

Carbon and nutrient deposition in a Mediterranean seagrass (*Posidonia oceanica*) meadow

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Abstract

The annual depositional flux of carbon (C), nitrogen (N), and phosphorous (P) to the sediments under a northeast Spain *Posidonia oceanica* meadow was evaluated, and the sources and fate of the material deposited elucidated. The annual deposition of carbon represented $198 \text{ g C m}^{-2} \text{ yr}^{-1}$, 72% of which was derived from the seston and 28% from *P. oceanica* detritus. The depositional flux was poor in nitrogen ($13.4 \text{ g N m}^{-2} \text{ yr}^{-1}$) and phosphorous ($2.01 \text{ g P m}^{-2} \text{ yr}^{-1}$), although comparable to the nutrient inputs required to support the growth of *P. oceanica*. Remineralization in the sediment only returned $15.6 \text{ g C m}^{-2} \text{ yr}^{-1}$, yielding a net carbon accumulation of $182 \text{ g C m}^{-2} \text{ yr}^{-1}$. Our results show that in the Mediterranean littoral *P. oceanica* meadows are important sites of net organic carbon burial, derived from sedimented sestonic particles and seagrass detritus.

Seagrass meadows tend to produce an excess of organic carbon over community requirements (Gattuso et al. 1998) and are believed to store an important fraction of the excess carbon they produce in the sediments (Duarte and Cebrián 1996). The deposition of organic carbon within seagrass meadows should be further enhanced through the effect of seagrass canopies on water flow and the trapping of sestonic particles (Short and Short 1984; Gacia et al. 1999). The deposition of organic matter within seagrass meadows must also be associated to a significant input of nutrients, which may play an important role in their nutrient budget. Seagrass growth is often nutrient limited in oligotrophic waters (Fourqurean et al. 1992; Alcoverro et al. 1997a), where seagrasses must satisfy their nutrient requirements largely through root uptake (Dennison et al. 1987). Nutrient inputs must be at least sufficient to compensate for nutrients lost with exported material, which represents, on average, about 30% of their net primary production (Romero et al. 1992; Pergent et al. 1997). The nutrient inputs associated to particle deposition within seagrass meadows are, however, yet to be evaluated.

The deposition of organic matter is likely to be particularly important within the meadows of the Mediterranean species *P. oceanica*, which develops communities with par-

ticularly high biomass (Duarte and Chiscano 1999) and the tissues of which decompose very slowly (Romero et al. 1992; Mateo and Romero 1997). Indeed, the enrichment of *P. oceanica* canopies in sestonic particles (Duarte et al. 1999) has been shown to be associated to an increase in deposition against the background of low sedimentation rate in undisturbed Mediterranean waters (Gacia and Duarte 2001). Moreover, the deposited materials are likely to be retained in the sediment because *P. oceanica* canopies significantly reduce resuspension (Gacia and Duarte 2001). The nutrient inputs associated to particle deposition may play an important role in the northwest Mediterranean *P. oceanica* meadows, which growth has been reported to be nutrient limited (Alcoverro et al. 1997a).

We here quantify the net annual sedimentary flux of carbon and nutrients (N and P) to the sediments under a *P. oceanica* meadow and elucidate the sources and fate of the material deposited. We do so using data derived from an annual monitoring of particulate organic carbon, nitrogen, and phosphorous deposition within a northeast Spanish *P. oceanica* meadow and use microscopic examinations of the settling material together with analyses of the stable carbon isotopic composition of the materials to identify the nature and sources of the deposition. We use this information to assess the relative importance of materials produced by *P. oceanica* and associated epiphytes versus sestonic particles in the sedimentary organic matter. The results derived here are combined with indicative estimates of organic matter mineralization in the sediments to yield an understanding of carbon and nutrient retention within *P. oceanica* sediments. Finally we evaluate the importance of the depositional nutrient input relative to the estimated N and P demands for *P. oceanica* growth.

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Methods

The study was conducted in a 15-m depth *P. oceanica* meadow at Fanals point (40°41'N, 2°52'E; northeast Spain), an exposed coastline occasionally supporting substantial wave action and along shore currents. Near-bottom velocities range from 2 to 10 cm s⁻¹ under moderate wind conditions (average of 7.92 ± 3.15 cm s⁻¹ during the study period, Granata unpubl. data), and the dominant forcing is provided by wind and swell waves with periods from 3 to 15 s (Granata et al. unpubl. data). Water temperature, chlorophyll *a* concentration, planktonic metabolism, and the δ¹³C isotopic signal of the seston were obtained from a weekly monitoring conducted in the area (Duarte et al. 1998; Duarte unpubl. data).

Particle deposition was measured at monthly intervals from May 1997 until June 1998 using sediment traps (cf. Gacia and Duarte 2001). The total depositional flux was measured by sediment traps consisting of 20.5-ml cylindrical glass centrifuge tubes with a height versus diameter ratio of 5, positioned at 20 cm above the bottom, thereby remaining within the seagrass canopy. The tubes were attached by groups of 5, about 4 cm apart from each other, to 30-cm long horizontal stainless rods. Previous studies showed that the variance between units mounted on the same frame was not significantly different to that between units mounted on different frames (ANOVA, *p* > 0.5). Thus, all sedimentation tubes were used as replicate units, whether mounted in the same or different frames, to estimate particle flux. Sediment traps of the same size were also fixed in groups of five to a central 1.5-m tall vertical pole, at heights of 20, 40, 60, 80, and 100 cm above the bottom to partition between primary (or net) versus resuspended deposition inside the meadow.

The resuspended load declines exponentially with increasing height above the sediment source and can, therefore, be estimated as the intercepts at the sediment surface (i.e., height = 0) of the fitted exponential relationships between the downward depositional flux and the height of the sediment traps above the bottom (Pejrup et al. 1996). Three replicated sediment trap arrays (five units each) for the estimation of total deposition at 20 cm height (i.e., a total of 15 replicated sedimentation tubes) and one structure with five units of five sediment traps each, positioned at 20, 40, 60, 80, and 100 cm above the bottom, were assembled by self-contained underwater breathing apparatus (SCUBA) divers inside the meadow. Traps were deployed at monthly intervals for a period ranging between 3 and 10 d (see Gacia and Duarte 2001 for further details).

