\mathrm{GR}_m\times\mathrm{DENSITY}_m \tag{10}$$

where GR$_m$ is the averaged growth rate of *Zostera noltii* plants, DENSITY$_m$ is the averaged shoot density.

2.3. Photosynthesis

To reduce the variability due to age-dependent effects on photosynthesis (Alcoverro et al., 1998), photosynthetic measurements were always performed on 2 cm fragments of the second outer leaf. Leaf pieces were excised some hours before measurements to minimize wounding effects (Mazzella et al., 1981; Dunton and Tomasko, 1994). Fresh weight, length and width were determined before the gas exchange measurements. Oxygen evolution was recorded at 17 °C with a Hansatech polarographic O$_2$ electrode (Hansatech Ltd.). Photosynthesis-irradiance (P–I) curves were performed in triplicate at 9 light intensities from 0 to 1700 μmol photons m^{-2} s^{-1}. P–I curve parameters were estimated by fitting biomass-normalized data to a rectangular hyperbola model (Baly, 1935), according to Eq. (11).

$$P_\mathrm{N}^\mathrm{B}=\frac{P_\mathrm{max}^\mathrm{B}\alpha^\mathrm{B}I}{P_\mathrm{max}^\mathrm{B}+(\alpha^\mathrm{B}I)}-R^\mathrm{B} \tag{11}$$

where P_N^B is net photosynthesis (μmol O$_2$ g DW^{-1} s^{-1}), $P_\mathrm{max}^\mathrm{B}$ is photosynthetic capacity (μmol O$_2$ g DW^{-1} s^{-1}), α^B is photosynthetic efficiency (μmol O$_2$ m^{-2} μmol^{-1} photons g DW^{-1}) and R^B dark respiration rate (μmol O$_2$ g DW^{-1} s^{-1}).

Photosynthetic photon flux density (PPFD) was measured within the incubation chamber using a Quantitherm light sensor (Hansatech Ltd.). After measurements, the chlorophyll concentration of plant tissues was measured spectrophotometrically according to Jeffrey and Humphrey (1975) after extraction in acetone (24 h in darkness).

2.4. Statistical analysis

Except for LLR, due to the lack of belowground information from punched plants, data from November 1997 were excluded from the statistical analysis of dynamic variables (i.e. GR, LER, and LAR). For each meadow, the temporal effects were tested using a one-way ANOVA, followed by the Fisher LSD test for multiple comparisons when necessary (Sokal, 1981) (Table 1). Heterocedastic data were log-transformed. For persistent heterocedastic data, a Kruskal–Wallis one-way analysis of variance by ranks was applied, followed by a multiple comparison (Siegel and Castellan, 1988). In all cases, the significance level was set at 5% probability.

3. Results

During the winter of 1997–1998, increased sand movement due to persistent storms was clearly fed and aggravated by the opening of a new inlet within the barrier island of Ançao (June 1997). These events seriously affected the nearby *Zostera noltii* beds. Consequently, the exposed meadow showed large and abundant gaps due to plant removal or plant burial (our personal observations). After the stormy period (i.e. March 1998), the remaining plants in the exposed site exhibited a strong peak in leaf loss rate (>2.8 cm plant^{-1} d^{-1}, Fig. 2). Despite this strong impact, the exposed population was able to recover efficiently in a period of 6 months. The process of recovery was coupled with large changes in plant morphometry and photosynthetic parameters. These responses are detailed in the following sections and compared with the results from a meadow, situated close to the exposed area, but protected from external hydrodynamic impacts.

3.1. Morphometric changes as an acclimative response

Large changes in plant morphometry were not reflected in annual patterns of biomass or shoot density. In the exposed and the protected meadows, biomass and shoot density exhibited unimodal annual patterns with a maximum in summer and minimum in winter (Fig. 2). However, when the exposed meadow was examined in more detail, a divergence between shoot density and biomass was observed after the disturbance, that was not observed in the protected site. In the exposed meadow, the shoot density doubled while the biomass remained unvaried (100 g DW m^{-2}, Fig. 2) between March and May 1998. Such uncoupling coincided with a remarkable morphometric change in plants within the exposed meadow (Fig. 3). Thus, plants at the exposed site had leaves 65% shorter (averaged leaf length decreased permanently from 25 to 7–10 cm) and 25% narrower than plants at the protected site (Table 1, Fig. 3A and B), as well as longer internodes and roots (Table 1, Fig. 3C and D). The leaf size of plants from the protected bed also varied during this period (Fig. 3A and B). However, the changes in the protected site were small and short-lived compared with those observed in the exposed site.

