

ORIGINAL ARTICLE

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Morphological and physiological differences between two morphotypes of *Zostera noltii* Hornem. from the south-western Iberian Peninsula

Received: 20 December 1998 / Received in revised form: 21 April 1999 / Accepted: 23 April 1999

Abstract The morphological and physiological differences between two morphotypes of *Z. noltii* Hornem. were studied in the intertidal meadows on the south-western Iberian Peninsula (Palmones river estuary and Ria Formosa). A small-leaved morphotype (SM) grows mainly at high intertidal sites, meadow edges or in recently deposited sandbanks, whereas a large-leaved morphotype (LM) generally thrives in well-structured beds or in deeper places. This study deals with the morphological, biochemical and physiological differences between these morphotypes as well as the ecological implications of the occurrence of different morphotypes in the same meadow. Shoot length, leaf width, rhizome internode length, roots per node, root length, leaf nutrient and pigment contents, and photosynthetic rates of both morphotypes were compared. The below-ground architecture (root and rhizome complex) of both morphotypes was more developed in sites characterized by higher hydrodynamics and/or a lower nitrogen content in sediments. Both morphotypes showed similar values for photosynthetic efficiency, dark respiration rate and compensation irradiance. On the other hand, the net photosynthetic capacity was much greater (5-fold) for the SM. This difference could explain the greater growth rate and faster leaf turnover rate of the SM compared with the LM. The occurrence of the SM in newly settled areas (and in the meadow edges) could be explained on the basis of its higher growth rate, which would allow a faster spreading of the meadow and/or better recovery after burial resulting from stormy weathers.

Key words Seagrass · *Zostera noltii* · Morphotypes · Growth

Communicated by H. Asmus and R. Asmus

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Introduction

Intraspecific morphological variability in seagrass communities, when growing under different environmental conditions, has been reported for *Zostera marina* (Ostenfeld 1908; Setchell 1929; Philip 1936; Biebl and McRoy 1971; Drew 1979; Phillips and Lewis 1983; Backman 1991; van Lent and Verschuure 1994a,b), *Z. japonica* (Harrison 1982), *Z. noltii* (den Hartog 1970; Pérez-Lloréns and Niell 1993b), *Z. capricorni* (Conacher et al. 1994), *Z. capensis* (Adams and Talbot 1992), *Halodule* spp. (den Hartog 1970), *Halophila ovalis* (den Hartog 1970) and *Thalassia testudinum* (McMillan and Phillips 1979), being mainly attributed to bathymetric gradients. Light, nutrients and temperature are the main variables controlling plant growth in subtidal beds (Short 1983), resulting in a decrease in length, width, and shoot density with increasing depth (Dennison and Alberte 1986; West 1990; Masini and Manning 1997). However, in intertidal systems, emersion effects (e.g. desiccation and temperature variability) result in a smaller leaf size and higher shoot density than in plants growing in the low intertidal zone (Cooper and McRoy 1988; Adams and Talbot 1992; Yabe et al. 1995). Such differentiation has been explained by the fact that high shoot density prevents desiccation during low tide by clumping (Pérez-Lloréns and Niell 1993b) and has been used as an indication of environmental stress (Phillips and Lewis 1983).

Responses of the seagrass root–rhizome system to environmental variability have also been reported, although direct measurements on below-ground parameters are scarce (Jacobs 1979; van Lent and Verschuure 1994a; Duarte et al. 1998; Sfriso and Ghetti 1998) and usually estimated from plastochron intervals (e. g. Vermaat et al. 1987). Light also plays an important role in below-ground development (Philippart 1995; Hemminga 1998) and, together with other variables (grain size, nutrient content in sediment and hydrodynamic regime), seems to trigger morphological responses. Short rhizome internodes with large, thin, and numerous roots have been found in sandy, nutrient-poor substrates because they al-

low a more effective nutrient uptake and a faster nutrient allocation by translocation. In contrast, thick, large, and poorly developed root hairs have been found in seagrasses growing in muddy, nutrient-rich beds (Short 1983; Marbà et al. 1996). Internode size has also been correlated with hydrodynamic conditions. In this sense, rhizomes with larger and thicker internodes have been found preferentially in exposed sites (Cooper and McRoy 1988).

