

Primary production, stocks and fluxes in the Mediterranean seagrass *Posidonia oceanica*

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ABSTRACT: Primary production in a *Posidonia oceanica* seagrass meadow (blades, sheaths and rhizomes) was estimated at 3 sites in Lacco Ameno Bay (Ischia, Italy). Foliar primary production ranged from 51 to 142 g dry wt m² yr⁻¹ for sheaths and 167 to 530 g dry wt m² yr⁻¹ for blades. Rhizome production ranged from 20 to 42 g dry wt m² yr⁻¹. The largest part of primary production was degraded *in situ* in the litter (42%); the remainder was either exported to other ecosystems (29%) or buried in the mat (29%). The loss of matter due to burial of sheaths and rhizomes in the mat, a phenomenon that is unique to *Posidonia oceanica* meadows, is considerable.

KEY WORDS: Seagrass · *Posidonia oceanica* · Primary production · Litter

INTRODUCTION

The seagrass *Posidonia oceanica* (Linnaeus) Delile is, with *Thalassia testudinum* Banks ex K nig, *Zostera marina* Linnaeus and several Australian seagrasses, one of the most productive marine phanerogams (Parker et al. 1963, Greenway 1974, Sand Jensen 1975, McRoy & McMillan 1977, Nienhuis & De Bree 1980, Hillman et al. 1989). Leaf production, measured by various techniques (Oxygen, carbon-14, leaf marking, lepidochronology) ranges from 300 to 2000 g dry weight m⁻² yr⁻¹ (Bay 1984, Thelin & Giorgi 1984, Libes 1985, Romero 1989, Pergent & Pergent-Martini 1991). As in most marine phanerogam-based ecosystems, only a small amount of the leaf production is consumed on the plant by macro-invertebrates (echinoderms, crustaceans) and fishes; most of the consumption of leaves occurs through the action of crustaceans, gastropods and microorganisms in the litter (Fenchel 1970, 1977, Wittmann et al. 1981). The flux of matter from primary production follows mainly 1 of 2 pathways: (1) When the leaves fall, the blade becomes detached from the plant and contributes to the litter, where decomposition occurs (Peres 1953, Picard 1965, Fenchel

1977, Francour 1990, Pergent-Martini et al. 1990, Romero et al. 1992). (2) The sheathing base of the leaf remains attached to the rhizome within the mat where the process of decay is very slow (Molinier & Picard 1952, Boudouresque 1986, Pergent 1990, Romero et al. 1992).

The primary production that goes into the litter either remains within the meadow, where it undergoes a kinetic process of rapid decay that can be accurately estimated (Pergent-Martini et al. 1990, Romero et al. 1992), or is exported to other ecosystems where it may represent a trophic input of considerable importance (Peres 1953, Picard 1965, Fenchel 1977). For example, the gut of the sea-urchin *Paracentrotus lividus* Lamarck in algae-dominated communities distant from *Posidonia oceanica* meadows can contain as much as 31% of *Posidonia oceanica* leaves (Verlaque & Nedelec 1983).

The primary production that is buried in the mat (sheaths and rhizomes) decays very slowly (Francour 1985, Pergent-Martini et al. 1990, Romero et al. 1992). The sheaths and rhizomes are in fact highly resistant to putrefaction, and may persist for thousands of years within the mat (Boudouresque et al. 1980). The con-

struction of a matte (living and dead rhizomes and roots, with the interstices filled with sediment) is one of the unique characteristics of *Posidonia oceanica* meadows (Pergent 1990).

In the present study, we attempted to quantify the flux of matter (dry weight) and of mineral elements (C, N, P) originating in the leaf primary production of *Posidonia oceanica* and to follow their distribution and dynamics both within and outside of the ecosystem, by analysing (1) consumption *in situ*, (2) litter degraded within the meadow, (3) litter exported to other ecosystems, and (4) stocking within the matte.

