

Nutrient mass balance of the seagrass *Posidonia oceanica*: the importance of nutrient retranslocation

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ABSTRACT: The seasonal nutrient mass balance of the dominant seagrass of the Mediterranean, *Posidonia oceanica* (L.) Delile, was evaluated in NE Spain in order to test the hypothesis that the effect of seasonal nutrient imbalance can be reduced by the reutilization of internal nutrient pools. To this end we investigated the seasonal and age-dependent variability of nitrogen and phosphorus concentration of the leaves, inferring from these data values of seasonal nitrogen and phosphorus incorporation, uptake, losses and retranslocation. Incorporation of nitrogen and phosphorus in leaves peaked in June and was lowest in September, thus following the seasonal growth pattern of the plant. Retranslocation of nitrogen and phosphorus was high from May to September and close to zero during the rest of the year. Losses of nitrogen and phosphorus were highest at the end of summer, associated with the major biomass losses. Nitrogen uptake by leaves reached maximum values in winter and was lowest during August-September, while phosphorus uptake was highest in spring and lowest in August-September. On an annual basis nitrogen and phosphorus uptake accounted for 60 and 41% of the total nutrient incorporation, respectively, while retranslocation of nutrients from old tissues accounted for the remaining 40 and 59%. Although roots and rhizomes function as sources of nutrients at the beginning of the summer, their contribution to the seasonal nutrient budget seemed to be minor.

KEY WORDS: Mediterranean Sea · Phosphorus · Nitrogen · Uptake · Incorporation

INTRODUCTION

Posidonia oceanica (L.) Delile is the dominant seagrass species of the Mediterranean Sea and one of the most important primary producers in its coastal waters (e.g. Buia et al. 1992). Several factors control the seasonality of the primary production of this seagrass. Large-scale factors such as light and temperature seem to be most important (Alcoverro et al. 1995), while nutrients, even though the Mediterranean is an oligotrophic sea (Poole & Atkins 1929, Weinberg 1976, Ivanoff 1977), seem to play a secondary role (Alcoverro et al. 1997). However, maintenance of high productivity requires high nutrient incorporation, especially in late spring-early summer, when seagrasses grow fast

and nutrient availability is low (Alcoverro et al. 1995). In terrestrial vegetation, one of the major mechanisms by which plants adjust to nutrient imbalance is by conservation through decreased losses by leaching (Tukey 1970) and by translocation of a large proportion of nutrients from senescing leaves before abscission (Shaver & Melillo 1984). Both these processes contribute to the high nutrient use efficiency of plants growing under nutrient-limited conditions (Vitousek et al. 1982).

Several authors investigated the chemical elementary composition of the seagrasses (see Duarte 1990). *Posidonia oceanica* shows high N concentrations during winter and a decline during spring and summer (Pellegrini 1971, Bay 1978, Pirc 1985, Pirc & Wollenweber 1988, Alcoverro et al. 1995). The general trend of a decline in nutrient concentration with increasing tissue age (Patriquin 1972, Harrison & Mann 1975, Thayer et al. 1977, Walker et al. 1989) indicates that nutrients are

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either leached to the external medium or retranslocated from old tissues before these are lost. Nutrient reclamation may be an important mechanism in the annual seagrass nutrient budget (Patriquin 1972, Borum et al. 1989, Pérez-Llorens & Niell 1989, Hemminga et al. 1991, Pedersen & Borum 1992, Stapel & Hemminga 1997). Leaching losses apparently seem low (Borum et al. 1989, Pedersen & Borum 1992) and most of the nitrogen lost from old tissues is recovered in young leaves.

In this paper, we test the hypothesis that seasonal nutrient imbalance in the seagrass *Posidonia oceanica* can be alleviated by nutrient conservation. A preliminary attempt to evaluate the role of retranslocation in the nutrient budget of the plant has been done in a previous work (Alcoverro et al. 1997), but was based on a very general leaf mass balance. Here we report results of a much more accurate balance from a totally new dataset, which includes an assessment of the tissue age as a source of variability and an evaluation of the role of below-ground organs. This allows more precise evaluation of nitrogen and phosphorus incorporation, uptake, losses and retranslocation.