In addition to morphological and structural variability, genetic and physiological differences between morphotypes have also been detected. Genetic distinction in *Z. marina* populations has been found in relation to habitat depth (Backman 1991; Fain et al. 1992). Drew (1979) reported higher photosynthetic rates in the narrow-leaved morphotype of *Z. marina* growing in the intertidal sites. Small morphotypes of *Z. noltii* occurring at high intertidal locations showed higher inorganic carbon uptake rates and lower carbon compensation points (measured in air and in water) than large morphotypes, with the differences increasing as the temperature rose (Pérez-Lloréns and Niell 1993b). This agrees with the finding that plants from high intertidal beds have higher tolerance to high temperatures (Biebl and McRoy 1971; McMillan 1984). Although these kinds of studies are rare, they are potentially useful for seagrass transplantation purposes (Williams and Davis 1996).

The data presented in this paper were obtained during the course of two research projects carried out at different times, locations and with different objectives. This explains why the parameters measured were not exactly the same for the two locations. Nevertheless, with the bulk of data presented, the following goals can be accomplished: (1) detecting and quantifying differences in plant architecture, biochemistry (elemental composition, chlorophyll content) and physiology (photosynthetic performance, growth) in *Z. noltii* Hornem. morphotypes occurring in the south-western Iberian Peninsula, and (2) examining the ecological implications of the occurrence of such morphotypes.

Materials and methods

Sampling sites

Plants were collected from two sites in the south-western Iberian Peninsula: Palmones river estuary and Ria Formosa. The Palmones river estuary is a small, shallow (2.5 km) eutrophic estuary located at Algeciras Bay (southern Spain), where seagrass beds are gradually being overgrown by ulvaceans (Hernández et al. 1997). The maximum tidal amplitude is 1 m. The large morphotype (LM) beds occurred at 0.10–0.25 m (height above lowest astronomical tide) in the main channel while the small morphotype (SM) was located at 0.75–0.90 m, at the edges of the main channel. Ria Formosa (southern Portugal) is a large tidal lagoon (50 km) with a strongly branched system of creeks and channels connected to the ocean by few outlets. The maximum tidal amplitude is 2.80 m and there are no permanent freshwater inputs, resulting in lower nutrient levels than in the Palmones river estuary. Extensive seagrass meadows (*Zostera noltii*, *Cymodocea nodosa* and occasional patches of *Z. marina*) are found. The distribution

of *Z. noltii* morphotypes in Ria Formosa differed from those in the Palmones river estuary. SM plants were found mainly in the intertidal mudflats of the principal channel, usually growing on newly settled sandbanks. LM plants largely occurred in lateral creeks (either in shallow pools or highly clumped in small and gently sloping elevations), where hydrodynamics are low and the emersion period is long.

Sediment analysis

Samples for granulometry, organic matter and elemental C and N composition were collected with cores (10 cm length, 3.2 cm i.d.) from meadows in the central channel and in a high intertidal belt of the Palmones river estuary. Core samples were cut in five cross-sections. Organic matter content was determined according to Håkanson and Jansson (1983). C and N contents were estimated with a Perkin-Elmer 240 CNH elemental analyzer. Sediment samples for granulometric analysis were weighed and sieved with 2, 1, 0.5, 0.25, 0.125, 0.0625 mm pore diameter sieves, after a drying period (24 h) at 70°C. The sedimentary particles were classified according to the Wentworth's classification of grain size (Fritz and Moore 1988).

Plant analysis

Plant material was collected during low tide and transported in an ice chest to the laboratory within 4 h of sampling. Shoot length, leaf width, rhizome internode length, roots per node and root length were measured.