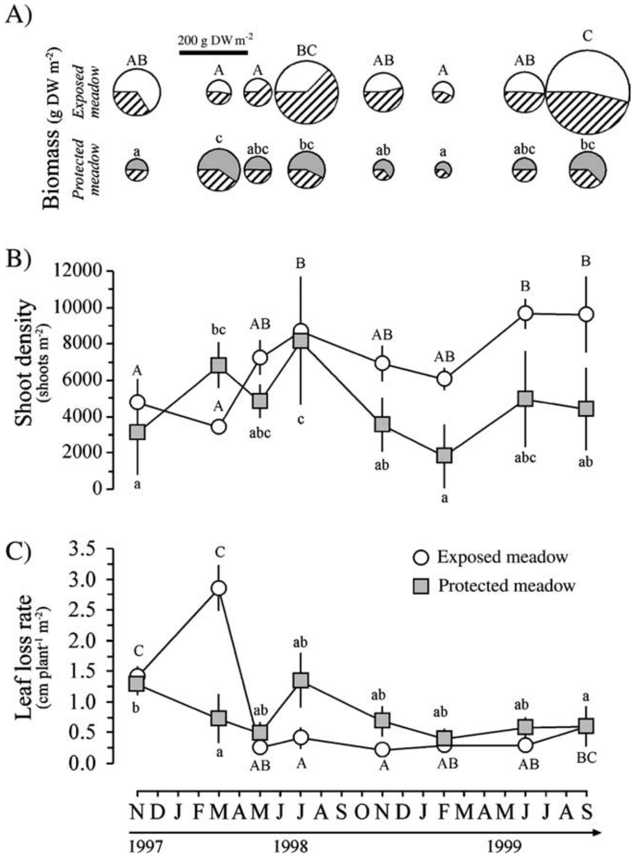

Fig. 2. Temporal variation of (A) biomass, (B) shoot density and (C) leaf loss rate of *Zostera noltii* in the two studied meadows. In Fig. 2A, the pie diameters are proportional to the corresponding values (reference in top black line). White and grey areas represent leaf biomass of exposed and the protected meadow, respectively, and patterned ones the root/rhizome systems. Significant differences among samplings are indicated by the alphabetic code. For each graph, capital letters correspond to the exposed meadow (white circles), and minor letters to the protected one (grey squares) (see Table 1 for statistical analysis).

In the protected meadow, leaf morphometric changes coincided with a reduction in leaf N content (Fig. 3A and 4A) reaching values below the 1.8% DW, level considered critical for nutrient limitation in seagrass leaves (Duarte, 1990). During the same period (May 1998), no significant