METHODS

The study was conducted in a *Posidonia oceanica* meadow located in the Medes Islands, NE coast of Spain (42° 2' N, 3° 13' E) near the upslope limit of the meadow (–5.0 m, see Alcoverro et al. 1995). Every 2 mo (i.e. 7 sampling events, from November 1992 to December 1993), leaf growth was estimated using a modification of the leaf marking technique (Zieman 1974, Romero 1989a). To do this, 10 shoots, distributed at random over an area of ca 100 m², were marked at each sampling event; all leaves within a shoot had 2 parallel holes punched in them with a hypodermic needle just above the ligula of the outermost leaf. At the same time, shoots marked in the previous visit were collected, and, in the laboratory, 'new' (tissue below the mark) and 'old' tissue were sorted, dried at 70°C and weighed to obtain leaf elongation (new tissue, g dry weight [dw] shoot⁻¹ d⁻¹) and biomass (new + old tissue, g dw shoot⁻¹).

At each sampling event, 30 additional shoots were collected at random over an area of ca 100 m². In the laboratory, epiphytes were removed using a razor blade, and shoots were sorted into different parts as follows: leaf sheaths (only in 5 sampling events), roots, rhizomes and leaf tissue of different ages. Tissue age was considered instead of leaf age due to the longevity of the leaves of *Posidonia oceanica*, which can include a wide age range, from apex to basal parts. Four age classes were considered: from 0 to 25 d (A1), from 25 to

50 d (A2), from 50 to 100 d (A3) and from 100 to 150 d (A4). Age determination was done according to the leaf growth curves of Romero (1989b) combined with direct data of leaf growth.

All these fractions were dried (70°C until constant weight), weighed, ground and analyzed for C, N and P concentrations. Total carbon and nitrogen were determined using a Carlo-Erba CHN Analyzer and phosphorus was determined by induced coupled plasma after wet acid digestion of the material (Mateo & Sabaté 1993). Since a single shoot did not provide enough material for the element analysis of the photosynthetic tissue, the 30 shoots were randomly sorted into 3 groups of 10 shoots each to ensure adequate replication; each analysis was performed in pooled material from these 10 shoots, resulting in a total of 3 replicates per age class and sampling event. For the rest of the plants (rhizome and roots) 3 to 6 replicated measures were done per sampling event.

For the photosynthetic parts of the plant (leaves), within-shoot yearly nutrient mass balance was computed using 25 d intervals; nutrient concentration and leaf growth were obtained by linear interpolation between sampled times and sampled age classes. The seasonal trend of both leaf growth and nutrient concentration in leaves seems to be robust enough (Romero 1989b, Alcoverro et al. 1995) to allow these interpolations.

Shoot biomass losses were computed as:

$$BL_i = 1/25 (B_{i-25} - B_i) + P_i \quad (1)$$

where BL_i are the biomass losses between i and $i-25$ (g dw shoot⁻¹ d⁻¹), i is the time (days) from the beginning of the experiment, B_i is the total shoot biomass (as g dw shoot⁻¹) at time i and P_i is shoot growth between $i-25$ and i (as g dw shoot⁻¹ d⁻¹).

The within-shoot tissue age composition was estimated using the following equation:

$$B_{ij} = B_{i-25, j-1} \text{ except for } j = 1, \text{ where } B_{i1} = P_i \times 25 \quad (2)$$

and except for those k ($k \leq n$) verifying

$$\sum_{j=1}^k B_{ij} > B_{i \bullet}$$

for which

$$B_{ik} = B_{ik+1} = \dots = B_{in} = 0 \quad (3)$$

and

$$B_{ik-1} = B_{i \bullet} - \sum_{j=1}^{k-1} B_{ij} \quad (4)$$

$$\text{with } B_{i \bullet} = \sum_{j=1}^n B_{ij}$$

where j is the age class in 25 d intervals, $n = 6$ being the total number of age classes, B_{ij} is the biomass (as g dw shoot⁻¹) of age class j at time i .