Sediments were sampled in August and November 1997 and in June 1998 using a 20-cm diameter corer. The sampling dates were chosen to encompass the seasonality in litter stocks observed in sediments from nearby *P. oceanica* meadows (Romero et al. 1992), where maximum litter accumulation was found in early winter and minimum in late spring. Three replicate cores, containing the top 5 cm of sediment, were collected from inside the meadow as well as from an adjacent (about 5 m apart) unvegetated area. Above-ground plant material including epiphytes was also collected in September and December 1997.

At the laboratory, the contents of the sediment traps were collected onto precombusted 25-mm GF/F filters for measurements of the dry weight, ash free dry weight, particulate organic carbon, nitrogen, and phosphorous, as well as the isotopic composition of the organic carbon of the sedimenting particles. A sample of the material collected in the sediment traps placed at 20 cm above the bottom was preserved with formaline for the microscopic examination of the particles. Three replicated subsamples of every sediment corer were used to conduct similar analyses for the sediment material except for the nutrient content. Plant samples, including the epiphytes, were ground to powder in an agate mortar, and subsamples were analyzed for particulate organic carbon. The isotopic composition of the organic carbon was analyzed for both seagrass and epiphyte mixed material, but also after separating seagrass tissue from the epiphytic community.

The dry weight of the material was measured after desiccation to constant weight (within 24 h) at 60°C in a drying oven. The ash free dry weight of the material was determined following combustion for 4 h at 450°C. The organic carbon content of plant, including the epiphytic community; trap; and sediment materials was determined on dried subsamples using a Carlo Erba CHN analyzer following treatment of the samples with HCl fumes to remove carbonates. Total nitrogen was measured on the particles collected on precombusted filters using a Carlo Erba CHN analyzer. Total phosphorous in the particles collected on acid-washed filters was determined after wet digestion in acidic persulfate at 120°C for 30 min following Koroleff (1976). The stable isotope composition of organic carbon in sediment trap material, sediment, plant tissue after scraping epiphytes, the epiphytes, and seston were determined using a Fisons elemental analyzer coupled online (via continuous flow interface) with a Finnigan Delta S mass spectrometer, after the removal of carbonates with HCl. Results of carbon isotope analysis are reported in the δ notation relative to the Vienna-PDB (Pee Dee Belemnite) standard. Reproducibility of the analysis was determined, based on replicate measurements, to be better than 0.1‰.

The seasonal variation of the carbon isotopic signal of the seagrass-epiphyte assemblage was derived from the product of the fractional leaf and epiphyte biomass (L_{bm} and E_{bm} , from Gacia and Duarte 2001 and Alcoverro et al. 1997b, respectively) and the isotopic signal for each of these components ($\delta^{13}\text{C}_L$ and $\delta^{13}\text{C}_E$, respectively) using the equation,

$$(L_{\text{bm}} \cdot \delta^{13}\text{C}_L) + (E_{\text{bm}} \cdot \delta^{13}\text{C}_E) = \delta^{13}\text{C}_{\text{LE}}$$

We described the seasonal variability in the relative abundance of different types of material (seagrass particles, inorganic particles, phytoplankton, filamentous algae, benthic diatoms, foraminiferans, zooplankton, and detritus of different sizes) using microscopic examination. Samples of settling material were examined, after being sonicated at low frequency for 15 min to disperse the particles, under transmitted light, on a Zeiss Axiovert 25 inverted microscope at 100 and 200 magnifications, depending on particle size. We assessed the relative abundance of the different particle types and measured the size of *P. oceanica* detritus (as projected area, in μm²) from the length of the main axes of the *P.*

oceanica fragments, determined using a micrometer fitted onto the eyepiece of the microscope. Other organic detritus was classified into three size classes (<20 μm , between 20 and 50 μm , and >50 μm). We determined particle abundance and size in duplicate subsamples by counting all particles in 20 fields of each subsample.

Long-term dissolved inorganic carbon (DIC) evolution rates in sediment subsamples encapsulated at the laboratory were used to quantify remineralization rates of the organic material present in the sediment, both under the canopy and on bare sand. Approximately 125 ml of sediment obtained after mixing the contents of the 5-cm corers from each of the vegetated and bare sites were diluted with 40 ml of filtered seawater in headspace vials previously flushed with N_2 to ensure an initial CO_2 -free atmosphere. This resulted in a slurry that was incubated at the laboratory in the dark at the ambient seawater temperature and assayed at time intervals of $t = 1, 30,$ and 60 d, encompassing the time scale of decay of *P. oceanica* detritus (Romero et al. 1992). These long incubations were necessary to have sufficient accuracy for these low activity samples. Moreover, Dauwe et al. (2001) observed linear total inorganic carbon production over more than 40 d. At each time interval, four replicate vials were opened and the pH and the alkalinity of the water were analyzed to estimate DIC concentrations and, from the slope of the time series of concentrations, the rate of DIC production. Mineralization rates based on slurry incubations may deviate from in situ rates because slicing and homogenization of the sediment horizons may disturb microgradients of nutrients and enlarge the solid-liquid ratio so that microorganisms have easier access to organic matter (Aller and Aller 1998). However, studies of the effects of slurry incubations on bacterial production rates are not equivocal (Burdige 1989). The presence of mineral surfaces may stimulate rates of incorporation of organic substrates, even by one order of magnitude in slurries (Meyer-Reil 1986), or inhibit incorporation rates compared to undisturbed sediments (Dobbs et al. 1989), depending on the substrate, mineral, and organisms involved.