Elemental composition was determined on samples of dried ground tissue. Previous to drying, plants collected from Palmones river estuary were sorted into outer (oldest), middle and inner (youngest) leaves (corresponding to leaves numbered 1, 2 and 3 respectively in Fig. 1 at t_0) and each sample was further sorted into apical (tip), central and basal fragments. This allowed a fine study of spatial gradients within the shoots. The material from Ria Formosa was sorted into above- and below-ground parts.

Pigment concentrations in plants harvested from the Palmones river estuary were estimated in leaf fragments as above. In plants from Ria Formosa, the fragments (2 cm) for pigment estimations were taken from the second outer leaf (middle leaf). The fragments were cut 2 cm above the sheath. Chlorophyll was extracted in acetone (24 h in darkness), and concentration was estimated according to Jeffrey and Humphrey (1975).

Since age-dependence of photosynthesis has been reported in leaf sections of seagrasses (Mazzella and Alberte 1986; Alcoverro et al. 1998), photosynthetic rates were always performed on 2-cm fragments of the second outer leaf to reduce variability. The pieces were excised some hours before the measurements to minimize wounding effects (Dunton and Tomasko 1994). Oxygen evolution was recorded with a Hansatech polarographic O_2 electrode at 17°C. Photosynthetic-PFR curves were performed in triplicate at 9 PFRs from 0 to 1700 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Photon flux was measured

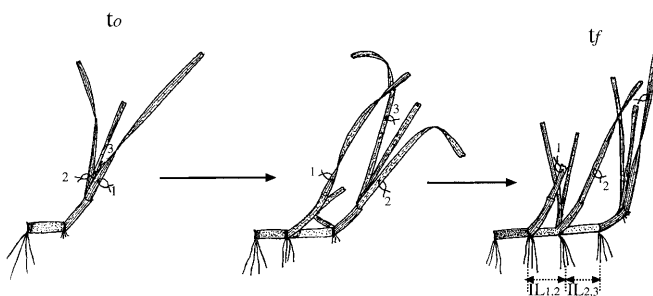


Fig. 1 Diagram showing the temporal evolution of a terminal punched shoot. Abbreviations are as defined in the text

within the incubation chamber with a Quantitherm light sensor (Hansatech)

Growth rates were estimated by a modification of the classical punching method described for seagrasses (Zieman 1974). Leaves from terminal shoots were marked with fine plastic fibres 1 cm above the sheath. For each morphotype, 19–21 terminal shoots were marked and collected after 8 days. Figure 1 shows a diagram of the temporal evolution of a terminal punched shoot. Leaf growth rates (G_L) were estimated according to the equation:

$$G_L = \frac{(\sum G_{nm} + \sum G_m)}{t}$$

(cm day⁻¹ shoot⁻¹), where G_{nm} is the growth rate of unmarked leaves (small and new leaves). $G_{nm} = TLL(t_f) - TLL(t_0)$, where TLL is total leaf length and t_0 , t_f are the days of marking and collection, respectively. G_m is the growth rate of marked leaves; $G_m = MLL(t_f) - MLL(t_0)$, where MLL is the length from the leaf base to the punching mark. $t = t_f - t_0$.

In a similar way, rhizome growth rates (G_R) were calculated according to:

$$G_R = \frac{\sum IL_{(i,i+1)}}{t}$$

(cm day⁻¹), where $IL_{(i,i+1)}$ is the internode length between leaf i and leaf $i+1$.

Statistical analysis

Parametric tests were applied whenever possible. However, some distributions showed either heteroscedasticity or deviations from normality, even after data transformations. In these cases, the equivalent non-parametric tests were applied (Zar 1984). Therefore, for each sampling site, morphological comparisons between morphotypes (shoot, root and internode length, leaf width and roots per node) were tested by a two-sample t -test or the non-parametric Mann-Whitney test. The former test was also applied to compare the characteristics of sediments from the Palmones river estuary. To compare C, N and pigment contents in leaves and leaf fragments of plants from Palmones river estuary, one-factor analyses of variance were applied. Multiple comparisons among means were done by the Tukey test. In all cases, the significance level was set at 5% probability.

