Biomass and leaf dynamics of *Cymodocea nodosa* in the Ria Formosa lagoon, South Portugal

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Abstract

We describe shoot density, aboveground and belowground biomass, form and leaf production per shoot over a one-year cycle for *Cymodocea nodosa* meadows in the Ria Formosa lagoon (South Portugal). Habitat conditions in Ria Formosa allow the development of lush meadows (up to 1752 shoots m⁻²), supporting high shoot biomass (up to 945 g DW m⁻²), high leaf productivity (up to 14 g DW m⁻² d⁻¹) and large shoots (up to 113 cm leaf length) despite being located at the northern limit of the distributional range in the Atlantic Ocean. Biomass in the meadows examined is higher than other Atlantic sites with *C. nodosa*, and comparable to the most productive seagrass meadows yet reported. Shoot morphometry and biomass distribution were variable within Ria Formosa, with the stands growing in muddy sediments having a lower ratio of belowground/aboveground biomass than those in sandy sites. *C. nodosa* had a clear unimodal growth cycle, reaching maximum leaf development in summer. Mean leaf length and number of leaves per shoot, the rate of appearance of new leaves and the rate of leaf fall, average leaf growth and leaf turnover rates (P/B) were minimal in February and March, and maximal in July and September. The high production of the meadows examined may be related to the high nutrient availability in Ria Formosa, evidenced by the high leaf nutrient content (3.4% of DW and 0.38% of DW for nitrogen and phosphorus, respectively).

Keywords: *Cymodocea nodosa*; leaf production; Portugal; Ria Formosa; seagrasses.

Introduction

The seagrass *Cymodocea nodosa* (Ucria) Ascherson is widely distributed throughout the Mediterranean Sea and the North-Atlantic coast of Africa, reaching its southern limit in Senegal (den Hartog 1970, Afonso-Carrillo and Gil-Rodríguez 1980, Lüning 1990). Most studies on the

phenology and biomass of the species have been conducted in the Mediterranean Sea (Caye and Meinesz 1985, Peduzzi and Vuković 1990, Buia and Mazella 1991, Terrados and Rós 1992, Pérez et al. 1994, Mostafa 1996, Rismondo et al. 1997, Agostini et al. 2003, Terrados et al. 2006), whereas research on the biomass and growth of the species in the Atlantic coast is limited to observations in North Africa, including those in the Canary Islands (Reyes 1993, Reyes et al. 1995), and Mauritania (Van Lent et al. 1991, Vermaat et al. 1993).

This seagrass forms extensive meadows in Ria Formosa in southern Portugal, which, together with scattered patches along the southwestern Portuguese coast (Alberto personal observations 2004), represents the known northern limit of the species in the Atlantic Ocean. Analysis of the genetic structure of the *Cymodocea nodosa* meadows in Ria Formosa suggested that this population was likely introduced from a single male “founder” clone (Alberto et al. 2001), which may be derived from either the northern Africa or the Mediterranean meadows. A further peculiarity of Ria Formosa as a habitat for *Cymodocea nodosa* is that it is a highly productive, nutrient-rich system [nitrate concentrations up to 8.8 µM, phosphates up to 5.6 µM and ammonium concentrations up to 108 µM (Falcão and Vale 1990)], whereas all other Atlantic meadows investigated grow in oligotrophic or mesotrophic environments (Wolff et al. 1993, Pérez et al. 1994). The growth of *Cymodocea nodosa* is often nutrient-limited (Pérez et al. 1994), so growth and production in Ria Formosa may be particularly high.

Here we describe density, biomass, form and leaf production per shoot over a one-year cycle of *Cymodocea nodosa* meadows in the Ria Formosa lagoon (southern Portugal). We first describe plant form, biomass, both aboveground and belowground, and shoot density at the time of maximal biomass in summer, and then examine leaf growth and leaf dynamics over one year to estimate the annual leaf production per shoot of sites of contrasting sediment conditions in Ria Formosa.