The net aboveground production of the *P. oceanica* at Fanals meadow was estimated from local shoot densities (Gacia and Duarte 2001) and a regression between net aboveground production and shoot density fitted for *P. oceanica* in the region [net aboveground production ($\text{g C m}^{-2} \text{ yr}^{-1}$) = $23.16 + 0.377$ shoot density (shoots m^{-2}); $r^2 = 0.79$] from data in Alcoverro et al. (1995). The seasonal nitrogen and phosphorous requirements for *P. oceanica* growth in Fanals were estimated from measurements of shoot density and individual shoot biomass conducted at each sampling event (Gacia and Duarte 2001) using regression equations between shoot biomass and nutrient requirements [N requirements ($\text{mg N shoot}^{-1} \text{ d}^{-1}$) = $0.026 + 0.108$ shoot biomass (mg DW shoot^{-1}), P requirements ($\text{mg P shoot}^{-1} \text{ d}^{-1}$) = $0.0012 + 0.0153$ shoot biomass (mg DW shoot^{-1}), $r^2 = 0.660$ and 0.885 , respectively] developed from direct measurements in five nearby *P. oceanica* meadows (Alcoverro et al. 1997a). The external nitrogen and phosphorous demands for growth were calculated as the differences between the nutrient-sufficient requirements and the average nutrient translocation, derived from estimates for

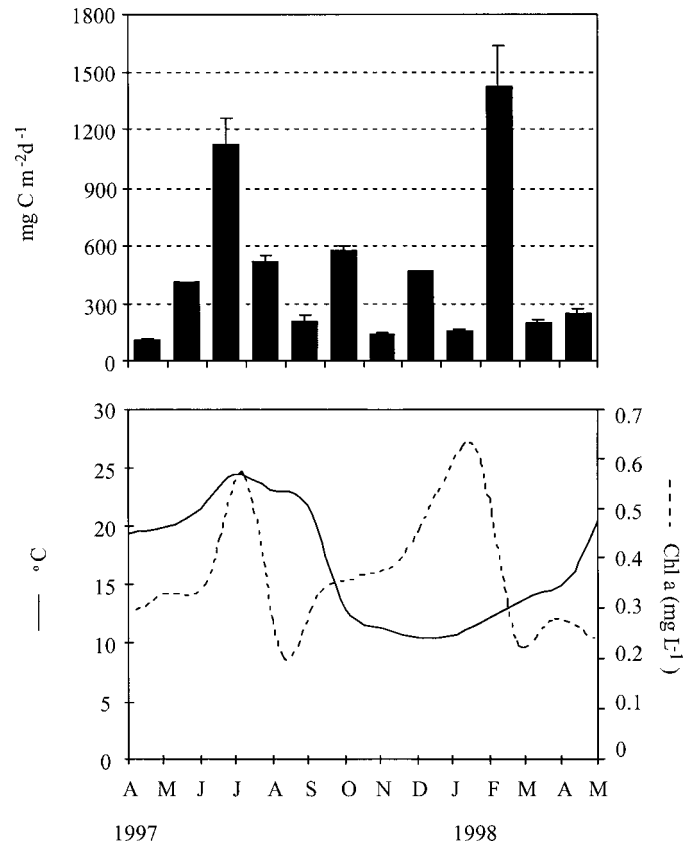


Fig. 1. Temporal variation in primary organic carbon deposition, chlorophyll *a* concentration, and surface seawater temperature at Fanals point from May 1997 to June 1998.

five nearby *P. oceanica* meadows (data from Alcoverro et al. 1997a).

Results

The primary (i.e., net) depositional flux of organic carbon inside the *P. oceanica* meadow at Fanals point varied over an order of magnitude, from a minimum of $110 \text{ mg C m}^{-2} \text{ d}^{-1}$ in May 1997 to a maximum of $1750 \text{ mg C m}^{-2} \text{ d}^{-1}$ in March of 1998 and paralleled the changes in chlorophyll *a* concentration in the water column (Fig. 1). The fraction of the settling material composed of organic matter (Fig. 2) was, in most cases, similar to that of the sestonic particles (25.6%, recalculated from data in Duarte et al. 1998), during phytoplankton blooms, with samples comprising a large percentage of *P. oceanica* fragments having higher organic contents.

The nutrient input associated to primary deposition (Fig. 3) varied tenfold for nitrogen (13 to $110 \text{ mg N m}^{-2} \text{ d}^{-1}$) and more than two orders of magnitude for phosphorous (0.1 to $17 \text{ mg P m}^{-2} \text{ d}^{-1}$). The calculated demands for *P. oceanica* growth in the area ranged between 17 to $45 \text{ g N m}^{-2} \text{ d}^{-1}$ and 1 to $9 \text{ g P m}^{-2} \text{ d}^{-1}$ (Table 1). The difference between the depositional nutrient inputs and the calculated seagrass demands showed a strong seasonality, characterized by excess nutrient demands relative to nutrient inputs from late

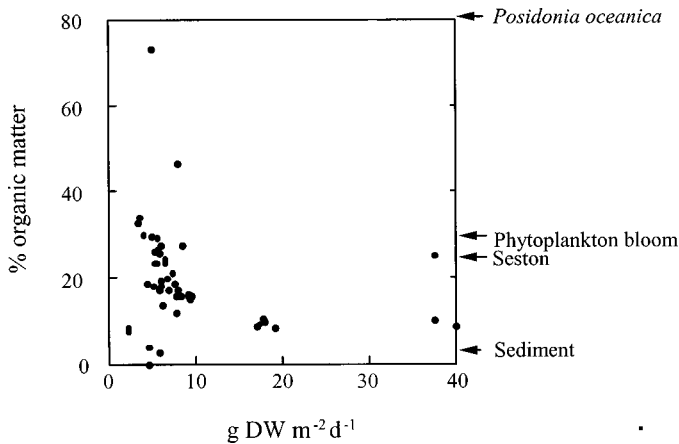


Fig. 2. The relationship between the percent organic matter in the settling material and the primary deposition at Fanals point. Arrows indicate reference average values for the seagrass, phytoplankton, seston, and sediment from the area.

spring to summer, the period of highest seagrass demands, and excess nutrient inputs relative to demands from late summer to the end of winter (Table 1).

The average annual organic C/N atomic ratio of the deposited material was 15 ± 1.3 , ranging from a minimum of seven to a maximum of 23 (Fig. 4). The C/P atomic ratio of the deposited material ranged from 78 in January 1996 to $>2,000$ in June 1997 and averaged 295 ± 63.8 . The C/N ratio of the depositional flux was high in the summer and low in the fall (Fig. 4), while the C/P ratio was also low in the fall and winter but varied significantly during the spring and summer (Fig. 5), thus suggesting variable nutrient sources in the area.