Results

Palmones river estuary

Sediment analyses (grain size, organic matter and C:N content)

LM and SM plants occurred in the central channel (CC) and high intertidal (HI) sites respectively. The sediments were composed mainly of mud and fine sand (Table 1).

No significant differences were found in the grain size composition between sites. However, very fine pebble was slightly more abundant in the CC, while the HI site was enriched in medium sand. The organic matter of the sediment was significantly higher in the HI site than in the CC (66 and 45 mg g DW⁻¹, respectively) as well as the C and N contents (Table 2). On the other hand, C:N atomic ratio displayed similar values at both sites with the highest values at 9.5 cm depth (16.8 in the CC and 19.0 in the HI).

Plant analyses (morphology, C:N ratio and chlorophyll contents)

Plants growing in the CC had longer and wider leaves as well as larger internodes, roots and more roots per rhizome node than plants occurring at the HI location (Table 3).

Both morphotypes showed similar C content in leaves (Table 4). However, a finer spatial analysis revealed some differences among leaves within the shoot. Differences were dependent on the morphotype. The C content decreased significantly with the leaf age in the LM, while the highest C content in the SM was found in middle leaves. No significant differences were found along any of the leaves in both morphotypes. N content was significantly higher in the LM than in the SM (Table 5). The pattern of N allocation within leaves was similar to that of C. The N content decreased with leaf age in the LM and the highest N content was found in middle leaves in the SM. Generally, no significant differences were found along leaves, except in the inner leaves of the LM, which showed a lower N content towards the apex, and the outer leaves of the SM, which showed significant differences among fractions. In

Table 1 Grain size fractions in sediments from the Palmones river estuary. CC Central channel, HI high intertidal site

Grain size fractions	Grain size (mm)	HI (%)	CC (%)
Fine pebble	>4	1.76	1.72
Very fine pebble	4–2	1.21	5.13
Very coarse sand	2–1	1.01	2.84
Coarse sand	1–0.5	4.30	3.57
Medium sand	0.5–0.25	23.7	16.6
Fine sand	0.25–0.125	25.4	26.8
Very fine sand	0.125–0.0625	11.4	12.3
Mud	<0.0625	31.2	31.0

Table 2 Organic matter (OM), C, N contents and C:N atomic ratio in sediments from the Palmones river estuary. CC Central channel, HI high intertidal site. Data represent mean±SD ($n=3$)

Depth (cm)	OM (mg g DW ⁻¹)		C (% DW)		N (% DW)		C:N atomic ratio	
	CC	HI	CC	HI	CC	HI	CC	HI
0.5	25.8	75.3	1.3±0.2	3.3±0.4	0.10±0.04	0.25±0.02	15.3±4.0	15.2±0.8
1.5	46.7	65.1	1.1±0.1	2.6±0.0	0.08±0.01	0.23±0.01	15.1±1.1	13.0±0.9
4.0	43.3	61.9	2.0±0.5	2.9±0.4	0.16±0.01	0.26±0.04	14.2±1.3	12.7±2.6
6.5	43.1	59.0	1.5±0.2	2.5±0.1	0.11±0.02	0.23±0.05	16.7±6.0	12.8±2.7
9.5	34.2	57.0	1.7±0.3	2.5±0.0	0.12±0.04	0.17±0.05	16.8±2.3	19.0±5.5

Table 3 Morphological characteristics of two *Z. noltii* morphotypes from the Palmones river estuary. Shoot length, leaf width, internode length and root length are expressed in cm. Data represent mean±SD; *n* is given in parentheses. Significant differences between morphotypes ($P<0.05$) are indicated by an asterisk

	Large morphotype	Small morphotype	<i>P</i>
Shoot length	13.2±3.8 (37)	6.8±2.7 (39)	*
Leaf width	0.17±0.04 (114)	0.09±0.02 (94)	*
Leaf FW/DW	4.6±0.5 (10)	5.3±0.7 (10)	*
Internode length	2.1±0.8 (114)	0.6±0.4 (37)	*
Root length	3.0±1.7 (75)	2.6±0.9 (56)	*
Roots per node	3.0±1.9 (24)	1.6±1.3 (73)	*

