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Detrital stocks and dynamics of the seagrass *Posidonia oceanica* (L.) Delile in the Spanish Mediterranean

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Abstract

Previous studies have shown that most leaf production (>90%) of the seagrass *Posidonia oceanica* is shed after senescence and that a substantial percentage (up to 80%) may thereafter be exported off the seagrass meadows by waves and currents. It has also been reported that *P. oceanica* meadows can accumulate large stocks of belowground detritus due to slow decomposition rates. However, the generality of these results across broad spatial scales is poorly known. In this report, we examine the fate of leaf production and the magnitude and dynamics of belowground detritus in 16 *P. oceanica* meadows distributed along the Spanish Mediterranean. Herbivores removed a small percentage of leaf production in all the meadows ($\leq 13\%$), with most leaf production (>85%) being shed after senescence. Most shed leaves (>90%) were exported off the meadows by physical agents, such as waves and currents. The amount of belowground detritus stored within 10–15 cm from the sediment surface varied from ca. 70 to 7500 g DW m⁻² among the meadows examined, and they accumulated at rates ranging from ca. 65 to 650 g DW m⁻² per year. These values are large when compared to other communities of aquatic and terrestrial macrophytes. Our results show that *P. oceanica* meadows in the Spanish Mediterranean support high values of secondary production in other systems by exporting large amounts of leaf detritus as well as acting as substantial carbon sinks by accumulating large reservoirs of belowground detritus. Therefore, the increasing anthropogenic threats on *P. oceanica* could entail an important loss of secondary production and carbon storage in Mediterranean coastal ecosystems. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: *Posidonia oceanica*; Primary production; Detrital stocks; Spanish mediterranean

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1. Introduction

Posidonia oceanica (L.) Delile is the most abundant seagrass species in the Mediterranean (Den Hartog, 1970), where it covers about 40,000 km² of the sea floor (Pergent, 1993). It forms extensive meadows and it contributes to the total meadow primary production with 150–3000 g DW m⁻² per year (Ott, 1980; Pergent, 1990; Pergent-Martini et al., 1994). Although herbivores may occasionally defoliate vast areas of *P. oceanica* (Laborel-Deguen and Laborel, 1977; Kirkman and Young, 1981; Shepherd, 1987), the intensity of herbivory on this seagrass is believed to be generally modest (Cebrian and Duarte, 1998). Past reports have shown that most leaf production ($\geq 90\%$) is channeled to higher trophic levels as detritus (Pergent et al., 1994; Cebrian et al., 1996; Pergent et al., 1997).

It has been found that, upon senescence and shedding, a substantial percentage (up to 80%) of *P. oceanica* leaf detritus is frequently exported off the meadows by waves and currents and decomposed in the receiving systems (Romero et al., 1992; Pergent et al., 1994; Pergent et al., 1997), although such percentage can be modest (10–20%, Mateo and Romero, 1997). Shed leaves remaining in the meadow decompose within a few months (Romero et al., 1992; Mateo and Romero, 1997; Pergent et al., 1997). On the contrary, belowground detritus (i.e. dead rhizomes and roots) are not usually exported off the meadow, where they decompose slowly. As a result, a significant percentage (25–35%) of the seagrass production is accumulated as refractory material within the meadow (Romero et al., 1994; Mateo et al., 1997; Mateo and Romero, 1997).

Nevertheless, the variability in the fate of *P. oceanica* leaf production and in the storage of belowground refractory detritus over large spatial scales is poorly known. More information would help to determine the general role of *P. oceanica* meadows in coastal ecosystems. For instance, *P. oceanica* meadows could support high levels of secondary production in neighboring communities if large quantities of leaf detritus are consistently exported off the meadows. In contrast, the general importance of *P. oceanica* leaf detritus as a food resource in neighboring communities could be of limited extent if high levels of export are observed only in a few locations. Similarly, *P. oceanica* meadows may represent a significant carbon sink for the coastal Mediterranean only if they consistently store large reservoirs of belowground detritus.

In this report, we examine the fate of leaf production and the magnitude and dynamics of belowground detritus in 16 populations of *P. oceanica* distributed along the Spanish Mediterranean. We first corroborate past observations that herbivores generally consume a small percentage of the seagrass production. We then show that the rates of leaf detritus export and accumulation of belowground detritus tend to be of considerable magnitude in the populations studied. We end up by discussing the implications of our results for the ecological role of *P. oceanica* meadows in Mediterranean coastal ecosystems.

2. Methods

We examined the fate of leaf production and the dynamics of belowground detritus in 16 populations of *P. oceanica* distributed between 36°41' and 42°22' along the Spanish Mediterranean coast (Fig. 1). The populations were sampled in September 1994, which