The abundance of the different sedimentary particles paralleled changes in the bulk depositional flux (Figs. 1 and 5). The flux was dominated by inorganic particles, but phytoplankton and benthic and filamentous cells were also im-

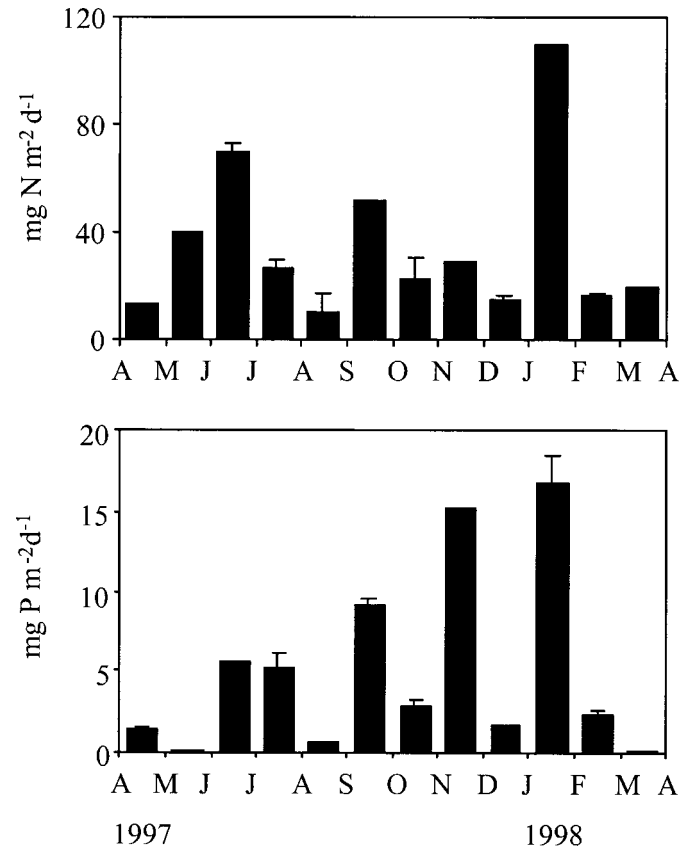


Fig. 3. Temporal variation in primary sedimentary nitrogen (upper panel) and phosphorous (lower panel) inputs to the *P. oceanica* meadow at Fanals point.

portant components. *P. oceanica* fragments were relatively infrequent but were large ($230 \pm 138 \mu\text{m}^2$). Foraminifers and fragments of zooplankton organisms were observed occasionally (Fig. 5). The isotopic composition of the organic

Table 1. Temporal variation in nitrogen and phosphorous input, nutrient demand, nutrient retranslocation and net requirements (after Alcoverro 1997a) for *Posidonia oceanica* growth at Fanals Point.

| Month | N input (mg N m ⁻² d ⁻¹) | N demand (mg N m ⁻² d ⁻¹) | N retrans- location (mg N m ⁻² d ⁻¹) | N require- ments (mg N m ⁻² d ⁻¹) | P input (mg P m ⁻² d ⁻¹) | P demand (mg P m ⁻² d ⁻¹) | P retrans- location (mg P m ⁻² d ⁻¹) | P require- ments (mg P m ⁻² d ⁻¹) |
|----------------------------------------------------|-------------------------------------------------------|--------------------------------------------------------|----------------------------------------------------------------------|-------------------------------------------------------------------|-------------------------------------------------------|--------------------------------------------------------|----------------------------------------------------------------------|-------------------------------------------------------------------|
| May | 13.1 | 50 | 0 | 50 | 1.38±0.19 | 6 | 0 | 6 |
| Jun | 40±0.23 | 64 | 0 | 64 | 0.09±0.01 | 8 | 0 | 8 |
| Jul | 69.5 | 75 | 0 | 75 | 5.59±0.05 | 9 | 3 | 6 |
| Aug | 26.6±3.77 | 43 | 5 | 38 | 5.23±0.90 | 5 | 3 | 2 |
| Sep | — | 36 | 13 | 23 | — | 4 | 4 | 0 |
| Oct | 10.1±3.12 | 30 | 13 | 17 | 0.58±0.02 | 3 | 3 | 0 |
| Nov | 52.0±7.29 | 17 | 9 | 8 | 9.12±0.46 | 1 | 1 | 0 |
| Dec | 22.6 | 21 | 4 | 16 | 2.80±0.45 | 1 | 3 | 0 |
| Jan | 28.8±7.61 | 24 | 1 | 23 | 15.2 | 2 | 1 | 1 |
| Feb | 14.6 | 27 | 0 | 27 | 1.59 | 2 | 0 | 2 |
| Mar | 110.1±1.54 | 26 | 0 | 26 | 16.86±1.66 | 3 | 0 | 3 |
| Apr | — | 33 | 0 | 33 | — | 3 | 0 | 3 |
| May | 16.4±0.69 | 41 | 0 | 48 | 2.35±0.17 | 6 | 1 | 5 |
| Annual (g DW m ⁻² yr ⁻¹) | 13.39 | 15.02 | 1.38 | 12.59 | 2.01 | 1.35 | 0.51 | 1.18 |

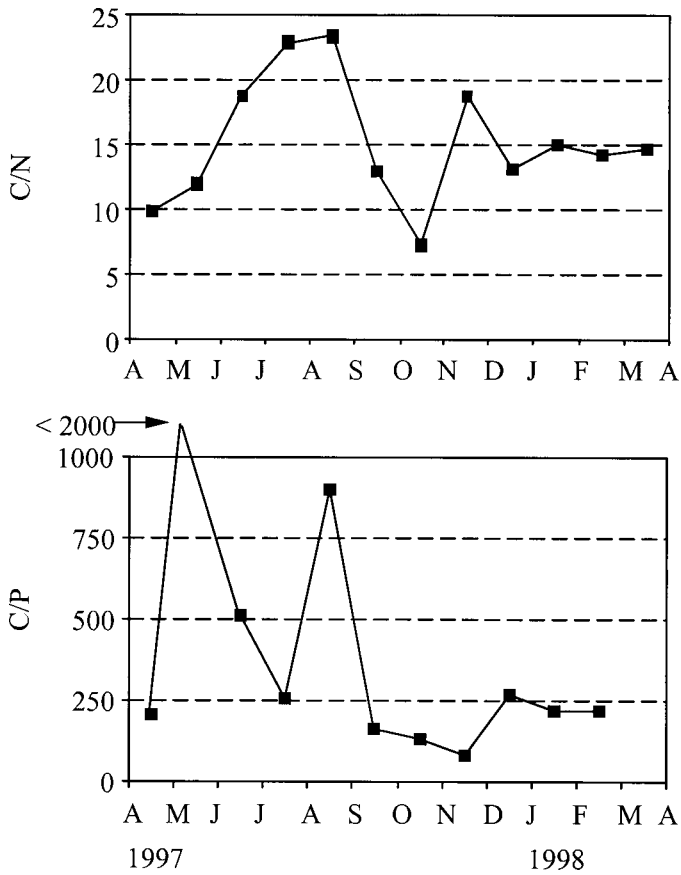


Fig. 4. Temporal variation in the C/N and C/P atomic ratios for the primary deposited material at Fanals point.