MATERIAL AND METHODS

Sampling sites. Samples were taken around the Island of Ischia (Gulf of Naples, Italy) within the *Posidonia oceanica* meadow of Lacco Ameno (Colantoni et al. 1982, Mazzella et al. 1989) at 3 sites (Fig. 1): LA05 (4 to 6 m depth), LA10 (10 to 12 m), and LA20 (20 to 22 m).

Estimation of primary production, using lepidochronological data. Twenty orthotropic rhizomes were collected at random by scuba diving (80 to 90% of rhizomes are orthotropic in this meadow), every month between July 1988 and July 1990, at the 3 sites. Meadow density (number of shoots per square meter) was estimated *in situ* using a 35 × 35 cm quadrat. In all, 21 measurements were taken for each site (meadow density is constant throughout the year for *Posidonia oceanica*).

For each rhizome, the sheaths were carefully detached and numbered starting from the older (near the base) to the more recent ones (near the living leaves). The length of each sheath was carefully mea-

sured and a thin cross section was made between 10 and 12 mm above the base of the sheath. Its thickness at the centre was measured under a microscope (Pergent 1990). These sheaths show cyclic variations in their thickness, each cycle corresponding to a 1 yr period. The study of these chronological cycles is termed lepidochronology (Pergent 1990).

Primary production was estimated following Pergent & Pergent-Martini (1991), on the basis of 3 parameters:

(1) Number of leaves produced annually. This parameter could be determined for the study period from the leaf renewal cycle estimated from lepidochronological data, and for previous years from the mean number of scales per cycle (Pergent 1990, Pergent & Pergent-Martini 1990).

(2) Leaf length. This corresponds to the mean length of the oldest blades and sheaths, determined for each month between July 1988 and July 1990. Only entire leaves (still possessing their apex) were taken into account (Pergent & Pergent-Martini 1991).

(3) Leaf density, i.e. leaf weight by unit of length (Sand-Jensen 1975). In the present study, the parameter taken into consideration was final density, just before shedding.

We also measured length, dry weight (dw), and C and N contents (Micro CHN Determinator, CHN 800) of the rhizome segments, determined between each pair of sheaths of minimum thickness, corresponding to a 1 yr period.

Number and biometry of living leaves (foliar shoots) were determined using the technique of Giraud (1979). Coefficient A (percentage of leaves which have lost their apex) was also noted. Constant dry weight (70°C) and C and N contents of the oldest leaf from each shoot were measured (calcareous epiphytes were previously removed by scraping with a razor blade).

Estimation of litter stocks. Samples were taken using a suction device inside a 35 × 35 cm quadrat every 3 mo (July and October 1988, January, April and July 1989) at LA05, LA10 and LA20 with 3 replicates in each case. The samples included all the material lying on the sediment, and the sediment itself, to a depth of 5 to 10 cm. The samples were sorted immediately, after thorough washing with running seawater, into 3 fractions according to Romero et al. (1992): (1) coarse leaf litter (>0.8 cm), (2) fine leaf litter (between 0.1 and 0.8 cm), (3) material from the belowground parts (dead rhizomes, roots and leaf base sheaths). These fractions were

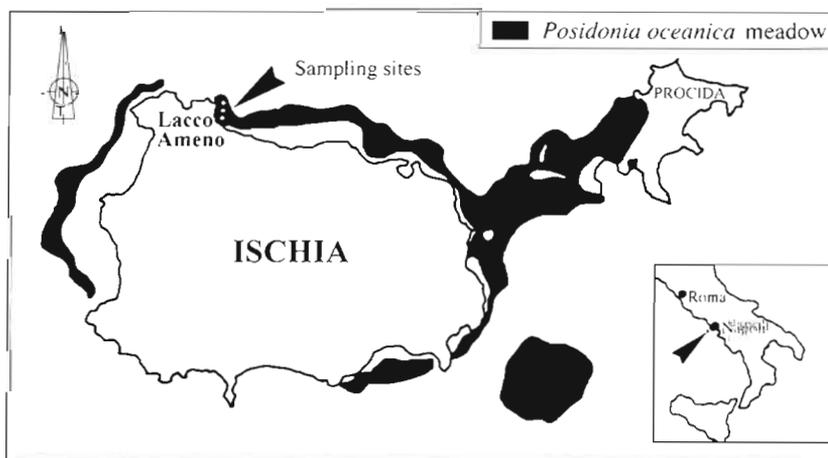


Fig. 1 Ischia island, Italy, showing the location of the study area. Location of *Posidonia oceanica* meadow shown according to Colantoni et al. (1982)

dried at 70°C until reaching a constant weight, then weighed separately.