Initial age distribution (for November) was obtained from Romero (1989b).

Assuming that retranslocation of nutrients occurs before loss of leaves take place, nitrogen and phosphorus leaf retranslocations were estimated as:

$$LR_i = 1/25 \left(\sum_{j=1}^n (C_{i-25,j} - C_{i,j+1}) B_{i-25,j} \right) \quad (5)$$

where LR_i is the leaf retranslocation (in mg element shoot⁻¹ d⁻¹) between time i and $i-25$ and C_{ij} is the concentration (as % relative to dw) of the given element for the age class j at time i .

Nutrient incorporation was estimated as:

$$NI_i = P_i \times C_{i1} \quad (6)$$

where NI_i is the nutrient incorporation (as mg element shoot⁻¹ d⁻¹) between time i and $i-25$, P_i is shoot growth between $i-25$ and i (as g dw shoot⁻¹ d⁻¹), C_{i1} is the element concentration (as % of dw) at time i of the youngest age class (0 to 25 d).

Nutrient losses were computed as:

$$NL_i = BL_i C_{ij_{\max}} \quad (7)$$

where NL_i are the nutrient leaf losses (as mg element shoot⁻¹ d⁻¹) between i and $i-25$, BL_i are the biomass losses (as g dw shoot⁻¹ d⁻¹) between i and $i-25$ and $C_{ij_{\max}}$ is the element concentration (as % relative to dw) of the oldest tissue age class which was present at time i .

Nutrient uptake per shoot was estimated as:

$$NU_i = NL_i + 1/25 \left(\sum_{j=1}^n B_{ij} C_{ij} - \sum_{j=1}^n B_{(i-25)j} C_{(i-25)j} \right) \quad (8)$$

where NU_i is the nutrient uptake (as mg element shoot⁻¹ d⁻¹) between i and $i-25$. This estimate covers total uptake per shoot and, thus, includes both root and leaf uptake.

No such detailed estimate was possible for the below-ground organs (roots and rhizomes), but the possibility of seasonal storage in these organs was evaluated by computing a budget of gains/losses between successive sampling events, as a product of standing biomass multiplied by nutrient concentration change (positive or negative). This approach is reliable in the case of *Posidonia oceanica* due to the peculiarities of its below-ground biomass. In effect, we assume here that rhizome + root biomass is constant throughout the year (see Cebrián et al. 1997) and equal to the values reported by Mateo & Romero (1997): 1.16 g dw shoot⁻¹ for rhizomes and 0.74 g dw shoot⁻¹ for roots. In addition, we also assume that processes such as nutrient incorporation are modest in relation to total nutrient pools: annual values of nutrient (N and P) incorporation and losses never exceed 6% of the total nutrients accumulated in these parts (Mateo & Romero 1997).

The potential role in the nutrient economy of the other non-photosynthetic plant parts (i.e. leaf bases or petioles) was also investigated using the same approach (mass budget).

Two-way ANOVA was used to partition the variance observed in nutrient concentration (nitrogen, carbon and phosphorus) of leaves into variance among sampling events (time), tissue type (A1 to A4) and their interaction. One-way ANOVA was performed to assess the variance in leaf sheath nutrient concentration due to differences among sampling events (Sokal & Rohlf 1981).

RESULTS

Leaf carbon concentration differed with leaf age (Table 1), with the highest values found in the youngest tissues (A1, Fig. 1a) and the lowest in the old tissue (A4, Fig. 1a). There were also significant differences among sampling events (Table 1), with the highest values observed in December and the lowest in May. However, both factors accounted only for a minor part of total variability (14 and 11%, respectively).