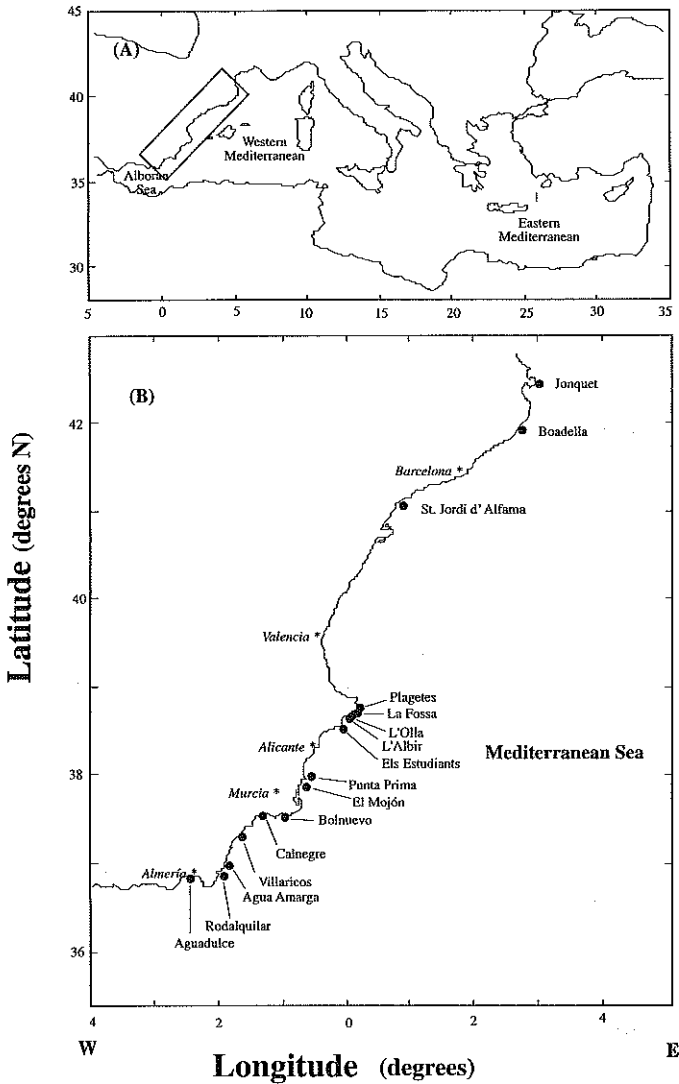


Fig. 1. (A) General location of the area examined; (B) detail of the populations sampled.

is the month of maximum leaf shedding (Ott, 1980; Romero, 1989; Mateo and Romero, 1997). In each population, we counted all the vertical shoots and apices of horizontal growth enclosed in each of three quadrats. The quadrats were tossed haphazardly within the meadow, and they covered 0.09 or 0.25 m² depending on the natural density of shoots in the population. We also collected all leaf-blade detritus enclosed in each of three more 0.25 m² quadrats haphazardly tossed in the meadow. This was done with an underwater suction pump, which has proven useful to collect seagrass leaf detritus (Romero et al.,

1992; Mateo and Romero, 1997; Pergent et al., 1997). This procedure only sampled detrital leaf fragments $>1 \text{ mm}^2$, since all suctioned material was collected into 1 mm^2 mesh bags. The bags were carried to the lab, leaf-blade detritus dried overnight (80°C), and the mean mass of leaf-blade detritus (g DW m^{-2}) calculated for each population.

The use of cores for sampling belowground material proved to be inoperative, since the hardness of the *P. oceanica* belowground “matte” (i.e. entangled net of rhizomes, roots and sediment) prevented us from digging the core more than a few centimeter into the sediment. Therefore, we extracted the seagrass belowground compartment by manually cutting off the matte with a long, sturdy knife down to a depth of 10–15 cm below the sediment. Three replicates, each consisting of 30–40 vertical shoots and attached belowground material, were haphazardly sampled in each population. Care was taken to minimize breakage of belowground organs from aboveground shoots when extracting the samples. In the laboratory, a subsample containing about 10 shoots and attached belowground material was randomly selected and severed out of each replicate in every population. Leaf sheaths, dead rhizome and dead roots were sorted out of each subsample and dried overnight. Finally, in each population, the mean standing stocks of sheaths, dead rhizome and dead roots (g DW m^{-2}) from the sediment surface to 10–15 cm down into the matte were calculated by multiplying the mean ratio of dry weight of sheaths, dead rhizome or dead roots per shoot (g DW per shoot) times the mean density of shoots in the population (shoots per square meter). S.E. was calculated with techniques of error propagation (Meyer, 1975).

In each population, we calculated annual leaf (blade + sheath) production on an areal basis (g DW m^{-2} per year) as the product between annual leaf production per shoot ($\text{g DW per shoot per year}$) and shoot density (shoots per square meter). Annual leaf production per shoot was derived as the product between the mean number of leaves produced per shoot yearly and the mean maximum biomass reached by intact (unbroken by herbivore or wave activity) fully-grown leaves. In previous surveys of these populations (Cebrian et al., 1996; Marba et al., 1996), we calculated the mean number of leaves produced per shoot yearly from the annual cycles of internodal length imprinted on the rhizome of vertical shoots. This is possible because each node on the rhizome corresponds to the insertion point of a shed leaf. This technique was generalized by Duarte et al. (1994), and has been satisfactorily applied to examine leaf growth dynamics in many seagrass species when only a limited number of sampling visits is possible (Gallegos et al., 1994; Vermaat et al., 1995; Kenworthy and Schwarzschild, 1998).

Herbivory was estimated from the bite marks imprinted by herbivores on leaf blades. In each population, we measured the area covered by all bite marks on the oldest leaf of each of 50 randomly collected shoots, and converted this area into DW from measurements of leaf specific weight (mg DW cm^{-2}). Then, for each population, we derived the mean consumption over the leaf life-span (mg DW per leaf) as the average of the 50 consumption values measured in the population. Annual leaf consumption per shoot ($\text{g DW per shoot per year}$) was calculated as the product between the mean consumption over the leaf life-span and the mean number of leaves produced per shoot yearly in the population. Finally, we divided annual leaf consumption per shoot by annual leaf production per shoot to express herbivory as a percentage of leaf production. This approach has been applied to other long-lived seagrass species with broad leaves where herbivore bites remain imprinted on the blades (Greenway, 1976; Thayer et al., 1984; Cebrian and Duarte, 1998). Yet, the estimates

of herbivory derived here could be somewhat skewed because our method assumes the consumption values measured in September are representative of mean annual values.