Decay experiments. Classic litter bag experiments were performed at sites LA05 and LA20 (Bocock et al. 1960, Godshalk & Wetzel 1978, Brock et al. 1985, Josselyn et al. 1986). A known amount (30 g fresh wt) of senescent leaves *Posidonia oceanica* was enclosed in a series of mesh bags (mesh size = 0.1 cm). The bags were then placed in the meadow and collected at increasing time intervals. At each sampling, 3 bags were collected at random and taken to the laboratory. There the samples were washed, the fauna was removed and the litter then sorted into 2 fractions (coarse leaf litter and fine leaf litter). These fractions were weighed separately after drying at 70°C to constant weight.

Belowground parts. Samples of rhizomes and roots were taken using a diver-held corer (Pirc 1983) at LA05 and LA20, penetrating to around 20 cm depth in the sediment. The samples were washed carefully, divided into 3 vertical sections and sorted into the following fractions: (1) living rhizomes, (2) dead rhizomes and remaining leaf sheaths, (3) living roots, (4) dead roots and (5) fine undifferentiated fraction (between 0.1 and 0.8 cm), the fractions were then weighed as described above. The criteria used in the fractioning of the belowground parts of the plant were those described in Francour & Semroud (1992).

Lepidochronological analysis was used to establish the exact year of formation of a given rhizome section or a given leaf base, and consequently the decay rate of the associated tissues (Pergent 1990, Pergent & Pergent-Martini 1990).

Chemical elementary composition. In order to assess the turnover of various biogenic elements in the different compartments, the elementary composition (carbon, nitrogen and phosphorus) was determined for subsamples, dried at max. 70°C, of the following items:

(1) litter from LA05 and LA20, (2) material from the decay experiments (LA05 and LA20), and (3) below-ground parts (sheaths and rhizomes).

The subsamples were ground to a fine powder to determine C and N content. P content was analysed using ICP (Induction Coupling Plasma) after wet acid digestion following Delgado (1986), adapted to a microwave digester as described by Mateo & Sabate (1989).

RESULTS

Leaf primary production

The mean number of leaves produced per shoot during a 1 yr period (average between data from July 1988 to July 1989 and from July 1989 to July 1990) ranged from 6.6 to 7.7 (Table 1).

Leaf density depends on the width and thickness of leaves, and varies according to age and season of formation (Bedhomme et al. 1983, Thelin & Giorgi 1984). It ranged from 7.7 to 9.9 mg dw cm⁻¹ for sheaths and from 3.6 to 4.1 mg dw cm⁻¹ for blades (Table 1).

Annual mean length for the oldest adult leaves ranged from 32.0 to 39.4 cm (Table 1).

Mean net production of leaves ranged from 0.86 to 1.42 g dw shoot⁻¹ yr⁻¹, depending on depth (Table 1); of this production, 21 to 23% was in the sheaths and 77 to 79% in the blades. Meadow density (from 253 ± 23 to 473 ± 44 shoots m⁻²) was used to evaluate net primary production of the meadow in each site (Table 1); it ranged from 218 to 672 g dw m⁻² yr⁻¹.

The mean proportion of carbon in the *Posidonia oceanica* leaves, measured at the 3 sites with a Micro CHN Determinator, was 27.4 ± 1.5% of dry weight (Pergent & Pergent-Martini 1991); the mean net primary production of leaves was 184, 128 and 60 g C m⁻² yr⁻¹ at 5, 10 and 20 m depth, respectively (Fig. 2).