Leaf nitrogen concentration was highly seasonal, with high values observed in winter and low values at

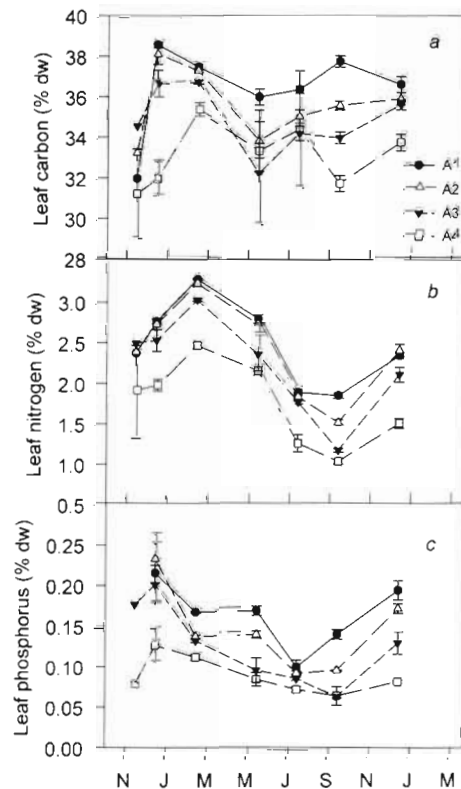


Fig. 1. Changes with time in concentrations of carbon, nitrogen and phosphorus in leaves of different age (as % of dw). Mean values and standard error

Table 1. ANOVA table summarizing the significance of the differences found in carbon, nitrogen and phosphorus concentration in leaves among age classes (Tissue) and among sampling events (Time) and in sheaths, rhizomes and roots (only Time factor considered)

Variable	Factor	df	MS	p	% variance
% carbon leaves	Time	6	17.3	0.026	11
	Tissue	3	42.0	<0.001	14
	Time × Tissue	18	5.5	0.684	–
	Error	83	6.8	–	–
% nitrogen leaves	Time	6	4.8	<0.0001	72
	Tissue	3	2.25	<0.0001	17
	Time × Tissue	18	0.05	0.176	–
	Error	83	0.042	–	–
% phosphorus leaves	Time	6	0.0290	<0.0001	50
	Tissue	3	0.0243	<0.0001	21
	Time × Tissue	18	0.0017	0.0150	9
	Error	85	0.0008	–	–
% carbon sheaths	Time	4	8.65	0.001	62
	Error	17	1.24	–	–
% nitrogen sheaths	Time	4	0.65	<0.0001	86
	Error	15	0.028	–	–
% phosphorus sheaths	Time	4	0.0027	0.0003	71
	Error	15	0.0003	–	–
% carbon rhizome	Time	6	11.01	0.123	–
	Error	44	6.15	–	–
% nitrogen rhizome	Time	6	1.56	<0.0001	62
	Error	40	0.13	–	–
% phosphorus rhizome	Time	6	0.0009	0.304	–
	Error	22	0.0007	–	–
% carbon root	Time	5	4.95	0.0001	68
	Error	21	0.56	–	–
% nitrogen root	Time	6	0.065	0.064	–
	Error	22	0.027	–	–
% phosphorus root	Time	6	0.0011	0.027	61
	Error	14	0.0003	–	–

the end of summer (Fig. 1b, Table 1). Nitrogen concentrations ranged from 3.3% of dry weight (young tissue, A1, in winter) to 1% of dry weight (old tissue, A4, in summer). Nitrogen concentrations decreased with tissue age, but the seasonal pattern was similar across age classes (non-significant interaction term). We observed a slightly lower concentration at the end of the sampling period (January 1993) compared to that of the previous year (January 1992) for all 4 age classes.

Phosphorus concentration also showed significant seasonal changes (Table 1), but with the maximum value preceding that of nitrogen (Fig. 1c). The highest values were again found among the youngest tissue (Fig. 1c). Seasonal pattern significantly but only slightly (see the significant interaction in Table 1) differed in oldest leaves (A3 and A4) from youngest ones (A1 and A3).

Carbon concentration in leaf sheaths was lowest in winter and highest in summer (Fig. 2a, Table 1). Con-

centrations of nitrogen and phosphorus in the leaf sheaths followed the same trend as in the leaves, although with lower values, and also showed a clear decrease at the end of the second year relative to the equivalent period of the previous year (Fig. 2b,c, Table 1).