Similarly, in each population we estimated annual sheath production (g DW m^{-2} per year) as the product between the mean number of leaves produced per shoot yearly, the mean sheath biomass of fully-grown leaves, and shoot density (Duarte et al., 1994). In addition, the number of leaves produced per shoot yearly was multiplied by the mean internodal weight and by shoot density to estimate the annual production of shoot rhizome (g DW m^{-2} per year) in each population (Duarte et al., 1994). We also estimated in each population the annual production of horizontal rhizome (g DW m^{-2} per year) as the product between the annual horizontal growth per apex ($\text{g DW per apex per year}$) and the density of apices (apexes per square meter). The annual horizontal growth per apex was derived in previous surveys (Marba et al., 1996) as the slope of the weight of horizontal rhizome between two consecutive shoots versus the age difference of the shoots (Duarte et al., 1994). Moreover, we estimated the annual root production on horizontal rhizomes (g DW m^{-2} per year) in each population as the product between the mean ratio of root biomass to horizontal rhizome biomass and the annual production of horizontal rhizome. This procedure may somewhat underestimate root production on horizontal rhizomes, since root turnover is unaccounted for (Duarte et al., 1998). Finally, in eight of the populations examined, we recorded the age of all the shoots collected and we calculated the annual rate of accumulation of belowground detritus (g DW m^{-2} per year) as the quotient between the mean standing stock of belowground detritus (sheaths plus dead rhizome and dead roots) and the mean age of the three oldest shoots sampled in the population.

3. Results

Annual production ranged about two-orders of magnitude among populations for all compartments (i.e. leaves, sheaths, rhizome and roots) (Table 1). This variability, however, was caused by the anomalously low values found in El Mojon. This population had been undergoing a severe decline due to nearby sewage outfalls and was, at the time of sampling, close to total disappearance. When this population is disregarded, the ranges of variability are reduced to about one-order of magnitude for leaf and rhizome production, and about five-fold for sheath and root production (Table 1). Leaves contributed the most to total production, from 81% in La Fossa to 95% in L'Olla. Herbivores consumed small percentages of leaf and, consequently, total production. Only the population in Els Estudiants lost little more than 10% of leaf production to herbivores, with more than half of the populations losing less than 5% (Table 1).

Leaf-blade detritus ranged over one-order of magnitude among populations, from $0.4 \pm 0.2 \text{ g DW m}^{-2}$ (mean \pm S.E.) in the declining population of El Mojon to $146.3 \pm 41.3 \text{ g DW m}^{-2}$ in the moderately productive L'Olla (Table 2). Yet most populations exhibited relatively low values, with up to 50% of them having less than 20 g DW leaf-blade detritus per square meter (Fig. 2A). Standing stocks of belowground detritus also varied greatly among populations, with sheaths and dead rhizomes ranging over two-orders of magnitude and dead roots over one-order of magnitude (Table 2). As a consequence, total detrital standing stocks (belowground + leaf-blades) also differed remarkably among populations, with

Table 1
Leaf (blade + sheath) production, the percentage consumed by herbivores, sheath production, production of shoot rhizomes (vertical rhizome), horizontal rhizomes production, root production on horizontal rhizomes, and total production (i.e. sum of all previous compartments) in the populations sampled^a

Population	Leaf production (blades + sheaths)	Leaf production consumed by herbivores (%)	Sheath production	Vertical rhizome production	Horizontal rhizome production	Root production	Total production
Jonquet	940.7	3.3	89.4	20.6	42.9	12.7	1016.9
Boadella	1228.5	2.5	120.6	71.1	57.6	8.1	1365.3
Sant Jordi d' Alfama	364.6	4.6	35.9	23.2	27.7	6.2	421.7
Plagetes	1115.0	7.2	122.4	76.1	52.5	18.4	1262.0
La Fossa	1240.5	5.6	111.9	185.5	93.5	10.5	1530.0
L'Olla	1071.9	0.5	89.1	41.9	10.2	2.7	1126.7
L'Albir	509.1	8.7	54.3	32.0	22.7	22.5	586.3
Els Estudians	1456.0	13	169.1	140.7	60.7	15.0	1672.4
Punta prima	910.6	4.1	149.8	79.3	26.1	0.6	1016.6
El Mojon	15.2	8.9	1.5	2.0	0.8	0.2	18.2
Bolnuevo	1062.9	3.7	88.4	47.7	41.4	6.5	1158.5
Calnegre	933.5	4.0	100.0	58.7	17.1	4.7	1014.0
Villaricos	130.3	5.4	24.5	18.6	6.2	1.1	156.2
Agnamarga	702.2	3.7	145.3	84.9	13.6	6.0	806.7
Rodalquilar	954.7	4.1	146.9	142.2	61.5	11	1169.4
Aguadulce	565.7	7.4	88.4	52.3	19.4	7.1	644.5

^a All values are expressed in g DW m⁻² per year, except percentage of leaf production consumed.

Table 2

Standing stocks (mean \pm S.E.) of leaf-blade detritus, sheaths, dead rhizome and dead roots, and the total detrital stock (sum of all previous compartments) in the populations sampled^a