Table 1. *Posidonia oceanica*. Net foliar primary production (per shoot and per m²) during a 1 yr period (average between July 1988 to July 1989 and July 1989 to July 1990), 3 sites at Lacco Ameno (Ischia, Italy)

Depth (m)	Leaf section	No. of leaves yr ⁻¹	Leaf density (mg dw cm ⁻¹)	Mean leaf length (mm)	Meadow density (m ²)	Leaf primary production	
						g dw shoot ⁻¹ yr ⁻¹	g dw m ⁻² yr ⁻¹
5	Sheath	7.65	9.9	39	473	0.30	142
	Blade	7.65	4.1	355	473	1.12	530
	Total			394		1.42	672
10	Sheath	7.55	9.0	41	351	0.29	102
	Blade	7.55	3.9	349	351	1.04	365
	Total			391		1.33	467
20	Sheath	6.55	7.7	40	253	0.20	51
	Blade	6.55	3.6	281	253	0.66	167
	Total			320		0.86	218

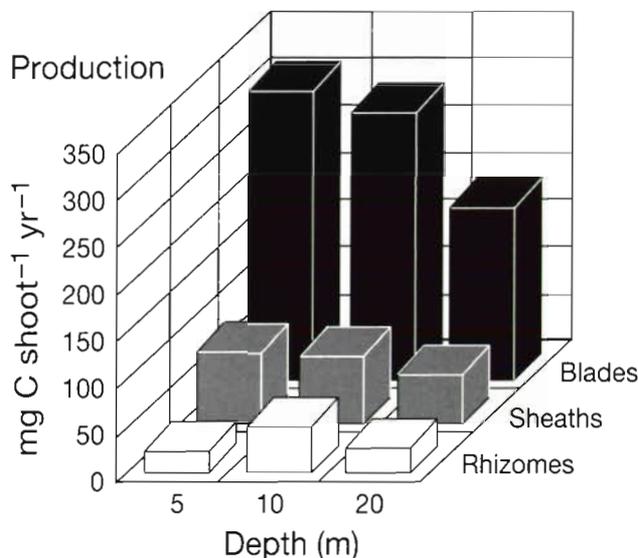


Fig. 2. *Posidonia oceanica*. Net primary production by depth around Ischia island, Italy

Rhizome production

Net rhizome production was low but not insignificant in comparison with leaf production: 0.08, 0.12 and 0.08 g dw shoot⁻¹ yr⁻¹ at 5, 10 and 20 m depth, respectively, or 37.8, 42.1 and 20.2 g dw m⁻² yr⁻¹ (between 6 and 9% of total production).

The mean percentage of carbon in segments of rhizomes that had appeared during the 2 yr of our study at Ischia was 34.8 ± 0.44%; mean rhizome production of the meadow (in g C m⁻² yr⁻¹) was, between July 1988 and July 1990, 13.0 at LA05, 14.7 at LA10 and 7.1 at LA20 (Fig. 2).

Table 2. Coefficient *A* for *Posidonia oceanica* leaves (%) in the Mediterranean (values are annual averages). Ad. = adult leaves; Int. = intermediate leaves

Locality	Mean depth (m)	Ad.	Int.	Average (Ad. and Int.)	Source
Algiers Bay (Algeria)	2	99.3	44.7	73.5	Semroud et al. (1990)
	8	93.9	30.6	63.7	
Urla-Iskele (Turkey)	2	74.0	11.2	48.1	Pergent & Pergent-Martini (1988)
	5	77.4	12.0	50.1	
Port-Cros (France)	2	64.6	27.0	51.2	Pergent & Pergent-Martini (1988)
	11	27.5	3.8	19.2	
	23	27.2	0.8	19.0	
Banyuls-sur-Mer (France)	2	94.9	41.7	79.4	Pergent & Pergent-Martini (1988)
	12	56.8	14.4	44.4	
	19	44.2	9.1	34.3	
Ischia (Italy)	5	43.1	5.9	30.9	Present study
	10	24.8	2.8	19.3	
	20	24.8	2.0	18.9	

Consumption *in situ*

Predation pressure from grazers was estimated using Coefficient *A*; it would appear that around the Island of Ischia, consumption of leaves on living plants is low (Table 2).