Table 4 Carbon content (% dry weight) in leaves of two *Z. noltii* morphotypes (large-leaved, *LM*, and small-leaved, *SM*) from the Palmones river estuary. For simplicity, the boxes show the mean value of each level within each factor (morphotype, leaf or leaf fraction) ($n=2, 3$). Different letters within a box indicate significant differences ($P<0.05$) between means

Morphotype	Leaf	Leaf fraction			
		Basal	Central	Apical	
LM 36.8 ^α	Outer	35.8 ^a	35.6 ^x	35.3 ^x	36.7 ^x
	Middle	36.8 ^{ab}	36.4 ^x	36.9 ^x	37.3 ^x
	Inner	37.8 ^b	38.1 ^x	36.9 ^x	38.4 ^x
SM 38.4 ^α	Outer	39.1 ^{ab}	37.9 ^x	40.2 ^x	39.2 ^x
	Middle	41.7 ^a	40.5 ^x	41.4 ^x	43.1 ^x
	Inner	34.5 ^b	36.4 ^x	33.6 ^x	33.4 ^x

Table 5 Nitrogen content (% dry weight) in leaves of two *Z. noltii* morphotypes (large-leaved, *LM*, and small-leaved, *SM*) from the Palmones river estuary. For simplicity, the boxes show the mean value of each level within each factor (morphotype, leaf or leaf fraction) ($n=2, 3$). Different letters within a box indicate significant differences ($P<0.05$) between means

Morphotype	Leaf	Leaf fraction			
		Basal	Central	Apical	
LM 4.25 ^α	Outer	3.5 ^a	3.5 ^x	3.6 ^x	3.4 ^x
	Middle	4.1 ^{ab}	4.6 ^x	3.9 ^x	3.8 ^x
	Inner	5.3 ^b	6.4 ^x	5.1 ^{xy}	4.5 ^y
SM 3.55 ^β	Outer	3.2 ^a	3.2 ^x	3.8 ^y	2.7 ^z
	Middle	4.5 ^b	4.6 ^x	4.6 ^x	4.4 ^x
	Inner	2.9 ^a	3.1 ^x	3.0 ^x	2.8 ^x

these leaves, the highest N content was found in the central fraction. Due to the relative constancy of the C content in the two morphotypes, the C:N atomic ratio was the mirror image of N. The C:N ratios were significantly greater in the SM than in the LM (Table 6). The C:N ratio increased significantly with the leaf age in the LM. However, the SM showed the lowest C:N ratio in the middle leaf. Regarding the leaf fractions, the LM showed the lowest C:N ratio in the base, except for the outer leaves, where no significant differences were observed. The pattern was different in the leaf fractions of the SM. Only the outer leaves showed significant differences in C:N ratios, being highest in the apex.

Table 6 C:N atomic ratio in leaves of two *Z. noltii* morphotypes (large-leaved, *LM*, and small-leaved, *SM*) from the Palmones river estuary. For simplicity, the boxes show the mean value of each level within each factor (morphotype, leaf or leaf fraction) ($n=2, 3$). Different letters within a box indicate significant differences ($P<0.05$) between means

Morphotype	Leaf	Leaf fraction			
		Basal	Central	Apical	
LM 10.4 ^α	Outer	11.9 ^a	11.9 ^x	11.4 ^x	12.5 ^x
	Middle	10.5 ^a	9.4 ^x	11.0 ^y	11.5 ^y
	Inner	8.5 ^b	7.0 ^x	8.5 ^{xy}	10.0 ^y
SM 13.2 ^β	Outer	14.5 ^a	14.0 ^x	12.5 ^x	17.1 ^y
	Middle	10.8 ^b	10.2 ^x	10.6 ^x	11.5 ^x
	Inner	14.4 ^{ab}	13.9 ^x	13.2 ^x	16.0 ^x