Population	Leaf-blade detritus	Sheaths	Dead rhizome	Dead roots	Total detrital stock
Jonquet	36.0 \pm 11.9	1508.6 \pm 446.9	445.6 \pm 171.6	758.2 \pm 276.7	2748.4 \pm 553.0
Boadella	47.4 \pm 31.5	1242.8 \pm 224.2	107.5 \pm 48.7	29.7 \pm 10.0	1427.4 \pm 231.8
Sant Jordi d'Alfama	3.3 \pm 0.6	706.9 \pm 254.5	161.6 \pm 48.3	74.3 \pm 8.8	946.1 \pm 259.2
Plagetes	6.3 \pm 1.5	3715.3 \pm 1746.3	959.4 \pm 629.1	436.4 \pm 323.8	5117.4 \pm 1884.2
La Fossa	4.1 \pm 1.5	879.6 \pm 301.1	1.0 \pm 0.3	43.4 \pm 25.0	928.1 \pm 302.1
L'Olla	146.3 \pm 41.3	1681.9 \pm 514.3	37.8 \pm 25.6	47.9 \pm 30.8	1913.9 \pm 517.5
L'Albir	23.7 \pm 6.8	916.1 \pm 329.4	95.6 \pm 57.0	150.0 \pm 142.9	1185.4 \pm 363.6
Els Estudiants	16.5 \pm 4.9	1206.1 \pm 352.8	210.4 \pm 128.2	40.2 \pm 13.6	1473.2 \pm 375.6
Punta Prima	5.3 \pm 2.0	1772.3 \pm 318.4	296.5 \pm 136.6	828.5 \pm 659.7	2902.6 \pm 745.1
El Mojon	0.4 \pm 0.2	56.0 \pm 43.2	3.9 \pm 3	10.1 \pm 9.2	70.4 \pm 45.4
BoInuevo	17.5 \pm 8.9	6488.8 \pm 1089.4	942.8 \pm 240.2	130.0 \pm 37.9	7579.1 \pm 1116.2
Calnegre	33.0 \pm 12.9	2835.3 \pm 945.3	910.8 \pm 418.9	208.6 \pm 93.3	3987.7 \pm 1038.3
Villaricos	10.0 \pm 5.2	355.0 \pm 34.5	96.7 \pm 20.6	133.0 \pm 13.2	594.7 \pm 42.6
Aguamarga	33.3 \pm 16.8	1447.1 \pm 216.1	88.3 \pm 23.8	220.3 \pm 38.0	1789.0 \pm 221.4
Rodalquilar	22.9 \pm 7.8	2161.8 \pm 843.2	512.4 \pm 277.9	100.7 \pm 79.9	2797.8 \pm 891.4
Aguadulce	52.8 \pm 11.1	1165.8 \pm 362.2	87.2 \pm 29.5	12.0 \pm 10.6	1317.8 \pm 363.9

^a All values are expressed in g DW m⁻².

values ranging from 70.4 \pm 45.4 to 7579 \pm 1116.2 g DW m⁻² (mean \pm S.E.). Most populations (>60%), however, stored total detrital stocks <2000 g DW m⁻² (Fig. 2B). Sheaths represented from 55 to 95% of the total detrital stock, with dead rhizomes and roots accounting for smaller percentages (from 1 to 25% for both of them) and dead leaves being mostly negligible (<5%, except 8% in L'Olla; Fig. 3).

The relationship between the total detrital stock and total production across the populations sampled showed two different domains (Fig. 4): a tendency towards larger stocks with higher production across populations with low to moderate values of production, and a lack of correlation across populations with high values of production. We arbitrarily set the threshold between the two domains at a production value of 1100 g DW m⁻² per year. This allowed us to describe the least-square regression equation between the total detrital stock (g DW m⁻²) and total production (g DW m⁻² per year) for populations with low to moderate production values:

$$\text{Total detrital stock} = -218.4 (\pm 362.5) + 3.1 (\pm 0.5) \text{ total production}$$

$$n = 9, R^2 = 0.82, P < 0.001$$

The rates of accumulation of belowground detritus ranged from 66.1 to 657.2 g DW m⁻² per year, with about 40% of the populations accumulating less than 200 g DW m⁻² per year (Fig. 5A). Across the populations compared, higher accumulation rates (g DW m⁻² per year) were conducive to larger belowground detrital stocks (g DW m⁻², Fig. 5B), as reflected by the least-squares regression equation:

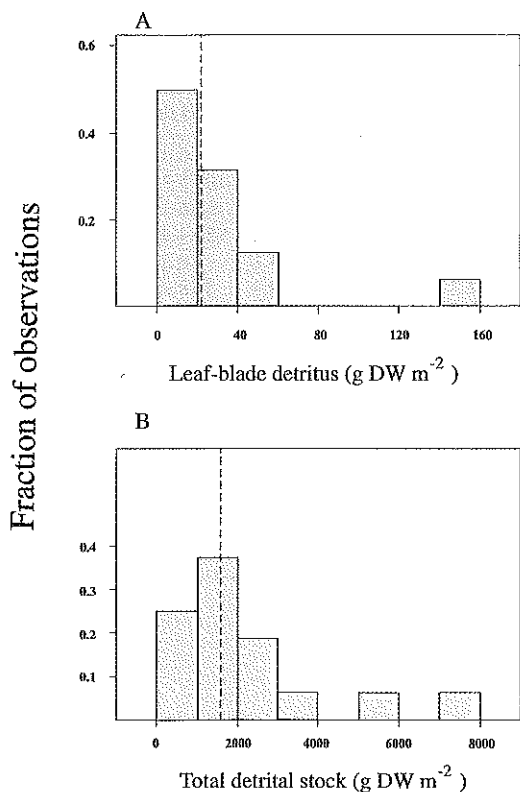


Fig. 2. The frequency histograms of the stocks of (A) leaf-blade detritus; and (B) total detritus in the populations studied. Dashed lines represent medians.

Belowground detrital stock = $384.2 (\pm 1071.2) + 8.0 (\pm 2.8)$ accumulation rate

$n = 8$, $R^2 = 0.51$, $P < 0.03$

There was, however, no significant relationship between accumulation rates and total production for these populations.

4. Discussion

Our values of leaf and rhizome production obtained using techniques of growth reconstruction (Duarte et al., 1994) are similar to those found in other populations of *P. oceanica* using different methods (see compilations by Pergent-Martini et al., 1994; Cebrian et al., 1997; Pergent et al., 1997). Reports of root production are scarce, but the few values available (Ott, 1980; Sanchez-Lisazo, 1993; Mateo and Romero, 1997; Duarte et al., 1998) lie within the range of our estimates. This suggests that our values of root production are not gross underestimates. Leaves accounted for the greatest percentage of total production in