Primary production contributing to the litter and kinetics of decay

We assumed that consumption of living leaves was insignificant (see 'Discussion'). Consequently, the amount of primary production contributing to the litter corresponds to that of the leaf blade; this is in fact the only part of the leaf that becomes detached, since the sheath remains attached to the rhizome. This material flux ranged from 46 (20 m depth) to 145 (5 m depth) g C m⁻² yr⁻¹.

The decay kinetics of *Posidonia oceanica* leaf blades, estimated on the basis of decay experiments (litter bags), followed a simple negative exponential model, with a high goodness of fit (Romero et al. 1992; Fig. 3). Weight loss was more rapid at 5 m than at 20 m depth for equivalent periods. The decay rate of *k* (exponent of the model) was around -0.0062 d⁻¹ for LA05 and -0.0033 d⁻¹ for LA20 (decay experiment between October and April).

Primary production stocked in the matte and kinetics of decay

The primary production that is stocked in the matte (belowground) corresponds to (1) the sheath bases of the leaves which remain attached to the rhizome, and (2) the rhizomes themselves. This represents a major part of the primary production, between 21 and 52 g of C m⁻² yr⁻¹, or an average of 29% of the total net primary production (Table 3).

The decay kinetics of the sheaths and rhizomes within the matte were estimated by means of lepidochronological data. Sheath decay was low; from these data, and again assuming a simple exponential model, a decay rate of *k* = -0.216 yr⁻¹ at 5 m and -0.110 yr⁻¹ at 20 m depth could be computed. Similarly, a model of rhizome decay was established but no weight loss was evident. This observation

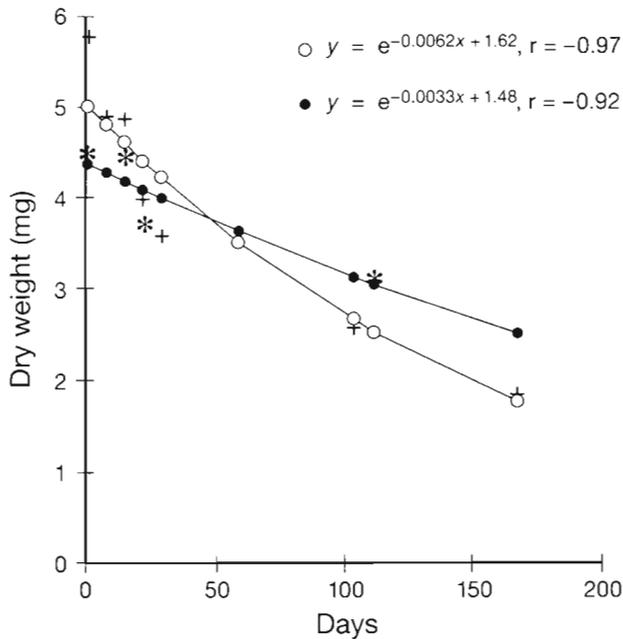


Fig. 3. *Posidonia oceanica*. Decay kinetics of leaves at Ischia, at 5 m (+) and 20 m (*) depth

is probably due to the fact that rhizomes remain alive for several years (Francour 1985).

Changes in C, N and P content of the belowground parts were analysed. There was a slight carbon loss with time in sheaths (principally at Sites LA05 and LA20; $r = 0.85$ and 0.84), while N and P content decreased sharply in the rhizomes but remained constant (N) or increased (P) in sheaths (Table 4).