Table 7 Total chlorophyll content (mg g DW⁻¹) in leaves of two morphotypes (large-leaved, *LM*, and small-leaved, *SM*) of *Z. noltii* from the Palmones river estuary. Boxes are comparison levels. For simplicity only mean values ($n=3$) are shown. Different letters indicate significant differences

Morphotype	Leaf	Leaf fraction			
		Basal	Central	Apical	
LM 7.5 ^α	Outer	7.4 ^a	4.6 ^x	7.5 ^{xy}	10.2 ^y
	Middle	7.1 ^a	2.9 ^x	5.9 ^{xy}	12.4 ^y
	Inner	8.1 ^a	4.5 ^x	8.9 ^y	10.9 ^y
SM 10.5 ^β	Outer	12.3 ^a	11.1 ^x	10.5 ^x	15.2 ^x
	Middle	10.2 ^a	4.2 ^x	11.8 ^y	14.6 ^y
	Inner	9.2 ^a	6.4 ^x	8.1 ^x	13.0 ^x

Table 8 Chlorophyll *a:b* ratio in leaves of two morphotypes (large-leaved, *LM*, and small-leaved, *SM*) of *Z. noltii* from the Palmones river estuary. Boxes are comparison levels. For simplicity only mean values ($n=3$) are shown. Different letters indicate significant differences

Morphotype	Leaf	Leaf fraction			
		Basal	Central	Apical	
LM 2.2 ^α	Outer	2.2 ^a	2.0 ^x	2.4 ^x	2.2 ^x
	Middle	1.9 ^b	1.7 ^x	2.0 ^x	2.0 ^x
	Inner	2.3 ^{ab}	2.3 ^x	2.4 ^x	2.4 ^x
SM 1.8 ^β	Outer	1.7 ^a	1.5 ^x	2.2 ^x	1.4 ^x
	Middle	2.1 ^a	2.1 ^x	2.0 ^x	2.3 ^x
	Inner	1.8 ^a	1.7 ^x	2.1 ^x	1.4 ^x

The total chlorophyll content was significantly higher in the SM than in the LM (Table 7). However, no differences in chlorophyll levels of the different aged leaves were recorded in either morphotype. Regarding the leaf fractions, the chlorophyll content decreased towards the base of the leaves. This pattern was more evident in the LM (Table 8). The chlorophyll *a:b* ratio displayed similar values in the two morphotypes (Table 8). The LM showed a significantly higher ratio in the internal leaves than in the middle ones. However, the SM displayed a similar chlorophyll *a:b* ratio within leaves. No trend among leaf fractions was found for the two morphotypes.

Table 9 Morphological characteristics, pigment content, photosynthetic parameters (*net* P_{max} : net photosynthetic capacity, R_d : dark respiration rate, α : photosynthetic efficiency and I_c : compensation irradiance) and growth rate of two *Z. noltii* morphotypes from Ria Formosa. Data represent mean \pm SD ($n=3$, excepting for morphology and growth measurements which are shown in parentheses). Significant differences between morphotypes ($P<0.05$) are indicated by an asterisk

	Large morphotype	Small morphotype	<i>P</i>
Morphology			
Shoot length (cm)	11.5 \pm 5.0 (20)	7.0 \pm 5.6 (14)	*
Leaf width (cm)	0.23 \pm 0.04 (20)	0.15 \pm 0.04 (14)	*
Internode length (cm)	1.2 \pm 0.7 (48)	1.6 \pm 0.7 (30)	
Root length (cm)	1.7 \pm 1.2 (24)	2.3 \pm 0.7 (29)	*
Roots per node	1.5 \pm 1.5 (17)	2.8 \pm 1.2 (11)	*
Pigments			
Chlorophyll (mg g DW ⁻¹)	7.1 \pm 0.2	7.9 \pm 0.4	*
Chlorophyll <i>a:b</i> ratio	2.3 \pm 0.1	2.5 \pm 0.0	*
Photosynthesis			
Net P_{max} ($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$)	1.04 \pm 0.64	4.98 \pm 0.78	*
R_d ($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$)	0.22 \pm 0.10	0.16 \pm 0.15	
α ($\mu\text{mol O}_2 \mu\text{mol}^{-1}$)	0.055 \pm 0.037	0.026 \pm 0.018	
I_c ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	5.6 \pm 5.2	5.8 \pm 3.9	
Growth			
Shoot (cm shoot ⁻¹ day ⁻¹)	1.5 \pm 1.1 (17)	2.7 \pm 1.3 (13)	*
Rhizome (mm day ⁻¹)	2.5 \pm 1.4 (17)	4.6 \pm 1.5 (13)	*
Leaf turnover rate (day ⁻¹)	0.04 \pm 0.03 (17)	0.14 \pm 0.03 (13)	*