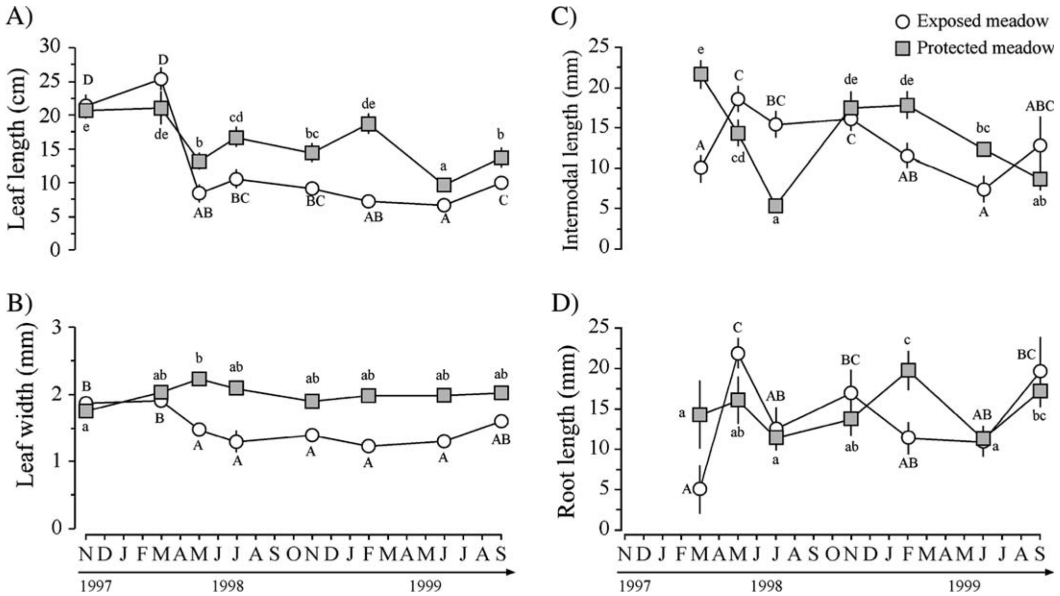

Fig. 3. Temporal variation of leaf (A and B) and root/rhizome morphometry (C and D) of *Zostera noltii* plants in the two studied meadows. Significant differences among samplings are indicated by alphabetic codes. For each graph, capital letter codes correspond to the exposed meadow (white circles), and minor letter ones to the protected one (grey squares) (see Table 1 for statistical analysis).

Table 1

One-way ANOVA on different variables of *Z. noltii* on the exposed and the protected meadows (effect:time)

Variables	Exposed meadow			Protected meadow		
		F, df	*p*		*F*, df	*p*
Biomass		5.078, 7	*		2.662, 7	*
Shoot density		3.092, 7	*		2.677, 7	*
Leaf length	T	22.2, 7	**	T	11.43, 7	**
Leaf width		4.434, 7	**	KW	20.63, 7, 121	*
Internodal length		4.166, 6	**		13.03, 6	**
Root length		3.139, 6	n.s.		3.63, 6	*
C_{leaf}	KW	12.94, 7, 24	n.s.	KW	14.43, 7, 23	*
$C_{\mathrm{root/rhizome}}$	KW	11.63, 7, 24	n.s.	KW	9.38, 7, 2	n.s.
N_{leaf}	KW	20.90, 7, 24	*	KW	18.18, 7, 23	*
$N_{\mathrm{root/rhizome}}$	KW	18.85, 7, 24	*	KW	15.48, 7, 2	*
Chlorophyll	T	15.63, 7	**		24.56, 7	**
$P_{\max}$	T	10.34, 7	**	T	10.72, 7	**
α		1.225, 7	n.s.	T	0.586, 7	n.s.
I_{sat}		0.832, 7	n.s.	KW	10.49, 7, 23	n.s.
GR	T	17.50, 6	**	KW	29.40, 6, 112	**
LER		4.254, 6	*		1.253, 6	n.s.
LAR	T	6.741, 6	**	KW	43.28, 7, 117	**
IER		12.20, 6	**	T	8.893, 6	**
IAR	T	8.577, 6	**		8.117, 6	**
RER	T	3.503, 6	*	T	2.643, 6	*
RAR	T	3.605, 6	*	T	1.769, 6	n.s.
PI		10.62, 6	**	T	5.47, 6	**
LLR	T	8.581, 7	**	KW	18.33, 7, 129	*

$^*p < 0.05$, $^{**}p < 0.001$, n.s. not significant.

The *F* value, degrees of freedom (df) and probability (p) for each particular ANOVA are included. Log-transformed data are indicated by the letter T. When necessary, a Kruskal–Wallis analysis of variance by ranks (KW) was applied. In those cases, data are H, df, n, and p. C_{leaf}, leaf carbon content; $C_{\mathrm{root/rhizome}}$, root/rhizome carbon content; N_{leaf}, leaf nitrogen content; $N_{\mathrm{root/rhizome}}$, root/rhizome nitrogen content; Chlorophyll, total chlorophyll content; $P_{\max}$, photosynthetic capacity; α, photosynthetic efficiency; I_{sat}, saturation irradiance; GR, growth rate; LER, leaf elongation rate; LAR, leaf appearance rate; IER, internodal elongation rate; IAR, internodal appearance rate; RER, root elongation rate; RAR, root appearance rate; PI, plastochrone index; LLR, leaf loss rate.