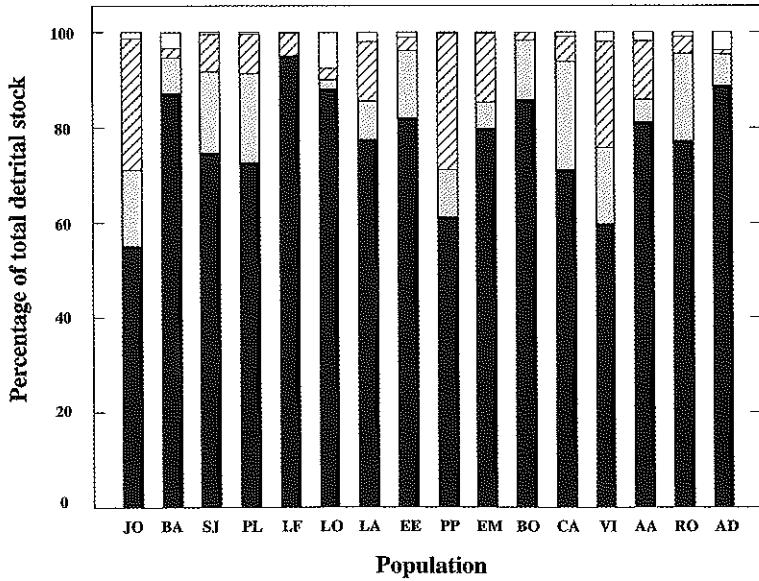


Fig. 3. The percentage of the total detrital stock represented by sheaths (black bins), rhizomes (grey bins), roots (hatched bins), and leaf-blades (open bins) in the populations examined; JO: Jonquet, BA: Boadella, SJ: St. Jordi d'Alfama, PL: Plagetes, LF: La Fossa, LO: L'Olla, LA: L'Albir, EE: Els Estudiants, PP: Punta Prima, EM: El Mojon, BO: Bolnuevo, CA: Calnegre, VI: Villaricos, AA: Aguamarga, RO: Rodalquilar, AD: Agudulce.

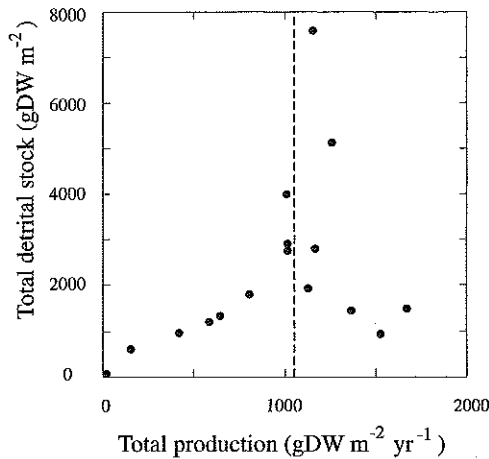


Fig. 4. The relationship between the total detrital stock and total production across the populations examined. The dashed line separates populations with production values lower than 1100 gDW m⁻² per year from those with higher values.

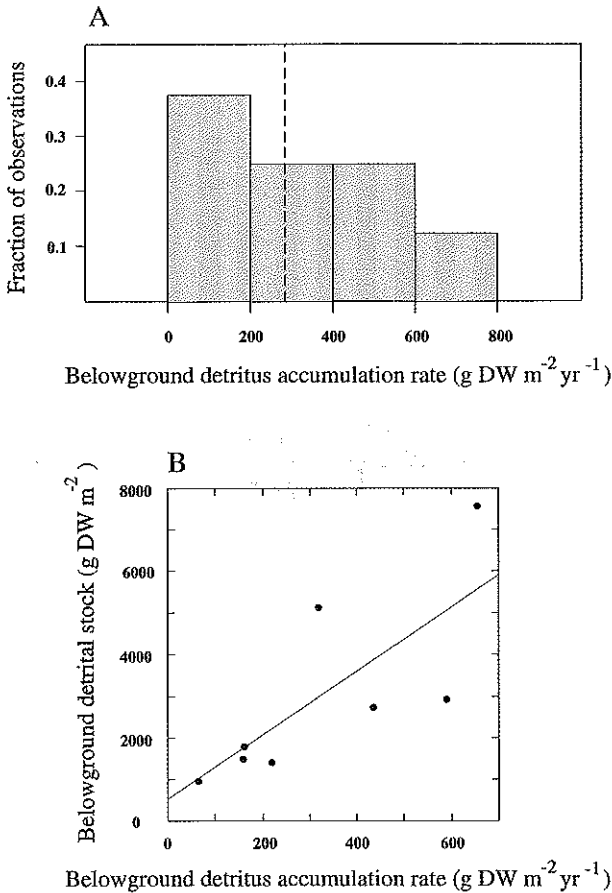


Fig. 5. (A) The frequency histogram of the rate of accumulation of belowground detritus in the eight populations where these measurements were taken. The dashed line represents the median; (B) the relationship between the belowground detrital stock and accumulation rate across the populations where accumulation measurements were taken. The continuous line depicts the equation fitted by least-square regression analyses.

all the locations examined (>80%), as it has been shown by previous reports (Ott, 1980; Sanchez-Lisazo, 1993; Pergent-Martini et al., 1994; Cebrian et al., 1997; Pergent et al., 1997; Mateo and Romero, 1997). Herbivores removed a small percentage of leaf production in all the populations studied ($\leq 13\%$), in accordance with most previous reports of herbivory on *P. oceanica* (<10% of leaf production; see compilation by Cebrian and Duarte, 1998). Therefore, although herbivores can occasionally consume larger percentages of *P. oceanica* leaf production, (around 30%; Kirkman and Young, 1981; Pergent et al., 1997), it seems that the intensity of herbivory on the seagrass is generally modest.