Ria Formosa

Plant analyses (morphology, chlorophyll content, photosynthesis and growth rates)

Above-ground characteristics of meadows in Ria Formosa differed from those in the Palmones river estuary. Plants growing at deeper sites, especially those occurring on newly settled sandbanks or at the edges of the meadow, showed shorter and narrower leaves as well as longer roots and more roots per node than plants growing in shallow, sheltered zones (Table 9). Although no significant differences were observed in internode length between morphotypes, the rhizome growth of the SM was significantly higher than that of the LM (Table 9). Total chlorophyll, chlorophyll *a:b* ratio, net photosynthetic capacity (P_{max}), shoot growth, rhizome growth and leaf turnover rate were significantly higher in SM, whereas no significant differences were found in other photosynthetic parameters (dark respiration, photosynthetic efficiency and light compensation irradiance; Table 9).

Discussion

Phenotypic plasticity in seagrass meadows is largely related to bathymetric location (light availability, air exposure) (den Hartog 1970), hydrodynamics (Fonseca and Kenworthy 1987), sediment texture and chemical composition (Short 1983). Large leaved morphotypes (LM) have usually been reported in deeper locations than the narrow leaved morphotypes (SM) (den Hartog 1970). It is the case in the Palmones river estuary, a sheltered system, where the LM grows mainly scattered in subtidal or low intertidal places (in the CC) and the SM occurs in the HI sites at high shoot densities. The relatively high water attenuation coef-

ficient (2–6.5 m^{-1} , Vergara et al. 1997) causes a strong decrease in the irradiance reaching the plants in the lower intertidal and subtidal sites. An increase in leaf length (or width) has been pointed out as a morphological adaptation to low irradiances, allowing a position higher up in the canopy (Spence et al. 1973). Another common adaptation to increasing depth is the enhancement of photosynthetic pigments (Falkowski and Raven 1997). On this basis, a higher pigment content would be expected in the LM plants. However, the highest values recorded in the SM could be partly explained on a self-shading basis. The highest shoot densities observed in the SM populations with an estimated leaf area index (LAI) of 3–5 (Pérez-Lloréns and Niell 1993a,c), together with some drifting *Ulva* or *Enteromorpha* mats deposited on the seagrass population at low tide, would result in a strong reduction in the light reaching the plants. As a result, this would affect not only the pigment levels, but also the growth rates of above- and below-ground parts (Philippart 1995; Vermaat and Verhagen 1996). However, clumping in intertidal plants has been suggested as an adaptation to prevent excessive desiccation (Glynn 1965), becoming very important in southern regions where temperature can easily reach extreme values in summer (40°C). The occurrence of dense SM meadows in the HI zone can be explained partly on a physiological basis. *Z. noltii* has the capacity to absorb atmospheric CO_2 during emersion at low tide (Leuschner and Rees 1993). Generally, SM shows greater tolerance to high temperatures than LM (McMillan 1984), as denoted by higher photosynthetic rates and lower compensation points for CO_2 when measured in air (Pérez-Lloréns and Niell 1993b).