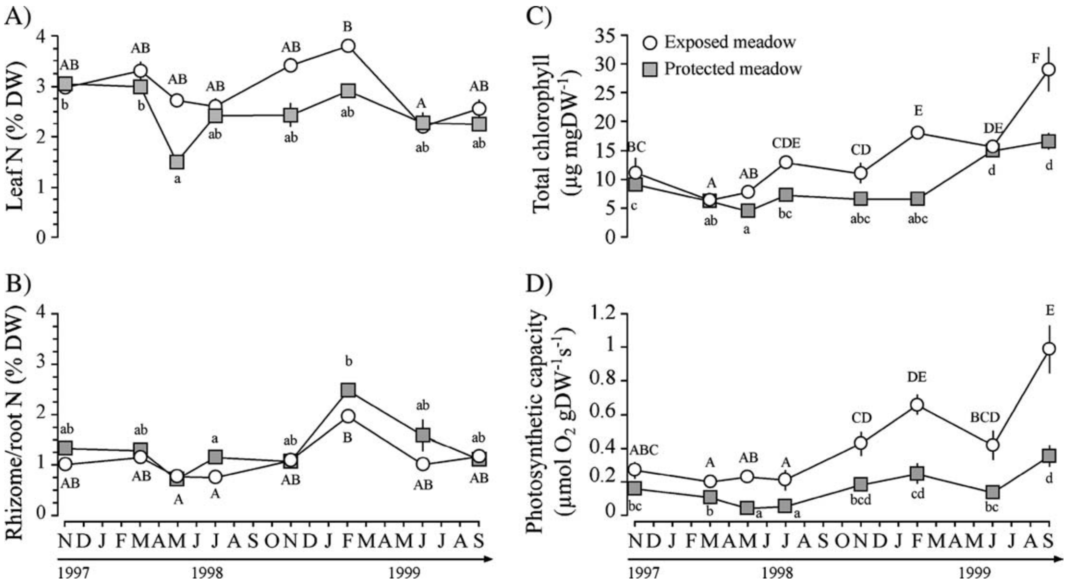

Fig. 4. Temporal variation of N content in leaves and root/rhizome of *Zostera noltii* plants (A and B), total chlorophyll (C) and photosynthetic capacity (D) of *Z. noltii* leaves in the two studied meadows. Significant differences among samplings are indicated by alphabetic codes. For each graph, capital letter codes correspond to the exposed meadow (white circles), and minor letter ones to the protected one (grey squares) (see Table 1 for statistical analysis).

reduction in the leaf N content of the exposed plants was observed and N content values were always higher than the critical level for seagrasses (Fig. 4A, Table 1).

Temporal variations in chlorophyll and photosynthetic parameters did not reveal any clear seasonal pattern in none of the meadows (Fig. 4C and D). However, after the morphometric change, plants from the exposed site showed an increasing temporal trend in chlorophyll content and photosynthetic capacity (P^{B}_{max}) (Fig. 4C and D, Table 1).

3.2. Dynamic acclimation

The range of variability in growth rate (GR) of *Zostera noltii* was unaffected by the morphometric differences detected between plants from the two sampling sites (1–4 mg DW plant^{-1} d^{-1}, Fig. 5A and Fig. 6A). However, the relative contribution of photosynthetic and non-photosynthetic tissues to the whole plant growth diverged considerably between the populations. GR of exposed plants peaked in May and July 1998 (3.7 and 2.9 mg DW plant^{-1} d^{-1}, respectively, Fig. 5A, Table 1). In May 1998, GR was mainly supported by the internodal and root growth (Fig. 5), with belowground production accounting for more than 70% of whole plant growth. By contrast, GR in July 1998 was largely maintained by increased leaf growth. The high production of the photosynthetic tissues lasted until November 1998. After that, GR remained about 1 mg DW plant^{-1} d^{-1} with a comparable contribution of photosynthetic and non-photosynthetic tissues. In the protected meadow, GR also peaked in May 1998 ($>$3.5 mg DW plant^{-1} d^{-1}, Fig. 6A) although the relative contribution of belowground parts to the whole plant growth was always below 55%, with a minimum in July 1998 (Fig. 6). In summary, although GR were similar in plants from both populations, recruitment rates (i.e. LAR, IAR and RAR) were higher in the exposed population (Figs. 5 and 6). Despite the maximum GR (on biomass basis) of the exposed meadow occurred in May 1998, the recruitment of new modules peaked in July 1998, when PI was extraordinarily short (4 days, Fig. 7).