carbon in the settling material did not vary much along the study (Fig. 6), averaging $-21.53 \pm 0.30\text{‰}$, intermediate between the values measured for the *P. oceanica* ($-12.24 \pm 0.18\text{‰}$) and its associate epiphytes ($-17.00 \pm 0.14\text{‰}$) and those of sestonic material ($-24.27 \pm 2.88\text{‰}$; Duarte unpubl. data), suggesting that these sources all contributed to the depositional flux (Fig. 6).

The organic content of the sediment was low, varying from 0.67% to 1.47%, and tended to be lower in unvegetated sediments (Table 2). The organic material in the sediment was mineralized slowly, with remineralization rates ranging between $4.8 \text{ mg C m}^{-2} \text{ d}^{-1}$ and $110 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Table 3). The mineralization rates in the sediments under the seagrass canopy tended to be higher than those in unvegetated sediments (Table 3) and resulted in an estimate average annual CO_2 release of $15.6 \text{ g C m}^{-2} \text{ yr}^{-1}$ from the meadow's sediments, compared to only $5.0 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the adjacent unvegetated sediments. The sedimentary organic material was characterized by a stable carbon isotopic signal slightly enriched on the heavy ^{13}C isotope inside the meadow ($-20.07 \pm 0.21\text{‰}$) compared to that in the adjacent unvegetated sediments ($-21.51 \pm 0.31\text{‰}$; *t*-test, $p < 0.02$), which was identical to the isotopic signature of the sedimenting material. These results indicate a detectable, but low, contribution of *P. oceanica* detritus to the organic matter pool under the plant's canopy.

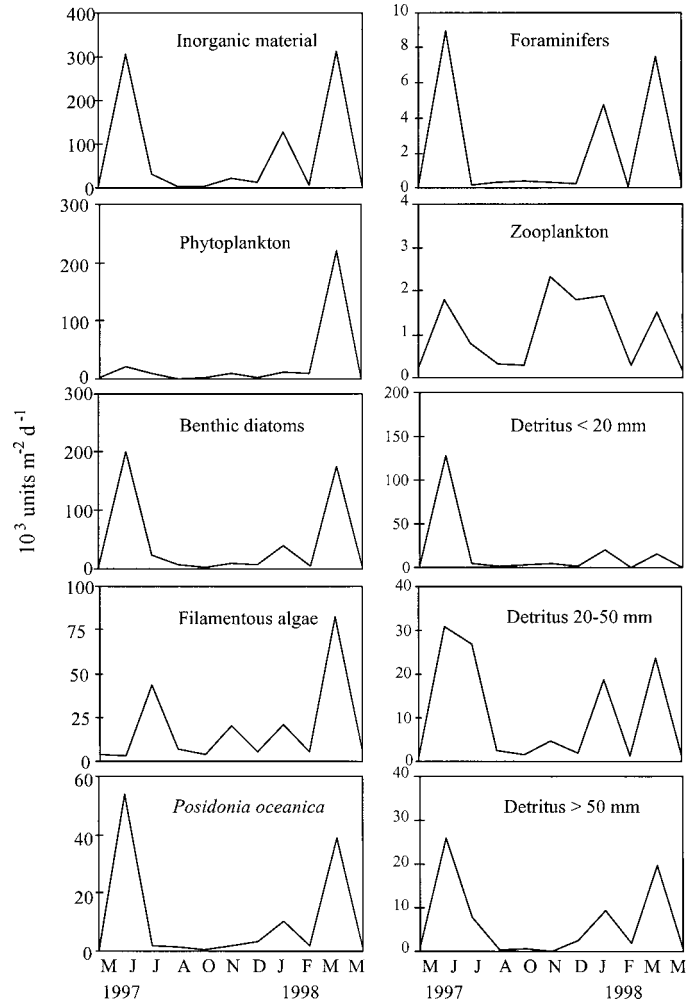


Fig. 5. Temporal variation in the different components of the total settling flux at Fanals point. Values are in $10^3 \text{ units m}^{-2} \text{ d}^{-1}$.

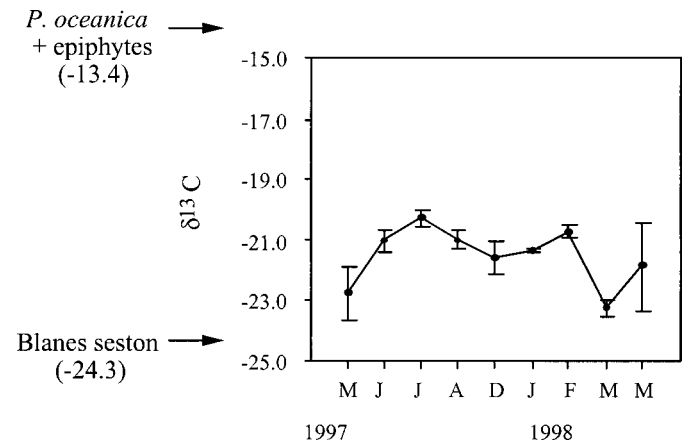


Fig. 6. Temporal variation in the stable carbon isotope signal for the primary deposition on the *P. oceanica* meadow at Fanals point.