Materials and methods

Study site

The Ria Formosa is a multi-inlet, barrier island system located in southern Portugal (37°10' N, 8°03' W, and 36°57' N, 7°31' W). Its present configuration consists of two peninsulas and five islands that extend over 50 km (Pilkey et al. 1989). Connection between the ocean and the back barrier area is made through six tidal inlets. According to Andrade 1990, the total area of this system is 1.7×10⁷ m², with the back barrier area consisting mainly of salt marsh and small sandy islands making up a

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complicated pattern of tidal channels and creeks. The saltmarsh species *Sarcocornia perennis*, *Spartina maritima*, and the seagrass *Zostera noltii* dominate the intertidal zone, while the seagrass *Cymodocea nodosa* dominates the subtidal zone with scattered patches of *Zostera marina* (Cunha and Duarte 2005). No meadows were observed in the intertidal zone, suggesting that *Cymodocea nodosa* cannot tolerate emersion.

Although the main navigation channel, the Faro channel, can reach 30 m in depth, the average depth of the lagoon is 2 m below mean sea level (msl) (Andrade 1990).

Fresh water input into the lagoon is low, and salinity remains close to 36 psu except during sporadic and short periods of winter run-off (Falcão and Vale 1990). Water temperature ranges annually from 12 to 26°C, and dissolved oxygen in the water column remains close to or above saturation levels (Falcão and Vale 1990). Tides in the area are semi-diurnal, average ranges are 2.8 m for spring tides and 1.3 m during neap tides; however, maximum ranges of 3.5 m can be reached. This pattern causes important semi-diurnal and fortnightly tidal fluctuations of water volume inside the system (Falcão and Vale 1990).

Morphometry, biomass, density and leaf nutrient content

Shoots and rhizomes of *Cymodocea nodosa* were collected during spring tides of August 1993 in stations S1, S2, MS3, M4, M5 (Table 1). We extracted six to nine 20 cm diameter cores from each site to a depth about 40 cm in the sediment (to include all living rhizomes). Cores were taken about 50 cm from one another. We counted all shoots of the rhizome pieces in the sample, counted and measured the lengths and widths of all entire leaves of each shoot and the sheaths, and counted and measured the length of the entire root. Leaf and root lengths reported are the sum of all leaves and roots, respectively. Leaves plus sheaths account for above-ground biomass. Leaves and sheaths, horizontal and vertical rhizomes, and roots were dried for 24 h at 70°C and weighed for total shoot biomass estimates.

Leaf nutrient contents were determined in duplicate sub-samples collected near station MS3 (August 1993). Nitrogen concentrations in leaves were determined using a Carlo-Erba (Milan, Italy) CHN analyzer, and tissue P concentrations were determined by colorimetry in dupli-

cate sub-samples after wet acid digestion (Koroleff 1983).

Leaf dynamics

Following a preliminary survey, we selected five *Cymodocea nodosa* meadows around the lagoon for leaf dynamics assessment. The criteria used for meadow selection was based on the choice of sites that would be representative of a range of substratum present in Ria Formosa, from mud to sand, S2, MS3, M4, M6, M7 (Table 1). All sampling sites were partially emergent during low-water tide periods allowing sampling without SCUBA.

Leaf growth was followed for 13 months (August 1993–September 1994). In each meadow, 20 shoots were marked by perforating all the leaves just above the bundle sheath with a pin (Zieman 1974); they were marked with a plastic strip attached to the shoot. The marked shoots were collected every 30 days. Shoot parameters such as total leaf length (the sum of the length of all leaves), total number of leaves, and new leaves per shoot were measured for each shoot. Leaf epiphytes were removed with a scalpel, and leaves were dried for 24 h at 70°C, and weighed.

Leaf growth ($\text{cm shoot}^{-1} \text{d}^{-1}$) was estimated by adding the growth in length of each shoot's leaves, and dividing by the number of days of growth. Shoot leaf production ($\text{g DW shoot}^{-1} \text{d}^{-1}$) was estimated from the amount of biomass that was produced by the leaves during the marking period, divided by the number of days of growth. We estimated the average turnover rate (P/B) by calculating the ratio between average shoot production and its total biomass, and dividing by the number of days of growth. New leaf appearance rate ($\text{leaves shoot}^{-1} \text{d}^{-1}$) was estimated for each marked period by:

$$\begin{aligned} \text{New leaf appearance rate} \\ = \text{no. of new leaves} / (\text{no. of marked shoots} \\ \times \text{days of growth}) \end{aligned}$$

The plastochrone interval (days) for each marking period (i.e., number of days between new and consecutive leaf appearance) was estimated as the inverse of the rate of new leaf appearance.