3.3. Consequences at the whole meadow level

Consequences of plant morphometry and dynamic divergences at the whole meadow level can be summarized in estimations of the seasonal production (Fig. 8). Large differences between meadows were detected during 1998. Production in the exposed meadow increased markedly from winter 1998 (5.8 g DW m^{-2} d^{-1}) to spring 1998 (26.6 g DW m^{-2} d^{-1}). The latter value, mainly supported by internodal production ($>$70%), was much higher than the estimated for the protected site. The same was observed in summer 1998, but in this case, production was largely supported by leaves. From summer 1998 onwards, similar production estimates were obtained at both meadows.

4. Discussion

The present study shows that morphometric variations (i.e. phenotypic variations) in *Zostera noltii* beds

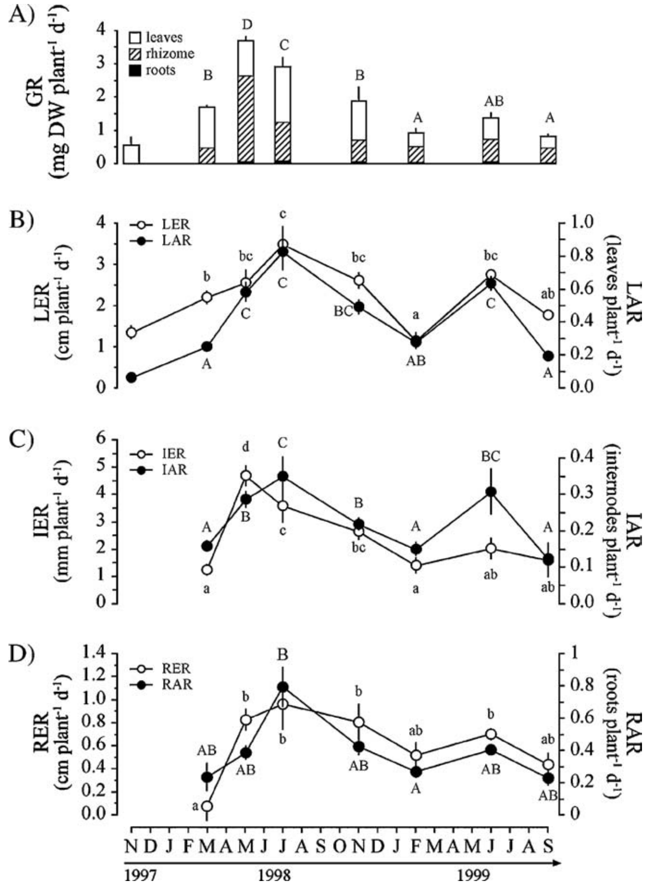

Fig. 5. Exposed meadow. Temporal variation of (A) whole plant growth rate (GR), (B) leaf growth rates, indicated as elongation (LER) and appearance of new units (LAR), (C) internodal growth rates, indicated as elongation (IER) and appearance of new units (IAR) and (D) root growth rates, indicated as elongation (RER) and appearance of new units (RAR), of *Zostera noltii* plants. Significant differences among samplings are indicated by alphabetic codes. For graphs B–D, capital letters correspond to black circles and minor letters to white ones (see Table 1 for statistical analysis).