Table 2. Initial organic carbon content, as percentage of the dry weight, of the sediment incubated for the experiments of the dissolved inorganic carbon production. Values are expressed \pm standard deviation of the mean.

| | | Percentage C_{org} |
|-----------|--------|-------------------------|
| 21 Aug 97 | meadow | 1.47 ± 0.855 |
| | sand | 0.76 ± 0.289 |
| 22 Dec 97 | meadow | 1.00 ± 0.031 |
| | sand | 0.67 ± 0.081 |
| 15 Jun 98 | meadow | 0.71 ± 0.088 |
| | sand | 0.80 ± 0.104 |

Discussion

The annual organic carbon deposition at Fanals point was estimated to be $198 \text{ g C m}^{-2} \text{ yr}^{-1}$, representing only a small fraction (4.7%) of the dry weight deposition in the area (Gacia and Duarte 2001). The settling flux was, therefore, dominated by inorganic material, as confirmed by the low organic content of the material collected and the dominance of inorganic particles in the particle pool. Examination of the materials comprising the settling flux revealed the diversity of particles involved, of which seagrass detritus represented only a modest fraction. Benthic diatoms and filamentous algae dominated the flux of organic materials, although phytoplankton cells were most abundant in March 1998, the time of the phytoplankton bloom in the area (Duarte et al. 1998). The general abundance of inorganic material, benthic diatoms, and detritus, as well as the presence of *P. oceanica* plant debris, provides indirect evidence of the importance of resuspension processes in the Mediterranean littoral (Dauby et al. 1995; Gacia and Duarte 2001).

The annual sedimentary input of nitrogen and phosphorus was estimated at $13.4 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $2.0 \text{ g P m}^{-2} \text{ yr}^{-1}$ (Table 1). These values are very close to, and not significantly different from, the calculated annual demands for *P. oceanica* growth ($15.0 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $1.3 \text{ g P m}^{-2} \text{ yr}^{-1}$; Table 1). However, remineralization rates are low, so that only a fraction of the sedimentary N and P will be available for plant uptake. In addition, there are important differences in the timing of nutrient inputs and organic matter sediment mineralization and plant demands for growth (Table 1), which is consistent with the nutrient limitation described for *P. oceanica* from late spring to summer in the area (Alcoverro et al. 1997a). Our calculations indicate that N and P regeneration from settling particles will be insufficient, both because of its magnitude and lack of phase with plant demands, to satisfy the plant requirements, implying that nutrient incorporation from the water column must also be significant. However, at the study site inorganic nutrient concentrations in the water column are below detection limit during most of the summer season (e.g., Duarte et al. 2000). Our understanding of the role of leaf versus root nutrient uptake is, however, rapidly changing. Earlier assumptions that these organs exploited different nutrient pools are being questioned as evidence that the sediment and water nutrient pools are linked by continuous exchange due to the subtidal

Table 3. Rates of mineralization in $\text{mg C m}^{-2} \text{ d}^{-1}$ at different times of the year after 1 and 2 months of sediment incubation.

| Starting incubation time | | 1 month ($\text{mg C m}^{-2} \text{ d}^{-1}$) | 2 month ($\text{mg C m}^{-2} \text{ d}^{-1}$) |
|--------------------------|--------|----------------------------------------------------|----------------------------------------------------|
| 21 Aug 97 | meadow | 110.0 | 51.3 |
| | sand | 7.6 | 30.6 |
| 22 Dec 97 | meadow | 9.8 | 15.0 |
| | sand | 4.8 | 7.9 |
| 15 Jun 98 | meadow | 44.1 | — |
| | sand | 23.7 | — |

pump processes (i.e., Huettel et al. 1996; Shum and Sundby 1996). This novel insight is redirecting previous polemics (Hemminga 1998) of root versus leaf uptake of pore or water-column nutrients, since these nutrient pools appear to be more closely linked than believed in the past.

The material deposited within the *P. oceanica* meadow was relatively depleted in nitrogen and, particularly, phosphorus. The C/N and C/P ratios were well above those characteristic of the particulate organic deposition in open (Copin-Montegut and Copin-Montegut 1983; Gadel et al. 1990) and coastal (Buscail et al. 1990; Dauby et al. 1995) Mediterranean waters. The high carbon to nutrient ratios indicate a significant contribution of nutrient-poor detrital material, likely derived from land inputs, to the particle flux at Fanals point.

The isotopic composition of *P. oceanica* leaves obtained at the 15 m Fanals meadow ($-12.24 \pm 0.14\text{‰}$) was similar to the average of $-11.9 \pm 4.1\text{‰}$ reported for the species (see Hemminga and Mateo 1996), and the $\delta^{13}\text{C}$ of *P. oceanica* epiphytes at Fanals point community ($-17.0 \pm 0.14\text{‰}$) was also within the range of previously reported values (-13.8 to -19.6‰ , Dauby 1989). Provided the seasonal variation in the isotopic signal of seagrass leaves and the biomass of epiphytic and aboveground material, we calculate the average $\delta^{13}\text{C}$ for the epiphyte-*P. oceanica* complex to be -13.4‰ .

The average isotope signal for the seston in Fanals was lighter than most values reported for littoral Mediterranean phytoplankton (e.g., -22.4‰ in Dauby 1989) and suggests a contribution of nonalgal land-derived material, probably discharged from the nearby Tordera River and the towns of Blanes and Lloret de Mar. An important input of land-derived organic carbon to this area has already been postulated in the past, as the carbon source that sustains net heterotrophic planktonic metabolism in this coastal area (Satta et al. 1996).

Knowledge of the stable carbon isotope composition of *P. oceanica* and its epiphytes and the sestonic material allows, when compared to that of the material collected in the sediment traps, the calculation of the relative contribution of the *P. oceanica*-epiphyte complex and seston to the settling carbon flux inside the meadow. We did so using a standard two-component isotope mixing equation of the form

$$\delta^{13}\text{C}_{\text{traps}} = \delta^{13}\text{C}_{P. \text{ oceanica}} \cdot f + \delta^{13}\text{C}_{\text{seston}} \cdot (1 - f)$$

where f is the fraction derived from the *P. oceanica*-epi-

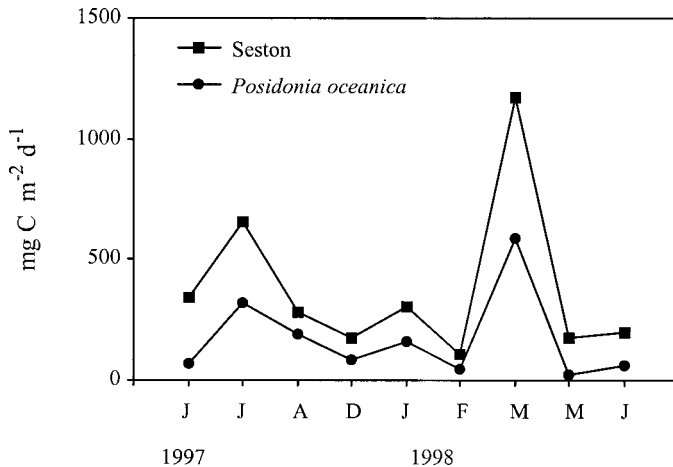


Fig. 7. The contribution of sestonic particles and *P. oceanica* detritus to the sedimentary carbon deposition on the meadow at Fanals point.