The rate of leaf loss ($\text{leaves shoot}^{-1} \text{d}^{-1}$) between two sampling events was estimated by:

$$\begin{aligned} \text{Leaf loss} = [(\text{no. of leaves}_{t_0} \\ + \text{no. of new leaves}) - \text{no. of leaves}_{t_0+t}] / t \end{aligned}$$

Table 1 *Cymodocea nodosa*: stations sampled in Ria Formosa; sediment and sampling type.

	Sediment type	Sampled for biomass	Sampled for leaf dynamics
S1	Sand	x	
S2	Sand	x	x
MS3	Mixed	x	x
M4	Mud	x	x
M5	Mud	x	
M6	Mud		x
M7	Mud		x

Biomass was sampled during August 1993, and leaf dynamics from August 1993 to August 1994.

Results

Morphometric data, biomass and leaf nutrient content at a peak season

The meadows were dense (up to 1752 shoots m^{-2} ; Table 2) and supported high total shoot biomass (up to 945 g DW m^{-2} ; Figure 1). The shoots had numerous short roots, and their combined biomass with the high rhizome biomass resulted in a high belowground biomass that exceeded the aboveground biomass for meadows grow-

Table 2 *Cymodocea nodosa*: leaf, sheath and root morphometry during peak season (August) for meadows S1, S2, MS3, M4, M5, and leaf nutrient content for MS3, in Ria Formosa.

	S1	S2	MS3	M4	M5
Leaves (shoot ⁻¹)	3.1±0.1	2.6±0.1	2.5±0.1	2.7±0.1	2.7±0.1
Total leaf length (cm shoot ⁻¹)	57.5±2.0	113±5.8	66.2±3.0	68.0±3.5	62.5±3.5
Leaf width (mm)	53±2	45±1	45±1	47±1.5	43±0.9
Leaf area index (m ² m ⁻²)	3.0	5.5	2.5	4.1	3.2
Sheath length (cm)	10.3±0.2	9.7±0.2	9.0±0.3	12.2±0.4	11.6±0.4
Shoot density (m ⁻²)	1005±96	1162±137	950±190	1752±468	1311±191
No. roots (shoot ⁻¹)	6.3±1.0	3.6±0.8	5.0±0.5	4.9±0.6	4.8±0.5
Total root length (cm shoot ⁻¹)	11.5±0.5	11.8±0.5	12.7±0.9	10.8±0.6	12.0±0.7
Ratio belowground/aboveground	1.9±0.1	2.2±0.1	4.2±0.4	1.1±0.1	0.8±0.1
Leaf nitrogen content (% DW)			3.4		
Leaf phosphorus content (% DW)			0.38		

Means±SE are reported (number of shoots examined per meadow=200). Site codes in Table 1.

ing in sand (S1 and S2) and mixed sediment (MS3). In meadows growing on mud (M4 and M5), the ratio of belowground/aboveground biomass was close to 1.0 (Figure 1). There was, however, considerable variation in shoot morphometry and biomass distribution within sites. Number of leaves per shoot varied from 2.5 in the mixed sediment site (MS3) to 3.1 in the sandy site (S2). The shoots had long leaves, with a total leaf length per shoot ranging from 57 cm to over 1 m in the sandy site. Leaf width varied from 43 mm in the muddy site to 53 mm in the sandy site. Leaf area index ranged from 2.5 to 5.5 m² m⁻² and sheath length from 9.0 to 12.2 cm (Table 2). Leaf nutrient content was measured for only the mixed sediment site and was 3.4% and 0.38% of DW for nitrogen and phosphorus, respectively.

Leaf dynamics

The meadows displayed a clear unimodal growth pattern, reaching maximum leaf development in summer, reflecting the high variation in water temperature, which during the period of study ranged from 5°C in winter to 28.5°C in summer. Mean leaf length per shoot varied from a minimum of 22.5 cm during March to 113 cm in July (Figure 2). The mean rate of new leaf appearance rate was low from December to March (0.008 leaves shoot⁻¹ d⁻¹) and high in July with a rate of 0.10 leaves per shoot per day (Figure 3). The average rate of leaf loss followed a similar pattern (Figure 3), with a minimum that varied between 0 to 0.02 leaves shoot⁻¹ d⁻¹ from December to March, and

a maximum ranging from 0.05 to 0.10 leaves shoot⁻¹ d⁻¹ during June and July.