As a consequence, most of the seagrass leaf production is shed after senescence. Shed leaf-blades can either be exported off the meadow or remain and decompose within the meadow. The standing stocks of leaf-blade detritus found in the populations examined here

are similar to values reported in other locations during the same season (Romero et al., 1992; Mateo and Romero, 1997; Pergent et al., 1997). Furthermore, our results imply a substantial export of shed blades from the meadows examined. We used the method proposed by Romero et al. (1992), which has also been used by many other authors (Pergent et al., 1994; Mateo and Romero, 1997; Pergent et al., 1997; Cebrian et al., 2000), to estimate a mean value of export for our populations from the mean rate of leaf shedding, the mean standing stock of leaf-blade detritus, and a mean (\pm S.E.) leaf decomposition rate of 0.0097 ± 0.0013 per day (Romero et al., 1992; Cebrian et al., 1997; Mateo and Romero, 1997; Pergent et al., 1997). The mean annual rate of leaf shedding (\pm S.E.) for the populations examined, calculated as leaf production minus the sum of sheath production and herbivory (Table 1), is estimated as 690.7 ± 87.2 g DW m^{-2} per year. Because about 75% of the leaves born in a year are shed between July and September (Ott, 1980; Romero, 1989; Cebrian et al., 1994), we can estimate that on the average 518 g DW (0.75×690.7) of dead blades per square meter are shed within that period in the meadows examined.

Therefore, if no export were occurring, the mean standing stock of leaf-blade detritus found in September should have equaled the amount of shed blades from July to September (518 g DW m^{-2}) plus the standing stock of leaf-blade detritus present in July minus the total amount decomposed from July to September. In turn, the amount of shed blades decomposed during the 60 day interval can be estimated as $518(1 - e^{-0.0097 \times (60/2)})$, which corresponds to 130.8 g DW m^{-2} . Hence, in September and under the hypothesis of no export, we would have found a standing stock of leaf-blade detritus equivalent to 387.2 ($518 - 130.8$) g DW m^{-2} plus the amount that was present in July but not yet decomposed by September. However, we only found an average (\pm S.E.) value of 28.7 ± 8.8 g DW m^{-2} , which indicates that a major percentage of blades shed during mid-late summer is readily exported off the meadow. This is in agreement with past observations that a substantial percentage of leaf production is frequently exported off *P. oceanica* meadows (40–80%, Romero et al., 1992; Pergent et al., 1994; Pergent et al., 1997), albeit this percentage may sometimes be modest (10–20%, Mateo and Romero, 1997).

This study and others (Romero et al., 1992; Mateo and Romero, 1997) show that most *P. oceanica* detritus is stored belowground. Sheaths, dead rhizomes and dead roots represent almost 100% of the total detrital stock in most of the populations examined here. This is due to the low decomposition and export rates of sheaths and rhizomes in comparison with those of leaves (Romero et al., 1992; Mateo et al., 1997). In turn, sheaths contribute more to the total detrital stock than dead rhizomes and dead roots do, which probably results from the fact that sheaths show higher production rates, but relatively similar decomposition rates, than rhizomes and roots (Romero et al., 1992; Mateo et al., 1997). Moreover, *P. oceanica* belowground detrital stocks are usually large, which is also a consequence of the slow decomposition rates of sheaths and rhizomes. In the populations examined here, the amount of detritus stored within 10–15 cm from the sediment surface ranges generally from several hundred to several thousand g DW m^2 . These values are similar to those found in other populations of *P. oceanica* (Romero et al., 1992; Mateo and Romero, 1997), and much higher than in populations of other seagrass species (Kenworthy and Thayer, 1984; Cebrian et al., 2000), when similar depths from the sediment surface are integrated. When deeper depths into the sediment are encompassed (≥ 1 m), detrital stocks as large as 5000 g C m^2 may be found in *P. oceanica* meadows (Romero et al., 1994; Mateo et al., 1997).

High rates of accumulation of *P. oceanica* belowground detritus are another consequence of the slow decomposition rates of sheaths and rhizomes, with higher accumulation rates resulting into larger detrital stocks. Our estimates of accumulation rates are similar to previous values that cover similar depth ranges from the sediment surface (≤ 20 cm; Pirc, 1983; Pergent et al., 1989; Semroud et al., 1990). When deeper depths are integrated, accumulation rates of belowground detritus tend to be smaller since long-term losses, such as decomposition of recalcitrant detritus, are included (Romero et al., 1994; Mateo et al., 1997; Pergent et al., 1997). Nevertheless, both short- and long-term accumulation rates of *P. oceanica* detritus are larger than those encountered in many other communities of aquatic and terrestrial primary producers (Cebrian, 1999). Large rates of detritus accumulation, along with a vast area covered (Pergent, 1993), render *P. oceanica* meadows important carbon sinks in the coastal Mediterranean. Using 3.1×10^3 km² as the area covered by *P. oceanica* in the Spanish Mediterranean (Mas et al., 1993), and our mean (\pm S.E.) accumulation rate (326.6 ± 76.1 g DW m⁻² per year), we estimate that a total of 1×10^{12} g DW per year are buried in the *P. oceanica* meadows of the Spanish Mediterranean over time scales < 30 years. In addition, the burial of refractory detritus within the matte represents, along with the export of detrital leaves, a loss of nutrients for the seagrass (up to 35%; Romero et al., 1992; Romero et al., 1994; Mateo and Romero, 1997). This loss needs to be counteracted by nutrients imported from allochthonous sources, such as terrestrial discharges, atmospheric deposition, nitrogen fixation or algal decomposition (Bethoux and Copin-Montegut, 1986), or from the exploitation of mineral-bound nutrient pools (Pedersen et al., 1997) if the seagrass production is to be maintained.