phyte complex. These calculations indicated a mixed contribution of the *P. oceanica*–epiphyte complex and the seston to the settling carbon flux within the meadow, with contributions of seston ranging from 59.5 to 89.9% of the carbon flux along the year (Fig. 7). At the annual scale, 72% of the sedimentary carbon flux was contributed by sestonic particles, with the remaining 28% being derived from detritus of *P. oceanica* and its associated epiphytes.

Similar calculations could be derived for the organic carbon present in the sediments inside the meadow. The average signal of $\delta^{13}\text{C}$ in the uppermost 5 cm of the sediment was slightly heavier than the annual average signal of the carbon present in the settling flux (ANOVA $p > 0.02$; Fig. 8), suggesting that there was an additional contribution of the *P. oceanica*–epiphyte complex to the carbon in the sediments compared to that in the depositional flux. Indeed, our calculations indicated that the *P. oceanica*–epiphyte complex contributed 43% of the organic carbon accumulated in the sediment. A similar enrichment in ^{13}C of sedimentary organic carbon has been reported for subtidal meadows of *Thalassodendron ciliatum* in Kenya, where 30% of the sediment organic carbon was derived from the seagrass (Hemminga et al. 1994). The enrichment of seagrass sediments with seagrass-derived carbon is expected to derive from (1) a potentially faster decomposition of the sestonic carbon compared to the more recalcitrant seagrass carbon and (2) the direct organic inputs to the sediments from seagrass rhizomes and roots.

Benthic decomposition rates inside the *P. oceanica* meadow at Fanals were low when compared to the rates measured in shallow vegetated sediments of *Zostera* species (e.g., Risgaard-Petersen et al. 1998; Hansen et al. 2000), but consistent with previous estimates for unvegetated oligotrophic Mediterranean (Vidal et al. 1997; Denis unpubl. data) sediments. Results from a concurrent study of sediment metabolism using core incubations from a nearby site (about 1 km away, 11 m depth) yielded an average \pm SE ($N = 5$ monthly experiments) respiration rate of 27.8 ± 5.74 mg C m⁻² d⁻¹ rates (Lucea and Duarte unpubl. data), not significantly dif-

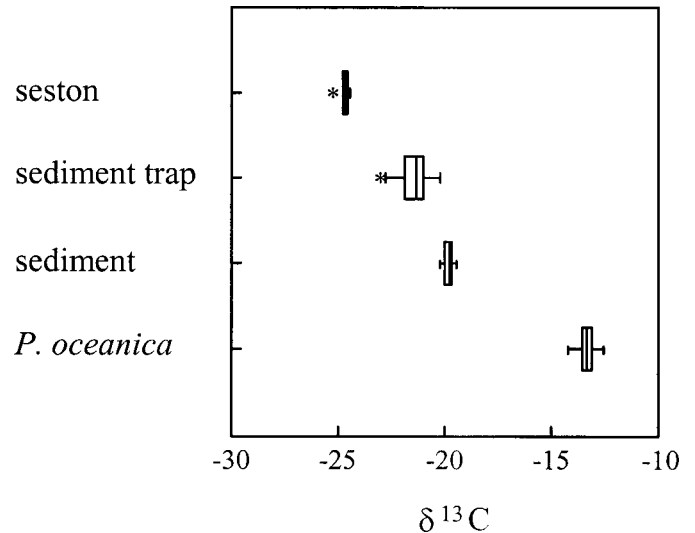


Fig. 8. Box plots showing the distribution of the carbon stable isotope signals for sources and sinks of carbon in the meadow at Fanals point. *P. oceanica* $n = 4$, Sediment $n = 5$, Sediment trap $n = 13$, and seston $n = 10$. Boxes encompass 50% of the values, the line represents the median value, bars extend to the 95% confidence limits, and asterisks represent observations beyond the 95% confidence limits.

ferent from the remineralization rate obtained using slurry incubations (Table 3). This observation agrees with results elsewhere that slurry-based estimates of carbon mineralization are in good agreement with rates of oxygen uptake in whole-core incubations Dauwe et al. (2001).

The low mineralization rates encountered in these vegetated sediments are, in part, explained by (1) the slow decomposition of the tissues of *P. oceanica* (Mateo and Romero 1997) compared to those of other seagrass species; (2) nutrient limitation of benthic remineralization, as demonstrated experimentally for *P. oceanica* sediments in the area (López et al. 1997); and (3) the fact that the studied meadow grows deeper (15 m depth) than the shallower (<1.5 m) meadows studied before, where easily degradable microphytobenthos may be a more important organic carbon source. In addition, the remineralization rates reported here are likely to be underestimates because in situ rates may be enhanced by hydrodynamic processes enhancing oxygen diffusion through the sediment. Indeed, interactions between microtopography and advective processes may enhance the fluxes of oxygen, nutrients, and particulate matter in permeable sediments (Huettel et al. 1996; Berninger and Huettel 1997). However, to date, significant methodological difficulties limit the capacity to incorporate these effects into estimates of organic matter mineralization (Jahnke et al. 2000).