In addition to the above-ground features, below-ground architectural differences were also detected. Longer internodes as well as more roots per node were recorded in LM growing in CC in the Palmones river estuary. The higher water flow and the lower sediment N

content in this site could result in a higher rhizome elongation and a greater root development, giving a more efficient anchorage and nutrient uptake from the sediment (Cooper and McRoy 1988; Short 1983). The most developed below-ground parts of LM plants seem to have an anchorage function since above-ground nutrient quota (N and P) in *Z. noltii* growing in Palmones never reached the critical limits for growth (Duarte 1990), nutrient limitation being unlikely (Pérez-Lloréns and Niell 1993a). The highest N content in the LM plants could be expected since they remain in the water for longer periods of time than the SM plants, having more access to the nutrients of the water column. It has been reported that there is a relatively high leaf uptake rates of N compared with roots (Hemminga et al. 1991) when nutrient levels in the water are high, as in the Palmones river estuary.

The leaf nutrient patterns in the LM are similar to those observed in other *Z. noltii* populations (Pérez-Lloréns et al. 1991), as well as in the seagrasses *Z. marina* (Umebayashi and Sasaki 1985; Pedersen and Borum 1992) and *Amphibolis antarctica* (Pedersen et al. 1997; Stapel and Hemminga 1997). A nutrient decrease in outer leaves has been associated with nutrient translocation from non-active growing (old) to active growing (new) leaves, resulting in a decrease in photosynthetic capacity of the oldest leaves (Alcoverro et al. 1998). This mechanism reduces the loss of valuable nutrients by leaf fall and increases the independence of external nutrient sources (Pedersen and Borum 1992; Pedersen et al. 1997). In *Z. noltii* these mechanisms are even more relevant for plant survival than other species because its thin and short-lived rhizomes have a small nutrient storage capacity (Marbà et al. 1996). However, a recent worldwide study of several seagrass species (Stapel and Hemminga 1997) concluded that the quantitative importance of resorption is probably limited, especially if herbivory and leaf detachment are taken into account. Regarding the SM, the low nutrient content of the outer leaves, as compared to the middle ones, could also be explained by a nutrient translocation process. However, the low nutrient content in the inner leaves contrasts with the pattern of the LM. This fact could be explained by a dilution effect due to rapid leaf growth (Stöcker 1980), where resources are utilized faster than they are taken up.

The distribution of both *Z. noltii* morphotypes occurring in Ria Formosa does not exactly match the pattern found in the Palmones river estuary. The former system is much more exposed than the Palmones river estuary and it is frequently subjected to storms. The SM grows mainly at meadow edges or in the recently deposited sandbanks, while the LM generally thrives in well-structured beds in more sheltered places (either in the high or in the low intertidal sites). Physical disturbance is considered one of the principal factors influencing the spatial structure of seagrass beds (Fonseca and Kenworthy 1987). Disturbances cause great mortality, followed by a conspicuous increase in the growth of the few surviving plants (Preen et al. 1995). *Z. noltii* lacks vertical rhizome growth to compensate for the fluctuations in sediment depth, being easily

damaged even by a slight burial. Its fast growth would be important for quick recovery following disturbance (Duarte 1991). The measured growth rates in both morphotypes from Ria Formosa were higher than those reported in other studies from the western Mediterranean meadows. For instance, Marbà et al. (1996) reported values for shoot and rhizome growth rates in *Z. noltii* of 0.9 cm day⁻¹ and 0.8 mm day⁻¹, respectively. Fast rhizome growth is related to a higher shoot recruitment, since new shoots are produced at regular intervals along the rhizome (Tomlinson 1974). From a rough estimation of plastochron interval (calculated from Table 9) SM produce, from each apical rhizome, a new internode every 3.5 days while 5 days are needed for LM. The higher (5-fold) net photosynthetic capacity in SM would contribute to its higher growth rates, allowing a faster regeneration of the meadow and a faster colonization of the substrate in disturbed or bare areas. In fact, Duarte et al. (1997) have reported that mortality caused by burial increased with decreasing seagrass size, whereas the potential to recover from this disastrous situation is enhanced with decreasing seagrass size.

Acknowledgements This work was supported by projects 12/REG II/6/96 from INTERREG II, and AMB96-0782 from the Ministerio Español de Educación y Cultura. The authors wish to thank two anonymous referees who provided valuable comments.

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