Larger detrital stocks are associated with higher production values only across populations reaching from low to moderate production levels (< 1100 g DW m⁻² per year). The reasons why the relationship between detrital storage and production would depend on the range of production values compared are unclear. Increasing seagrass production may change the stoichiometry of sediment organic matter (Kenworthy et al., 1982; Williams, 1990). These changes reflect shifts in the balance between nutrient inputs into the sediment (i.e. sedimentation, mobilization from water column or from mineral-bound fractions and nitrification) and outputs from the sediment (i.e. remobilization to the water column through plant exudation or detrital export and denitrification) that occur across a gradient of seagrass production (Hemminga et al., 1991). In addition, site-specific factors, such as the nature of anthropogenic eutrophication, sediment inorganic composition, and the intensity of detrital export, may also condition the evolution of the stoichiometry of sediment organic matter across a gradient of seagrass production. For instance, Pedersen et al. (1997) show that sediment organic matter is enriched in nitrogen, but not in phosphorus, with higher *Cymodocea nodosa* production in an estuarine system subject to intense anthropogenic nitrogen loading and with carbonate-rich sediments. In turn, changes in the stoichiometry of sediment organic matter may affect the rates of detritus decomposition and storage (Cebrian, 1999). We conjecture that the influence of the interaction between increased seagrass production and site-specific properties on the nutrient ratios of sediment organic matter and, therefore, on the rate of detritus storage in highly-productive *P. oceanica* populations (> 1100 g DW m⁻² per year) disrupts the association between larger detrital stocks and higher production found for populations with smaller production values. Research on the evolution of the nutrient content and decomposition rates of sediment organic matter across a gradient of seagrass

production, anthropogenic eutrophication and sediment inorganic composition is needed to explore this conjecture.

In conclusion, our results generalize for *P. oceanica* meadows in the Spanish Mediterranean past observations of the fate of leaf production and detritus dynamics obtained in specific populations. Herbivores consume a modest percentage of leaf production and, hence, most is shed over senescence. Most shed leaf-blades are exported off the meadow, thereby supporting high values of secondary production in the receiving communities. *P. oceanica* meadows are also important carbon sinks, because the seagrass belowground organs have slow decomposition rates. It has been suggested that a general decline of *P. oceanica* could be occurring (Zavodnik and Jaklin, 1990; Marba et al., 1996). Our results indicate that such a decline could entail an important loss of secondary production and carbon storage in Mediterranean coastal ecosystems. The close-to-disappearance population in El Mojon represents an example. *P. oceanica* stands out, therefore, as a crucial species to be preserved in the Mediterranean.

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References

- Bethoux, J.P., Copin-Montegut, G., 1986. Biological fixation of atmospheric nitrogen in the Mediterranean sea. *Limnol. Oceanogr.* 31, 1353–1358.
- Cebrian, J., 1999. Patterns in the fate of production in plant communities. *Am. Nat.* 154, 449–468.
- Cebrian, J., Duarte, C.M., 1998. Patterns in leaf herbivory on seagrasses. *Aquat. Bot.* 60, 67–82.
- Cebrian, J., Marba, N., Duarte, C.M., 1994. Estimating leaf age of the seagrass *Posidonia oceanica* (L.) Delile using the plastochrone interval index. *Aquat. Bot.* 49, 59–65.
- Cebrian, J., Duarte, C.M., Marba, N., Enriquez, S., Gallegos, M., Olesen, B., 1996. Herbivory on *Posidonia oceanica*: magnitude and variability in the Spanish Mediterranean. *Mar. Ecol. Prog. Ser.* 130, 147–155.
- Cebrian, J., Duarte, C.M., Marba, N., Enriquez, S., 1997. Magnitude and fate of the production of four co-occurring Western Mediterranean seagrass species. *Mar. Ecol. Prog. Ser.* 155, 29–44.
- Cebrian, J., Pedersen, M.F., Kroeger, K., Valiela, I., 2000. Fate of seagrass *Cymodocea nodosa* (Ucria) Ascherson production across a process of meadow formation. *Mar. Ecol. Prog. Ser.* 204, 119–130.
- Den Hartog, C., 1970. The sea-grasses of the world. North-Holland, Amsterdam, pp. 275.
- Duarte, C.M., Marba, N., Agawing, N., Cebrian, J., Enriquez, S., Fortes, M.D., Gallegos, M.E., Merino, M., Olesen, B., Sand-Jensen, K., Uri, J., Vermaat, J., 1994. Reconstruction of seagrass dynamics: age determinations and associated tools for the seagrass ecologist. *Mar. Ecol. Prog. Ser.* 107, 195–209.