Carbon concentration in the rhizomes did not vary among sampling events (Fig. 3a, Table 1). In contrast, nitrogen concentration in the rhizomes did differ between sampling events but there was no seasonal trend. Maximum values were reached in May and December 1993, while the concentration reached in December 1992 was half that found the following year (Fig. 2b). Although the time course of phosphorus concentrations was similar to that of nitrogen (Fig. 3b,c), these differences proved to be non-significant (Table 1).

The carbon concentration in roots reached minimum levels in November, and was relatively constant the rest of the year (Fig. 4a). Nitrogen and phosphorus concentrations in the roots showed a common trend

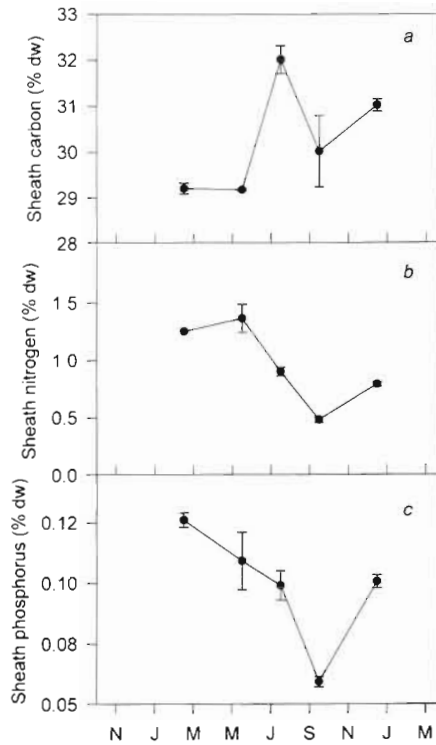


Fig. 2. Changes with time in concentrations of carbon, nitrogen and phosphorus in leaf sheaths (as % of dw). Mean values and standard error

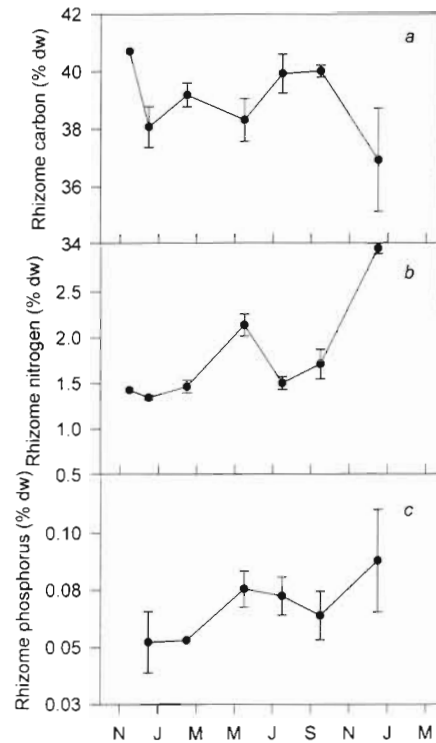


Fig. 3. Changes with time in concentrations of carbon, nitrogen and phosphorus in rhizomes (as % of dw). Mean values and standard error

with 2 peaks, one in November-December and another one in May, although the variation in nitrogen was not significant (Fig. 4b,c, Table 1).

The incorporation of nitrogen and phosphorus in leaves reached a maximum in June and a minimum in September (Fig. 5), thus following the growth pattern of the plant (Table 2). Retranslocation of nitrogen was high from March to September (up to $92 \mu\text{g N shoot}^{-1} \text{d}^{-1}$) while retranslocation of phosphorus was high from January to September (highest value: $4.5 \mu\text{g P shoot}^{-1} \text{d}^{-1}$). Retranslocation of both nutrients was very low during the rest of the year (Fig. 5). Nitrogen and phosphorus losses were highest at the end of summer, associated with the major biomass losses (Table 2, Alcoverro et al. 1995), being more irregular the rest of the year (Fig. 5). Nitrogen uptake reached maximum values in winter ($113 \mu\text{g shoot}^{-1} \text{d}^{-1}$, Fig. 5) and the minimum levels in August-September ($0 \mu\text{g shoot}^{-1} \text{d}^{-1}$). Uptake of phosphorus was highest in spring and fall (up to $6.1 \mu\text{g shoot}^{-1} \text{d}^{-1}$, Fig. 5) while the slowest uptake (close to zero) was found again in late summer (August-September). On an annual basis, nitrogen and phosphorus uptake accounted for 60 and 41% of the nutrient incorporation, respectively, while retranslocation from old tissues potentially accounted for the remaining 40% for nitrogen and 59% for phosphorus (considering leaching close to zero).