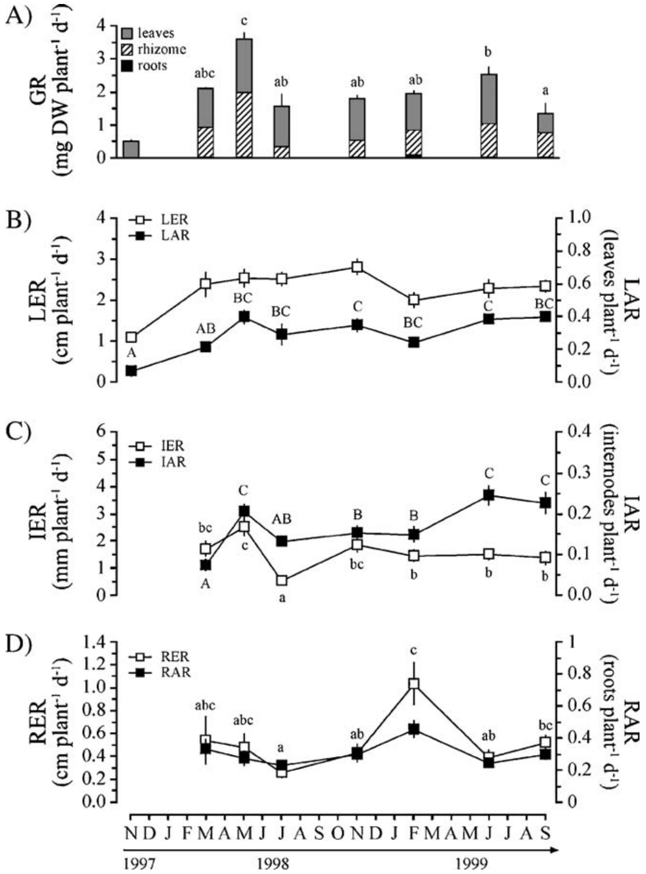

Fig. 6. Protected meadow. Temporal variation of (A) whole-plant growth rate (GR), (B) leaf growth rates, indicated as elongation (LER) and appearance of new units (LAR), (C) internodal growth rates, indicated as elongation (IER) and appearance of new units (IAR) and (D) root growth rates, indicated as elongation (RER) and appearance of new units (RAR), of *Zostera noltii* plants. Significant differences among samplings are indicated by alphabetic codes. For graphs B–D, capital letters correspond to black squares and minor letters to white ones (see Table 1 for statistical analysis).

work as acclimation mechanisms at several organization levels (i.e. plant modules, whole plant and meadow). Causes, mechanisms and effects of the acclimation process at each level will be discussed in the next sections.

4.1. Phenotypic variations: causes and mechanisms

Changes in hydrodynamics and in sediment-erosion patterns are common in areas close to a new inlet (Hofstede, 1999; Dennis et al., 2000; Dean and Dalrymple, 2002). In Ria Formosa, persistent storms further affected the area during the achievement of the inlet dynamics (winter 1997–1998; A. Vila, pers. comm.). Storms increased the sediment deposition within the lagoon affecting seriously the nearby seagrass beds (i.e. the exposed meadow). After that (March 1998), the exposed meadow underwent deep structural changes manifested by the high leaf loss rate, the marked drop in biomass and in shoot density and the appearance of numerous gaps. These effects on seagrass meadows have been previously attributed to increases in current velocity and/or sediment deposition episodes (Bell et al., 1999; Schanz and Asmus, 2003). However, and in contrast to previous studies, there was a re-establishment of the disturbed meadow (within 3–6 months) with a new morphotype with shorter and narrower leaves, but longer internodes (small-leaved morphotype, SLM). Changes in morphometry have been previously attributed to seasonal patterns and/or limited growth. However, none of these possibilities seem to support satisfactorily the changes observed in the exposed meadow. Seasonal patterns previously described for *Zostera noltii* that correlate biomass changes with shoot density (Vermaat and Verhagen, 1996) can explain suitably the changes observed in the protected meadow, but not in the exposed one where