- Duarte, C.M., Merino, M., Agawin, N.S.R., Uri, J., Fortes, M.D., Gallegos, M.E., Marba, N., Hemminga, M.A., 1998. Root production and belowground seagrass biomass. *Mar. Ecol. Prog. Ser.* 171, 97–108.
- Gallegos, M.E., Merino, M., Rodriguez, A., Marba, N., Duarte, C.M., 1994. Growth patterns and demography of pioneer Caribbean seagrasses *Halodule wrightii* and *Syringodium filiforme*. *Mar. Ecol. Prog. Ser.* 109, 99–104.
- Greenway, M., 1976. The grazing of *Thalassia testudinum* in Kingston Harbour, Jamaica. *Aquat. Bot.* 2, 117–126.
- Hemminga, M.A., Harrison, P.G., van Lent, F., 1991. The balance of nutrient losses and gains in seagrass meadows. *Mar. Ecol. Prog. Ser.* 71, 85–96.
- Kenworthy, W.J., Schwarzschild, A.C., 1998. Vertical growth and short-shoot demography of *Syringodium filiforme* in outer Florida Bay, USA. *Mar. Ecol. Prog. Ser.* 173, 25–37.
- Kenworthy, W.J., Thayer, G.W., 1984. Production and decomposition of the roots and rhizomes of seagrasses, *Zostera marina* and *Thalassia testudinum*, in temperate and subtropical marine ecosystems. *Bull. Mar. Sci.* 35, 364–379.
- Kenworthy, W.J., Zieman, J.C., Thayer, G.W., 1982. Evidence for the influence of seagrass on the benthic nitrogen cycle in a coastal plain estuary near Beaufort, North Carolina, USA. *Oecologia* 54, 152–158.
- Kirkman, H., Young, P., 1981. Measurement of health and echinoderm grazing on *Posidonia oceanica* (L.) Delile. *Aquat. Bot.* 10, 329–338.
- Laborel-Deguen, J., Laborel, F., 1977. Broutage des Posidonies a la Plage du Sud. *Trav. Sci. Parc. Nation. De Port-Cross* 3, 213–214.
- Marba, N., Duarte, C.M., Cebrian, J., Gallegos, M.E., Olesen, B., Sand-Jensen, K., 1996. Growth and population dynamics of *Posidonia oceanica* on the Spanish Mediterranean coast: elucidating seagrass decline. *Mar. Ecol. Prog. Ser.* 137, 203–213.
- Mas, J., Franco, I., Barcala, E., 1993. Primera aproximacion a la cartografia de las praderas de *Posidonia oceanica* en las costas espanolas. Factores de alteracion y de regresion. *Publ. Espec. Inst. Esp. Oceanogr.* 11, 111–122.
- Mateo, M.A., Romero, J., 1997. Detritus dynamics in the seagrass *Posidonia oceanica*: elements for an ecosystem carbon and nutrient budget. *Mar. Ecol. Prog. Ser.* 151, 43–53.
- Mateo, M.A., Romero, J., Perez, M., Littler, M.M., Littler, D.S., 1997. Dynamics of millenary organic deposits resulting from the growth of the Mediterranean seagrass *Posidonia oceanica*. *Estuar. Coast. Shelf Sci.* 44, 103–110.
- Meyer, S.L., 1975. *Data Analysis for Scientist and Engineers*. Wiley, New York, p. 513.
- Ott, J., 1980. Growth and production in *Posidonia oceanica* (L.) Delile. *P.S.Z.N.I. Mar. Ecol.* 1, 47–64.
- Pedersen, M.F., Duarte, C.M., Cebrian, J., 1997. Rates of changes in organic matter and nutrient stocks during seagrass *Cymodocea nodosa* colonization and stand development. *Mar. Ecol. Prog. Ser.* 159, 29–36.
- Pergent, G., 1990. Lepidochronological analysis in the seagrass *Posidonia oceanica*: a standardized approach. *Aquat. Bot.* 37, 39–54.
- Pergent, G., 1993. L'herbier a *Posidonia oceanica* (L.) Delile. Approche structurale, fonctionnelle et appliquee. *Diplome d'Habilitation a Diriger des Recherches, Univ. Corse, Fr.*, p. 141.
- Pergent, G., Boudouresque, C.F., Crouzet, A., Meinesz, A., 1989. Cyclic changes along *Posidonia oceanica* rhizomes (lepidochronology): present state and perspectives. *P.S.Z.N.I. Mar. Ecol.* 10, 221–230.
- Pergent, G., Romero, J., Pergent-Martini, C., Mateo, M.A., Boudouresque, C.F., 1994. Primary production, stocks and fluxes in the Mediterranean seagrass *Posidonia oceanica*. *Mar. Ecol. Prog. Ser.* 106, 139–146.
- Pergent, G., Rico-Raimondino, V., Pergent-Martini, C., 1997. Fate of primary production in *Posidonia oceanica* meadows of the Mediterranean. *Aquat. Bot.* 59, 307–321.
- Pergent-Martini, C., Rico-Raimondino, V., Pergent, G., 1994. Primary production of *Posidonia oceanica* in the Mediterranean Basin. *Mar. Biol.* 120, 9–15.
- Pirc, H., 1983. Belowground biomass of *Posidonia oceanica* (L.) Delile and its importance to the growth dynamics. In: *Proceedings of the International Symposium on Aquatic Macrophytes, Nijmegen*, pp. 77–81.
- Romero, J., 1989. Seasonal pattern of *Posidonia oceanica* production: growth, age and renewal of leaves. In: *Boudouresque, C.F., Meinesz, A., Fresi, E., Gravez, V. (Eds.), Proceedings of the Second International Workshop on Posidonia Beds, GIS Posidonie Publishers, Marseille, Fr.*, pp. 92–99.
- Romero, J., Pergent, G., Pergent-Martini, C., Mateo, M.A., Regnier, C., 1992. The detritic compartment in a *Posidonia oceanica* meadow: litter features, decomposition rates and mineral stocks. *P.S.Z.N.I. Mar. Ecol.* 13, 73–83.
- Romero, J., Perez, M., Mateo, M.A., Sala, E., 1994. The belowground organs of the Mediterranean seagrass *Posidonia oceanica* as a biogeochemical sink. *Aquat. Bot.* 47, 13–19.

- Sanchez-Lisazo, J.L., 1993. Estudio de la pradera de *Posidonia oceanica* (L.) Delile de la reserva marina de Tabarca (Alicante): fenologia y produccion primaria. Ph.D. Thesis, Universidad de Alicante, Spain, p. 130.
- Semroud, R., Mezegrane, S., Soltane, L., 1990. Etude lepidochronologique de *Posidonia oceanica* dans la region d'Alger (Algerie): donnees preliminaires. Rap. Commun. Int. Mer. Medit. 32, 10.
- Shepherd, A., 1987. Grazing by the sea-urchin *Paracentrotus lividus* in *Posidonia oceanica* beds at Banyuls, France. In: Boudouresque, C.F. (Ed.), Colloque International sur *Paracentrotus lividus* et les oursins comestibles, GIS Posidonie Publishers, Marseille, Fr., pp. 83–96.
- Thayer, G.W., Bjorndal, K.A., Ogden, J., Williams, S., Zieman, J., 1984. Role of larger herbivores in seagrass communities. Estuaries 7, 351–376.
- Vermaat, J.E., Fortes, M.D., Agawin, N.S.R., Duarte, C.M., Marba, N., Uri, J., 1995. Meadow maintenance, growth and productivity in a mixed Philippine seagrass bed. Mar. Ecol. Prog. Ser. 124, 215–255.
- Williams, S.L., 1990. Experimental studies of Caribbean seagrasses bed development. Ecol. Monogr. 60, 449–469.
- Zavodnik, N., Jaklin, A., 1990. Long-term changes in the Northern Adriatic marine phanerogam beds. Rap. Commun. Int. Mer. Medit. 32, 15.