Leaf production varied between 0.5 mg DW shoot⁻¹ d⁻¹ in spring, and 8.3 mg DW shoot⁻¹ d⁻¹ in summer (Figure 2). Leaf turnover rate (P/B) varied between 0.009 d⁻¹ in winter and 0.034 d⁻¹ in summer (Figure 2). The number of leaves produced per shoot in one year was 14 for the stand at M4 station (the only station that we were able to follow for 13 months), calculated directly through the leaf marking method. This implies that the plastochrone interval was 26 days for this meadow.

Discussion

The *Cymodocea nodosa* population described in this study, growing at the northern limit of the distributional range in the Atlantic Ocean, has comparable and sometimes higher growth rates than stands in locations to the south and east. Leaf area index (LAI) during peak season growth was comparable to those generally found in the Mediterranean Sea (3.9 m² m⁻², Caye and Meinesz 1985; 4.0 m² m⁻², Pérez 1989; 1.8 m² m⁻², Terrados and Rós 1992) and the Canary Islands (3.9 m² m⁻², Reyes 1993), but lower than in plants in the Bay of Piran (7.2 m² m⁻², Peduzzi and Vuković 1990) and in the lagoon of Venice (8.2 m² m⁻², Rismondo et al. 1997). Although shoot density is somewhat lower than those found in other sites (2060 shoot m⁻², Caye and Meinesz 1985; 2000 shoot m⁻², Pérez 1989; 1900 shoot m⁻², Terrados and Rós 1992; 1928 shoot m⁻², Reyes 1993; 2302 shoots m⁻², Rismondo et al. 1997; 1520 shoots m⁻², Agostini et al. 2003), with the exception of plants growing in Montazah Bay (404 shoots m⁻², Mostafa 1996) and Banc d'Arguin (576 shoots m⁻², Van Lent et al. 1991), the shoots in Ria Formosa occur at higher biomass than those generally observed in the Mediterranean Sea, Mar Menor (170 g DW m⁻², Terrados and Rós 1992), Alfaques Bay (785 g DW m⁻², Pérez et al. 1994), Montazah Bay (287 g DW m⁻², Mostafa 1996), as well as those from the few Atlantic meadows on the North African coast that have been studied, viz. Canary Islands (592 g DW m⁻², Reyes 1993), Banc d'Arguin (391 g DW m⁻², Vermaat et al. 1993). However, biomass results are comparable to the growth observed in the Bay of Piran (1020 g DW m⁻², Peduzzi and Vuković 1990), lagoon of Venice (1710 g DW m⁻²,

Figure 1 *Cymodocea nodosa*: mean total shoot (leaves and sheath, rhizomes and roots) biomass during peak season (August) at five sites (S1, S2, MS3, M4, M5) in Ria Formosa.

Figure 2 *Cymodocea nodosa*: total mean leaf length (cm) (+SE), rate of mean leaf production (g DW shoot⁻¹ d⁻¹) (+SE) and mean leaf turnover rate (P/B; +SE) through the year for the five sites sampled (S2, MS3, M4, M6 and M7).

Rismondo et al. 1997) and the lagoon of Urbino (1090 g DW m⁻², Agostini et al. 2003). *Cymodocea nodosa* biomass is dependent on the nutrient status of the meadow (Pérez et al. 1994), suggesting that the eutrophic nature of Ria Formosa lagoon is a determining factor for the large *Cymodocea nodosa* shoots there. Indeed, *C. nodosa* leaf nutrient concentrations in Ria Formosa are the highest yet reported for this species (Duarte 1990). The high values of biomass and production found for the Bay of Piran in the Gulf of Trieste (Peduzzi and Vuković 1990), lagoon of Venice (Rismondo et al. 1997) and for the

lagoon of Urbino (Agostini et al. 2003) might also be related to nutrient availability in these lagoons. Indeed, Diaz and Rosenberg (1995) describe the Gulf of Trieste as being an eutrophic region, and Bianchi et al. (2004) found a high concentration of nitrates and ammonium in the lagoon of Venice. There are no published nutrient records for the lagoon of Urbino.

There was, however, considerable variation in shoot morphometry and biomass distribution within Ria Formosa, with the stands growing in muddy sediments having a lower ratio of belowground/aboveground biomass

Figure 3 *Cymodocea nodosa*: rates of new leaf production and loss (leaf fall and leaf appearance) for five sites (S2, MS3, M4, M6 and M7).

than those in sandy sites. These findings are similar to observations by Terrados and Rós (1992) in the Mar Menor and Reyes (1993) in the Canary Islands.