DISCUSSION

Coefficient *A* (Giraud 1979) is purely descriptive and can only be considered an overall estimation. Loss of the apex may in fact be due either to consumption *in situ* of part of the plant by a grazer, or to hydrodynamic action, especially in shallow sites. Coefficient *A* is therefore insufficient to allow quantitative estimation of this trophic flux and can, at best, serve for comparison between localities or between

depths. The low *A* value recorded in the Lacco Ameno meadow, compared with other Mediterranean sites, would appear to suggest that this flux is particularly weak at Ischia (Table 2). This finding is no doubt related to the fact that, in this meadow, we observed very small numbers of macro-grazers, which are generally responsible for most of this consumption *in situ* [e.g. *Sarpa salpa* Linnaeus (Harmelin-Vivien & Francour 1992), *Paracentrotus lividus* (Bulteel et al. 1992)]. In addition, it would appear that most of this material flux is returned to the litter after passing through the digestive system of the grazers, and that it is mostly the leaf epiphyte which are assimilated, at least for *S. salpa* (Dauby & Coulon 1993). It may thus be suggested that the main result of grazer action is the mechanical fragmentation of the leaves, which favours the action of detritus feeders in the litter. This phenomenon has also been noted by other investigators for other phanerogam species (Ogden 1980, Thayer et al. 1984). In fact, the seagrass grazers apparently are not efficient digesters and typically absorb less than 50% of the ingested material (Thayer et al. 1984). Also, in some cases, this recycling may be functionally more important in transferring nutrients to adjacent ecosystems than in supplying nutrients to the seagrass ecosystem; defecation may not occur in the feeding area but rather in the area where the animal rests (Ogden 1980).

Nevertheless, even if direct consumption of marine phanerogam leaves by grazers appears to be generally slight (McRoy 1966, Mann 1972, Greenway 1976, Ott & Maurer 1977, Hemminga et al. 1991), this material flux varies considerably according to the species in question, the site and particularly grazer density (Greenway 1976, Ott 1981). Even in *Thalassia testudinum*, where direct consumption by grazers (e.g. sea urchins) appears to be particularly high for a marine phanerogam (Ott 1981), blade consumption by grazing ranges from between 5 and 10% (Zieman et al. 1979) to 50% (overgrazing by echinoids; Greenway 1976). In *Posidonia australis*, 3% of leaf consumption (in carbon) is by grazers, whereas in *P. oceanica*, Ott & Maurer (1977) suggest a value of 4% of standing stock (or 9% of net production).

Table 3. Estimation and distribution of *Posidonia oceanica* net primary production around Ischia island

Site	Production ($\text{g C m}^{-2} \text{ yr}^{-1}$)			Flux ($\text{g C m}^{-2} \text{ yr}^{-1}$)		
	Sites	Blade	Sheath	Exportation	Decay	Matte
LA05	145.1	38.9	13.2	50.8	94.3	52.1
LA10	100.0	27.9	14.7	49.0	51.0	42.6
LA20	45.7	13.9	7.0	16.9	28.8	20.9

The part of the primary production entering the litter appeared to be the largest, ranging from 69 to 74% of total annual production (in carbon). The litter stock fluctuates over the year according to input (e.g. leaf fall) and output (export and decay). On the basis of (1) the bathymetric distribution of litter, (2) inputs of new litter, i.e. shedding of leaf blades, in the meadow (from primary production of blades), and (3) the

Table 4. *Posidonia oceanica*. Decay kinetics of sheaths and rhizomes (C, N, and P content) in the matte

Site Year	Sheaths			Rhizomes		
	% C	% N	% P	% C	% N	% P
LA05						
1989	36.6	0.31	0.017			
1988	34.4	0.36	0.016	42.1	3.79	0.26
1987	33.1	0.33	0.019	42.2	2.06	0.14
1986	34.3	0.35	0.015	41.6	1.63	0.11
1985	32.1	0.48	0.026	42.3	0.76	
LA10						
1989	36.0	0.39				
1988	36.3	0.52	0.019	42.7	3.92	0.063
1987	35.9	0.34	0.018	43.0	3.43	0.040
1986	36.9	0.41	0.022	43.7	2.04	0.030
1985	37.7	0.36	0.021	43.3	1.36	0.031
1984	35.2	0.41	0.025	42.5	0.56	0.028
1983	36.2	0.35	0.123			0.029
1982	35.4	0.43	0.026	42.3	0.94	
LA20						
1989	31.2	0.35	0.014			
1988	32.0	0.34	0.016	40.5	3.80	0.094
1987	31.1	0.37	0.021	41.2	3.68	
1986	30.1	0.31	0.012	41.0	2.06	
1985	30.5	0.34	0.027	42.2	0.99	0.039
1984	30.4	0.39	0.026	41.2	0.89	0.043
1983	29.8	0.37	0.022	40.6	0.89	0.031
1982	30.6	0.42	0.036	42.4	0.63	0.035
1981	29.4	0.29	0.028	41.9	2.69	0.030
1980	29.2	0.39	0.030	40.8	0.56	0.030