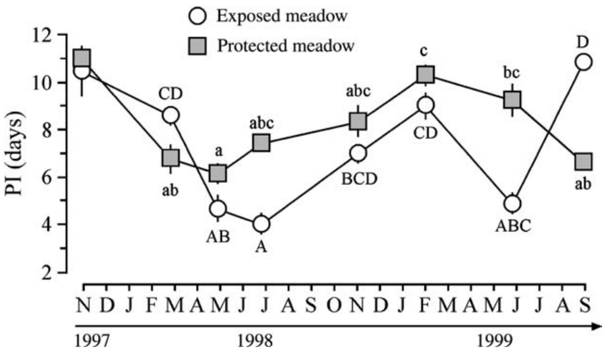

Fig. 7. Temporal variation of the plastochrone index (PI) in *Zostera noltii* plants from the exposed and the protected meadows. Significant differences among samplings are indicated by the alphabetic code. Capital letters correspond to the exposed meadow (white circles) and minor letters to the protected one (grey squares) (see Table 1 for statistical analysis).

shoot size and shoot density changed simultaneously. Similar LER during March and May 1998 was observed in exposed plants, even when the whole GR doubled. Consequently, leaf production decreased when the entire plant production increased. This change in relative growth between photosynthetic and non-photosynthetic tissues cannot be explained only by increases in light availability or by nutrient limitation. Enhanced light availability may explain increases in root-rhizome GR, but only as a proportion of the whole plant growth (Peralta et al., 2002). On the other hand, the pattern observed in the exposed meadow could be driven by nutrient limitation (Short, 1983; Short et al., 1985; Short et al., 1995; Brun et al., 2002). However, the high leaf N content (>2.5% DW) together with the high GR (>3.5 mg DW plant^{-1} d^{-1}) makes this hypothesis unlikely. Another cause that could trigger this response was the environmental disturbance suffered after the new inlet opening. Previous studies have also suggested that seagrasses exposed to high currents tend to decrease the leaf size (Schanz and Asmus, 2003) and increase the relative proportion of belowground tissues (Fonseca and Kenworthy, 1987; Peralta et al., 2000). Nevertheless, these studies (including ours) are based on descriptive observations and further research would be necessary to quantify any relationship between hydrodynamics and seagrass growth patterns.

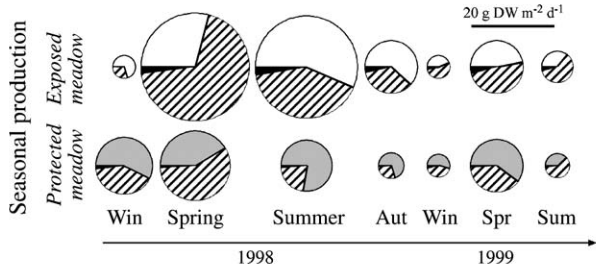

Fig. 8. Seasonal production estimations for exposed and protected meadows of *Zostera noltii* during the sampling period. The pie diameter is proportional to the corresponding value of production (reference value is indicated on the top black line). The compartments in each pie represent the root (black sections) and rhizome contribution (patterned sections). Plain sections represent the leaf contribution on the exposed meadow (white sections) and the sheltered one (grey sections).

The mechanisms responsible for the morphometric change of *Zostera noltii* in a short period (<3 months) may involve either external recruitment, genetic variation (i.e. adaptation) or reversible acclimation. On one hand, external recruitment requires the washing out of propagules from neighborhood populations and their settlement in the host area. Since the storms only occurred during the first winter and the exposed meadow was also affected by washing out, the settling of external shoots would be rather unlikely. On the other hand, the annual recruitment of *Z. noltii* depends largely on vegetative growth due to limited seed germination (Vermaat and Verhagen, 1996; Hemminga and Duarte, 2000; Brun et al., 2003). Therefore, the genetic variability in *Z. noltii* populations must be restricted to increases in the abundance of existing genotypes. Even in such case, phenotypic variations must result from simultaneous changes in PI, LER and IER (as observed from March to May 1998 in plants from the exposed site) (Brun, pers. comm.). Hence, the results indicate that plants from the exposed meadow were affected by physical impacts (i.e. hydrodynamics and sediment deposition) that triggered coordinated changes in plant dynamic variables, favouring a phenotypic change.