Mineralization rates were three times greater inside the meadow than over bare sand, consistent with previous reports of enhanced benthic bacterial activity inside seagrass meadows (e.g., Moriarty et al. 1990). Despite the enhanced mineralization, the sediments under the seagrass canopy contained a higher organic load than those on bare sand, confirming the enhanced organic carbon inputs to *P. oceanica*

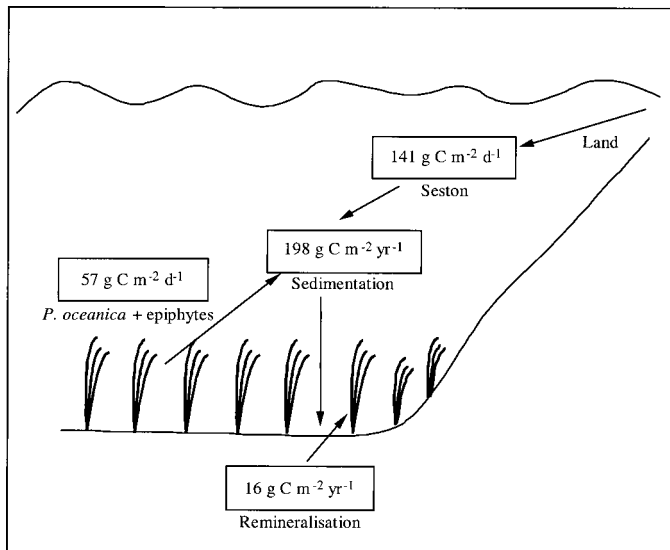


Fig. 9. Summary of the estimated organic carbon fluxes in the *P. oceanica* meadow at Fanals point.

sediments (Duarte et al. 1999). The reduced resuspension rates below *P. oceanica* canopies (Gacia and Duarte 2001) may, together with a higher organic carbon input, further explain the enrichment in organic matter of vegetated relative to unvegetated sediments since organic sediment particles have a low density and are resuspended more easily compared to inorganic materials.

The decomposition rates measured for the *P. oceanica* sediment at Fanals involved the remineralization of only 7.8% of the organic carbon inputs. Despite the net accumulation of organic carbon in the sediments, their organic content remains low (<1.5%; Table 2) because organic inputs represent a small percent of the total sediment inputs. While remineralization of nitrogen and phosphorous is faster than that for carbon (Valiela 1995), the recycling of the deposited nutrients is incomplete and leads to significant N and P burial in *P. oceanica* sediments (Romero et al. 1994). Correspondingly, the nutrient supply from remineralized sedimentary inputs must be below the seagrass demands, which must derive additional nutrients from the water column, resulting in nutrient-limited growth of seagrass in the region (Alcoverro et al. 1997a).

The results obtained allow the depiction of a tentative budget of particulate organic carbon deposition in the seagrass meadow studied (Fig. 9). The *P. oceanica*–epiphyte complex contributed 29% of the 198 C m⁻² deposited annually, which represents an input of 57 g C m⁻² yr⁻¹ as settling material. This is about half of the calculated production of the *P. oceanica* meadow, which, after correction for 10% herbivory losses (Pergent et al. 1997), was estimated at 110 g C m⁻² yr⁻¹, plus a conservative additional 20% due to epiphyte production (cf. Ballesteros 1987). The remaining 75 g C m⁻² yr⁻¹ of aboveground material produced by the *P. oceanica*–epiphyte complex must be exported or respired during decay (Mateo and Romero 1997). Litter export rates estimated for *P. oceanica* meadows at similar depths in the Medes Islands (northeast Spain) and

the island of Ischia (Italy) are somewhat lower (Romero et al. 1992; Mateo and Romero 1997), but these locations are sheltered compared to the greater exposure of Fanals point to waves and currents. Deposition of seston material should provide an input of 141 g C m⁻² yr⁻¹ to the seagrass sediments. Phytoplankton production is insufficient to supply this input, for the plankton community in the area is net heterotrophic, with community respiration exceeding primary production by fourfold (Satta et al. 1996). Hence, substantial allochthonous, i.e., land-derived, carbon inputs are necessary to allow the maintenance of both an important depositional flux of organic carbon and an excess carbon demand by planktonic heterotrophs.

Only a small fraction (<10%) of the organic carbon entering the sediments is respired, so that most of these inputs contribute to a net accumulation of organic carbon, estimated at about 182 g C m⁻² yr⁻¹, which, if maintained beyond the annual scale encompassed by our study, would imply a significant carbon (and nutrient) burial in this *P. oceanica* meadow. Moreover, because organic carbon is only a minor component of the settling flux, the sedimentation rate reported here implies a net sediment accretion within the meadow at Fanals of 0.2 cm yr⁻¹ (see also Gacia and Duarte 2001). These estimates, derived from observations of settling fluxes at the annual time scale, are in remarkable agreement with reports derived from examination of millenary deposits within Mediterranean *P. oceanica* meadows. For instance, long-term net sediment accretion rates under *P. oceanica* meadows have been estimated at 0.06 and 0.41 cm yr⁻¹ (Mateo et al. 1997), and long-term carbon burial in *P. oceanica* meadows has been estimated at 19 to 191 g C m⁻² yr⁻¹ (Romero et al. 1994). In fact, our estimate of the carbon accumulation rate in the sediments studied must be conservative, since our organic carbon burial estimate does not include the accumulation of carbon derived from below-ground production, which is significant in this species (Duarte and Chiscano 1999).

The results presented point to high carbon deposition rates in *P. oceanica* meadows. The seagrass and its associated epiphytes contribute 29% of the sedimentary flux of organic carbon but represent 43% of the organic carbon present in the sediments, indicating that inputs from below-ground organs and the low decomposition rate of *P. oceanica* relative to other detritus are important. While benthic remineralization rates are threefold higher in the vegetated sediments, the remineralization rate represents a small fraction (<10%) of the input, resulting in high carbon and nutrient burial rates in the *P. oceanica* meadows. The rates derived from our relatively short-term (1 yr) balance are remarkably consistent with those derived from long-term (millenary) balances, both supporting the conclusion (Duarte and Cebrián 1996) that seagrass meadows can be important sites for carbon burial in the ocean. The causes for this role are not only found on the high excess production, relative to respiratory demands, in seagrass meadows but on the enhanced sedimentation rates within seagrass meadows and, particularly, the high retention of materials derived from the attenuated sediment resuspension under seagrass canopies. These effects, which should be applicable to meadows other than those formed by *P. oceanica*, should be studied further to increase our

understanding of the magnitude and fate of particulate carbon and nutrient inputs to seagrass sediments.

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