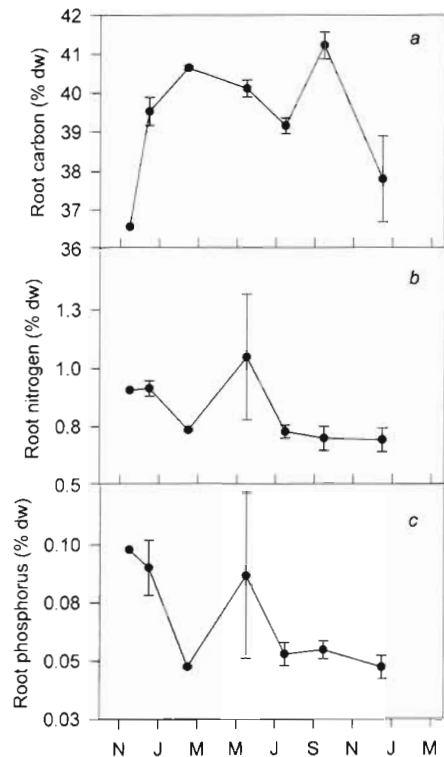


Fig. 4. Changes with time in concentrations of carbon, nitrogen and phosphorus in root (as % of dw). Mean values and standard error

Table 2. Leaf biomass, growth and leaf biomass lost during the sampling period. Values represent averages of 10 replicates (standard error). Values without standard error were obtained by linear interpolation (estimation)

Month	Shoot biomass (mg shoot ⁻¹)	Shoot growth (mg shoot ⁻¹ d ⁻¹)	Shoot lost (mg shoot ⁻¹ d ⁻¹)
Nov	320 (15.2)	4.0 (0.19)	
Dec	340 (21.4)	3.8 (0.27)	3.13
Jan	374 estim	3.5 estim	2.41
Feb	442 estim	3.1 estim	0.78
Mar	477 (41.3)	2.8 (0.31)	1.63
Apr	510 estim	4.1 estim	2.97
May	578 estim	5.0 estim	2.76
Jun	612 (80.0)	7.9 (0.64)	6.76
Jul	858 (39.9)	5.0 (0.51)	-3.2
Aug	430 (39.9)	2.6 (0.43)	16.87
Sep	200 (93.8)	2.0 (0.21)	9.66
Oct	238 estim	2.4 estim	1.13
Nov	315 estim	3.2 estim	0.63
Dec	354 (33.2)	3.6 (0.18)	2.3

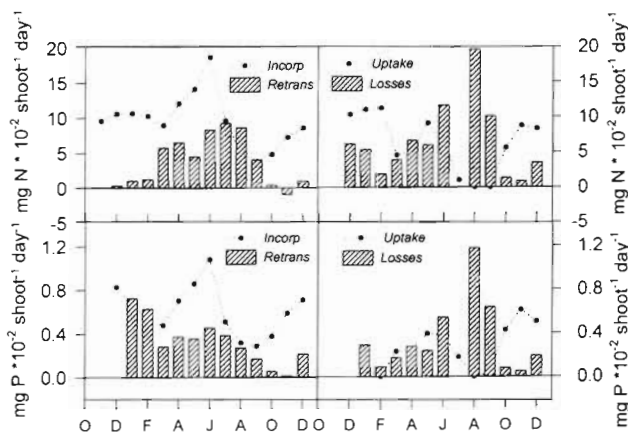


Fig. 5. Changes with time in incorporation, retranslocation, uptake and losses of nitrogen and phosphorus in leaves