4.2. Consequences of morphometric changes at the module level

Diversity in plant size has been previously related to interspecific ecophysiological differences (Duarte, 1991). Moreover, it has been reported that small-leaved morphotypes of *Zostera noltii* have higher $P^{\mathrm{B}}_{\mathrm{max}}$ than large-leaved ones (Pérez-Lloréns and Niell, 1993; Peralta et al., 2000). It suggests an inverse relationship between leaf size and photosynthetic capacity in *Z. noltii*, in agreement with the inverse correlation found between the leaf width and the photosynthetic capacity observed in this study (Fig. 9), Thus, in small leaves, with increased surface to volume ratio, chlorophyll could be distributed more efficiently, requiring less DW for the same photosynthetic surface, as described for steppe plants (Voronin et al., 2003). This hypothesis could largely explain the high GR measured in the present study for the SLM that appeared after the disturbance, as well as the lack of seasonality in pigment content and photosynthetic parameters. Unfortunately, experimental or even descriptive studies combining leaf width with photosynthetic performance are uncommon in literature and more detailed studies are necessary to test this dependence.

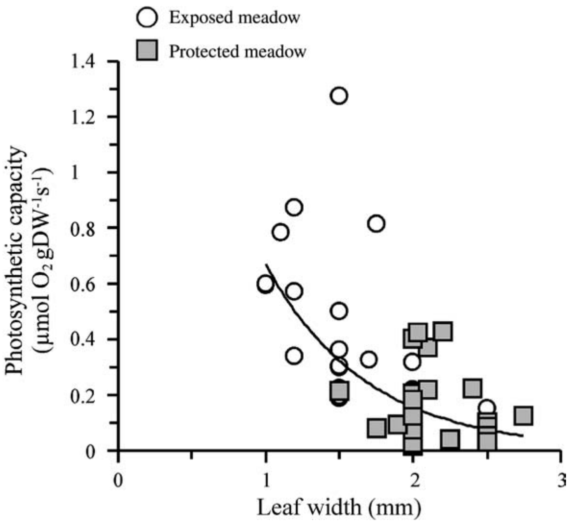

Fig. 9. Correlation between leaf width and photosynthetic capacity (P_{max}) in *Zostera noltii* plants from exposed (white circles) and protected (grey squares) meadow.

4.3. Consequences of morphometric changes at the plant level

Changes in biomass partitioning (i.e. above–belowground ratio) may modify the whole plant C-balance, by alteration of the photosynthesis/respiration ratio (Hemminga, 1998). It has been demonstrated that the oxygen consumption for leaves is 2.4–5 times higher than for roots/rhizomes in several seagrass species (Fourqurean and Zieman, 1991; Kraemer and Alberte, 1993; Dunton and Tomasko, 1994; Masini et al., 1995; Dunton, 1996). This suggests that total plant respiration must in part be dependent on the biomass allocation between leaves and roots/rhizome system (Hemminga, 1998). Therefore, enhanced belowground biomass, as observed in exposed plants in May 1998, may have benefited the acclimation process by reducing the biomass-normalized respiration rate. Nevertheless, the advantage of an increased roots/rhizome system should be carefully judged. A large root–rhizome system can be considered an asset only when light availability exceeds plant demands (Hemminga, 1998). Therefore, for the exposed meadow, the timing of the impact (winter) may have been critical in the success of the acclimation (spring). The success of recovery by increasing belowground tissues would probably be lower if the acclimation did start in late summer. Accordingly, the study of the appropriated temporal planning for coastal works as an early protecting method for nearby seagrass beds is suggested.

4.4. Consequences of morphometric changes at the population level

The present results show that phenotypic changes contributed to the re-establishment of the exposed meadow. Firstly, shoots that appeared after the disturbance were smaller (SLM) than the previous ones (LLM, identical to that of the protected site) but with similar growth capacity (see previous sections). Secondly, the shoot density increased considerably. As a result, production increased in the exposed meadow. Morphometric and demographic differences between plants from protected and exposed meadows still persisted even when the latter was re-established in 1999. After the recovery, the SLM exhibited lower plant growth rates than the LLM from protected site. Feedback effects (i.e. self-shading and reduced hydrodynamic stress) could largely account for the reduction in growth rate observed in SLM after the meadow recovery (Gambi et al., 1990; Koch, 2001). Nevertheless, in 1999, differences in plant growth rate and shoot density resulted in similar production values for the two meadows. These results show that the phenotypic plasticity of *Zostera noltii* may favor the formation of new stable states in a disturbed meadow.

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