Leaf production estimates during peak season (up to 14 g DW m⁻² d⁻¹) was substantially greater for Ria Formosa than those estimated for the Mediterranean regions of Bay of Piran (2.8 g DW m⁻² d⁻¹, Peduzzi and Vuković 1990) and for the Mar Menor (1.5 g DW m⁻² d⁻¹, Terrados and Rós 1992), but are quite close to the leaf production observed in the lagoon of Venice (12.3 g DW m⁻² d⁻¹, Rismondo et al. 1997) and the Urbino lagoon (17.5 g DW m⁻² d⁻¹, Agostini et al. 2003). The extent of annual variability in leaf size, growth, production and appearance and loss rates in the *Cymodocea nodosa* meadows studied was high, as observed for other temperate *C. nodosa* meadows, exceeding that for the Mar Menor meadows (0.5–0.8 mg DW shoot⁻¹ day⁻¹ for May–July; Terrados and Rós 1992) and subtropical meadows in the Canary Islands (Reyes et al. 1995). Leaf growth was highest from June to July, and leaf productivity per shoot per day peaked during July and August,

whereas these parameters were minimal during February. Reyes et al. (1995) found a similar leaf growth pattern in the Canary Islands, although the minimum values in Ria Formosa are delayed by two months in relation to the Canary Islands. The period of minimal and maximal leaf number found for meadows in Ria Formosa is also delayed by one to two months in relation to that in the Canary Islands. The high seasonality of *C. nodosa* in Ria Formosa is likely related to the very broad temperature range recorded there (23°C). Although the range of values differed, the rate of leaf appearance is similar in temporal patterns to those observed in Mediterranean meadows (Terrados and Rós 1992, Pérez et al. 1994) and on the Canary Islands (Reyes et al. 1995). As observed by these authors, the maximal and minimal rates of leaf appearance and leaf fall coincide in time, which reflects the higher rates of leaf renovation in spring and summer (May–July). The rate of leaf loss observed by Reyes et al. (1995) in the Canary Islands was minimal in February (0.012 leaf shoot⁻¹ d⁻¹) and maximal (0.049–0.057 shoot⁻¹ d⁻¹) in May and July, one month earlier than in Ria

Formosa. Leaf turnover rates are in the same range as those found for Mar Menor (0.004–0.028, Terrados 1992), but the maximum turnover rate for *C. nodosa* populations in Ria Formosa (0.034, this study) is the highest reported to date (0.003–0.018 in Delta del Ebro, Pérez 1989; and 0.012–0.018 in the Canary Islands, Reyes 1993).

The number of leaves produced in one year is close to estimates using the reconstruction methods for the same population in Ria Formosa (Cunha and Duarte 2005) and for other locations (11 leaves shoot⁻¹ y⁻¹, Caye and Meinesz 1985; 13 leaves shoot⁻¹ y⁻¹, Pérez 1989; 10 leaves shoot⁻¹ y⁻¹, Peduzzi and Vuković 1990; 11–12 leaves shoot⁻¹ y⁻¹, Terrados 1991, Terrados and Rós 1992; 13 leaves shoot⁻¹ y⁻¹, Reyes 1993) and confirm that the annual number of leaves produced by *Cymodocea nodosa* shoots is relatively constant. In summary, the results reported here indicate that habitat conditions in the Ria Formosa lagoon allow the development of lush meadows supporting highly productive and large shoots, despite being located at the northern limit of the distributional range in the Atlantic Ocean. Production of the meadows examined is comparable to the most productive seagrass meadows yet reported (Duarte and Chiscano 1999).

The factors limiting the distribution of *Cymodocea nodosa* in the Atlantic Ocean are unlikely to be determined by poor growth conditions or low temperatures. *C. nodosa* meadows in Ria Formosa appear to derive from a single (male) clone (Alberto et al. 2001), implying that sexual reproduction is limited in Ria Formosa. The limit of distribution of the plant in the Atlantic Ocean may be imposed by perturbations to the reproductive system, or other bottlenecks in the plant's life cycle, or to disturbance. The origin of this population (from Mediterranean, African or Macronesian stocks) is now being addressed (Alberto unpublished data).

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