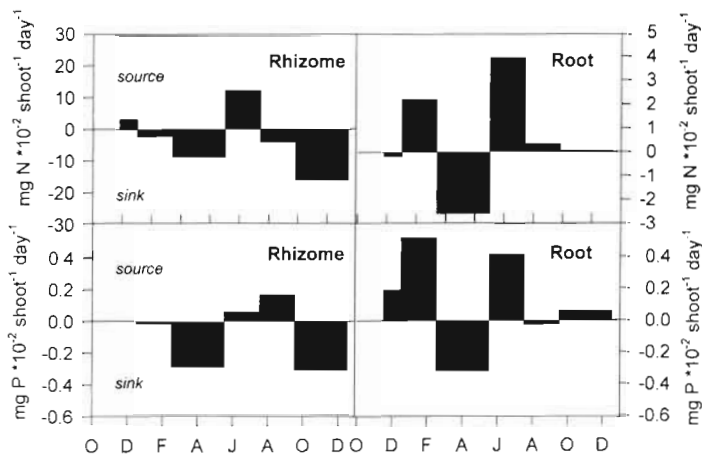


Fig. 6. Time course of nutrient (nitrogen and phosphorus) translocation from/to rhizomes and roots

The buffering capacity of rhizomes and roots suggests that the rhizomes acted as a source of nutrients during summer and as a sink during the rest of the year (Fig. 6). Roots presented a less clear pattern with 2 periods acting as a source (winter and summer) and an intermediate period acting as a sink (spring).

DISCUSSION

Nutrient concentration in each *Posidonia oceanica* age class followed a seasonal pattern similar to that observed in whole shoots (Alcoverro et al. 1995). This pattern of variability in nitrogen concentration has also been observed in *Zostera marina* (Pedersen & Borum 1993). Some authors have suggested that the seasonality found in shoot nutrient concentration (higher in winter, lower in summer) was induced by the seasonality in shoot age composition (Pellikaan 1984, Pirc & Wollenweber 1988). However, our results showed a clear seasonal pattern in nutrient concentrations (non-significant interactions in Table 1, except for phosphorus) across tissue age classes, with a clear accumulation of nutrients during winter for all the age classes.

With this new methodological approach that contemplates age classes instead of leaves for obtaining the nutrient curves, we are able to improve our nutrient retranslocation estimates. Consequently we can now assess annual values of retranslocation (40% N and 59% P) that are more precise and unequivocally higher than those obtained in previous works (20% N and 18% P in Alcoverro et al. 1997).

Nutrient balance studies in terrestrial plants have evidenced the importance of the seasonal nutrient recycling (e.g. Jonasson & Chapin 1985). Retranslocation of nutrients in seagrasses also varies seasonally, at least in temperate seagrass species (Pedersen & Borum 1993, this work). This is consistent with the seasonal uncoupling of growth and nutrient availability (Thom & Albright 1990, Alcoverro et al. 1995); therefore this has to be taken into account when we infer retranslocation values from short-time sampling (e.g. Patriquin 1972, Harrison & Mann 1975, Borum et al. 1989, Stapel & Hemminga 1997).

Along the seasonal growth cycle of *Posidonia oceanica*, 3 strategies are used to fit the nutrient demand of the plant: (1) acquisition from external sources (i.e. the water column or the sediment pore water), (2) re-use of internal pools, which potentially include nutrient retranslocation from old leaves and nutrient retranslocation from other organs (roots and rhizomes), and (3) use of nutrients stored in the

leaves themselves. During winter, nutrients are generally taken up from the external medium in excess of that of carbon, and the nutrient concentration in leaves increases (Alcoverro et al. 1995, this work). From spring to the end of summer, nutrients are exhausted in the sediment pore water and in the water column, (Ballesteros 1989, Alcoverro et al. 1995, Vidondo & Duarte 1995, Cebrián et al. 1996), while leaf growth attains its maximum (Alcoverro et al. 1995, this work). The nutrient demands are then met by the use of internal pools, among which the process of nutrient reclamation from old leaves may be important. However, the incorporation of carbon is still in excess of that of nutrients, with a concomitant decrease in nutrient concentration, eventually leading to nutrient shortage. This pattern is consistent with previous findings at the Medes Island site, where *P. oceanica* responded to experimental nutrient addition in spring and summer, while no response was observed in winter-fall (Alcoverro et al. 1997).