decay rate of leaf litter *in situ* (from decay experiments), Romero et al. (1992) established a simplified model for deducing the amount of litter exported out of the ecosystem. They estimated it to be, on average, 50% for the whole meadow between 1 and 32 m depth, with wide variations according to depth. Using this model with our own primary production data, for the 3 stations studied, we estimate the exportation rate (in carbon) to be 35, 49 and 37% of litter (or 26, 34 and 25% of total primary production), at 5, 10 and 20 m depth, respectively (Table 3). These values are similar to those reported by Francour (1990) at Port-Cros (Var, France) between 3 and 11 m depth (40% exported on average), and by Ott (1980) at Ischia (3 to 6 m depth), who estimated that 55% of blade production was exported.

For other seagrasses, Hemminga et al. (1991) demonstrated that the exportation rate may vary widely according to the station studied (1 to 30% for *Zostera marina*: in Josselyn et al. 1983, Bach et al. 1986), or the species (1% for *Thalassia testudinum*: Zieman et al. 1979; 27 to 79% for *Syringodium filiforme*: Fry & Virnstein 1988).

The relative stability of the values recorded for *Posidonia oceanica* (between 35 and 55% exported) may

be explained, on the one hand, by the similarity of the sites studied (Ischia and Port-Cros), in particular with regard to bathymetry and hydrodynamism, and on the other by the fact that the measurements were carried out in meadows situated at relatively great depth (3 to 20 m) and therefore less exposed to hydrodynamic variations than shallow water meadows.

There is little recycling of the primary production that is buried in the matte (sheaths and rhizomes), and most of this production is lost to the ecosystem (29% of the net primary production). In contrast to above-ground primary production, where the turnover time is low (on the order of months), for the belowground part the turnover time is much longer (from years to centuries). Our data would appear to indicate that the *Posidonia oceanica* ecosystem acts as a sink for the various biogenic elements.

CONCLUSION

With the exception of the part of primary production that is consumed *in situ*, but which contributes for the most part to the litter (faeces), we have quantified the various fluxes derived from primary production (Fig. 4). It appears that most of the primary production (in carbon) decays *in situ* (42%), while the remainder is distributed more or less equally between export (29%) and burial in the matte (29%). The main process by which the primary production in the *Posidonia oceanica* community is used is consumption by detritus-feeders.

Both immobilization (in the matte) and export represent net losses of biogenic elements for the system. The loss of matter due to burial of sheaths and rhizomes in the matte, a phenomenon that is unique to *Posidonia* meadows, is considerable.

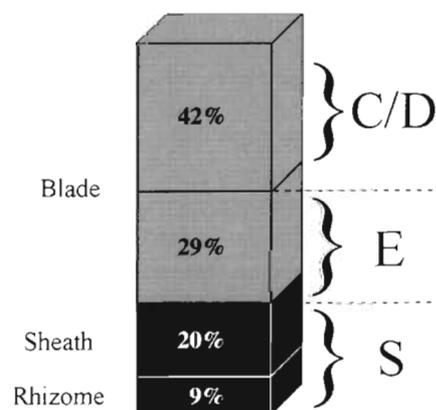


Fig. 4. *Posidonia oceanica*. Fluxes derived from the primary production: C/D, consumption and degradation *in situ*; E, exportation; S, stocked in the matte

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