It should be acknowledged that the method used has a serious drawback, in the sense that a nutrient mass balance does not permit one to discriminate between nutrient recovery and nutrient release to the external medium (leaching). Moreover, direct experimental measurements would have been needed to elucidate in detail which part of the nutrient decrease in old leaves would correspond to leaching. Hence the reported values of retranslocation should be viewed as maximum potential values. Nevertheless we must remember that direct measurements of leaching have been proved to be very complex, especially in plants such as *Posidonia oceanica* that grow with difficulty in a laboratory. The few reports that have measured leaching by direct methods state the marginal importance of this process in the nutrient budget of seagrasses. In *Zostera marina*, presumably the better known case, leaching never exceeds 10% of the total nutrient losses (Borum et al. 1989, Pedersen & Borum 1992). Hence, we conclude that the proposed retranslocation rates, although presumably overestimated, should be very close to the real values.

Other plant parts can also contribute to the supply of nutrients during spring-summer, but their role is, apparently, only minor. In the case of the leaf bases or petioles, seasonal changes in nutrient concentrations were similar to those found in the leaves. Lower values have been reported in dead petioles relative to living ones (see Manzanera et al. 1998), indicating that possible nutrient reclamation can also occur on these organs. However, their contribution to the overall nutrient budget should be modest, due to their low biomass relative to leaves and their low nutrient concentration. The seasonal changes in nutrient concentra-

tions of rhizomes and roots were less clear and even if they act as a nutrient source in early summer (Fig. 6) their contribution to the overall nutrient mass balance seems relatively small. In any case, the role of rhizomes and roots as short-time or long-time nutrient buffers remains to be examined in detail.

Our data suggest that retranslocation of nutrients in *Posidonia oceanica* constitutes a mechanism for optimizing nutrient use, which becomes important during times of nutrient shortage. This is also the case in other seagrasses and in terrestrial plants (e.g. Chapin & Bloom 1976, Jonasson & Chapin 1985, Chapin et al. 1986, Pedersen & Borum 1993). However, in general terms, relationships (across species) between leaf nutrient status and leaf nutrient retranslocation capacities have shown to be very weak in most terrestrial plants and seagrasses (Del Arco et al. 1991, Aerts 1996, Stapel & Hemminga 1997). Other plant features, such as the increase of leaf longevity, seem to be better correlated with nutrient availability, and constitute a significant adaptation for increasing the efficiency in the use of nutrients (Escudero et al. 1992).

Based on a general nutrient budget at the ecosystem level, Mateo & Romero (1997) proposed that nutrient losses were relatively small in *Posidonia oceanica* meadows, and that most phosphorus and, probably, most nitrogen (i.e. 80 to 90%) were recycled within the system. The data presented support this notion, and indicate that retranslocation could be one of the main mechanisms by which nutrient conservation is accomplished. In effect, retranslocation represented 40% of the requirements for nitrogen and 59% for phosphorus in *P. oceanica* on an annual basis. These values are higher than the average values of nutrient retranslocation reported for seagrasses (15% for nitrogen and 21% for phosphorus, Stapel & Hemminga 1997) and closer to those found in terrestrial plants (Jonasson & Chapin 1985, Chapin & Shaver 1988, Escudero et al. 1992, Reich et al. 1995). A tentative hypothesis to explain this is the long lifespan of *P. oceanica* leaves (around 150 d on average, maximum of 300 d: Romero 1989b), higher than those of most seagrass species (Duarte 1991). This persistence of leaves allows a more efficient nutrient recovery than in the case of an early abscission (Escudero et al. 1992). In addition, leaf longevity also implies a greater residence time of nutrients in the plant, and a reduction of nutrient demands.

Species with long-lived leaves like *P. oceanica* may minimize their dependence upon external nutrients through an effective internal retranslocation and conservation of nutrients. This can contribute to the understanding of why this species has colonized vast areas under nutrient-poor conditions.

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