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Nutrient resorption from seagrass leaves

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Abstract The resorption of nutrients (C, N and P) from senescent leaves of six seagrass species from nine different locations in tropical (Indonesia and Kenya), Mediterranean (Spain) and temperate (The Netherlands) regions has been investigated. Resorption was quantitatively assessed by calculating the difference in nutrient content between the leaves with the highest content, and the oldest leaves. In order to do so, the leaves were classified according to their age. The nutrient contents of leaves of a given age category were calculated by multiplying the measured nutrient concentration in this age category with its corresponding modelled leaf biomass. N- and P-concentrations declined during ageing and senescence of the leaves in all of the investigated situations but two. The decline in concentration varied up to 58% for N and up to 66% for P. The C-concentration declined on three of the investigated occasions and varied up to 24%. Despite a decline in concentration, the leaf C-content did not change, indicating no resorption of carbon. The efficiency of N-resorption from intact seagrass leaves varied between 3.8 and 29% (average: 15%), while the efficiency of phosphorus resorption varied between 0 and 51% (average: 21%). The resorption efficiency was not significantly different in seagrasses with a relatively high and a relatively low nutrient concentration, although within-species comparisons showed that in some cases resorption efficiency was positively related to the nutrient concentration of the leaves. Premature loss of leaves and leaf fragments (by e.g. herbivory) may substantially interfere with the resorption process. In Indonesian seagrasses we estimated that as a result of fragmentation and premature detachment only between 56 and 77% of the physiological resorption potential actually was realised. It is concluded that internal resorption may play a role in the nutrient dynamics of seagrass plants, but that its quantitative importance probably is limited. Nutrient resorption from senescent seagrass leaves may reduce the nutrient requirements for seagrass leaf production by approximately 10% for nitrogen and 15% for phosphorus.

Introduction

Seagrass beds rank among the most productive submerged aquatic ecosystems. To sustain a high productivity, a substantial amount of nutrients is required. The death of leaves and other plant parts, however, leads to a constant drain of nutrients, as nutrients are a component of these lost plant parts. The nutrients lost have to be replenished to allow the continued growth and persistence of the seagrasses (Hemminga et al. 1991). Numerous studies have shown that terrestrial plants resorb nutrients from senescent leaves. These nutrients may be reused for the growth of new leaves or roots and rhizomes. As a result, the dependence on an external nutrient supply is reduced (Jonasson and Chapin 1985). The amount of nutrients resorbed from senescent leaves of terrestrial plants varies widely, i.e. between 0 and 79% for N and between 0 and 90% for P (Chapin and Kedrowski 1983). Seagrasses, descendants of land plants that have invaded the marine environment, similarly may possess mechanisms to reclaim part of the nutrients from ageing leaves. Very little is known, however, about nutrient resorption in seagrasses. Some data on the decrease of nutrient concentrations during leaf development are available. C-decline ranges between 5 and 36% (Harrison and Mann 1975; Thayer et al. 1977; Alcoverro 1995). The decline in nitrogen ranges between 20 and 80% (Patriquin 1972; Harrison and Mann 1975; Thayer et al. 1977; Pedersen and Borum 1993; Alcoverro 1995), while for phosphorus, a decline between 30 and 40% is reported (Walker and McComb 1988; Alcoverro 1995). Most of these figures, however, did not distinguish between a decline due to leaf growth (dilution) and a de-

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cline due to resorption during senescence. Borum et al. (1989) and Pedersen and Borum (1992, 1993) concluded that internal reclamation of nitrogen accounted for 12 to 27% of the annual nitrogen requirements of *Zostera marina*. Alcoverro (1995) calculated that in *Posidonia oceanica* 37 and 44% of the annual nitrogen and phosphorus demand is met by resorption from senescent seagrass tissue. A general figure for nitrogen resorption is given by Hemminga et al. (1991), who estimated that approximately 25% of the seagrass' total nitrogen demand can be met by internal resorption. Resorption, however, presumably will vary between seagrass species, and possibly also within species in response to varying environmental nutrient availabilities, as is the case in terrestrial plants (Chapin and Kedrowski 1983; Pugnaire and Chapin 1993).

The aim of this study is to compare the nutrient resorption of several seagrass species in different geographic regions of the world (Indonesia, Kenya, the Mediterranean and The Netherlands).

Materials and methods

Study sites

The leaves of several seagrass species were collected from a range of environments (Table 1). Barang Lompo in Indonesia is a coral island located approximately 14 km off the coast. The reef flat of the island is covered by mixed seagrass beds, dominated by *Thalassia hemprichii* (Ehrenb.) Aschers., *Enhalus acoroides* (L.*f.*) (both climax species) and the pioneer species *Cymodocea rotundata* Ehrenb. & Hempr. ex Aschers. Parts of the reef flat occasionally run dry during low water. Samples of the three species were taken in the wet season, during February and March 1994. Gusung Tallang, also in Indonesia, is an intertidal mudflat, located on the coast of South Sulawesi, in between the mouths of the Maros River in the north and the Tello (a tidal creek) in the south. This area is characterised by narrow sandbars perpendicular to the coastline, with well-developed seagrass vegetation between these sandbars, dominated by *E. acoroides*. At the fringes, mixed beds with smaller seagrass species occur, notably *T. hemprichii*. Samples of both species were taken in the wet season, during February and March 1994. Bira, at the utmost southeast of South Sulawesi, Indonesia, is a shallow coastal area exposed to a relative strong wash of waves. This site is dominated by the robust climax species *Thalassodendron ciliatum* (Forssk.). Samples of this species were taken at the end of the wet season in April 1994.

Gazi Bay is situated 50 km south of Mombassa on the Kenyan coast, and is dominated by a mangrove forest on the northern part of the bay. Intertidal flats and shallow subtidal areas covered by seagrass meadows are found in between the mangrove forest and coral reefs in the south. Intertidally growing *Thalassodendron ciliatum* was sampled (October 1994) from three sites at increasing distance from the mangrove forest.

Medes Islands is a group of small islands and rock pinnacles in the Mediterranean, 1.5 km off the coast of Girona, Spain. A *Posidonia oceanica* (L.) Delile meadow extends on the west side of the islands, from 3 to 15 m depth (Alcoverro et al. 1995; Mateo 1995). Shoots of this plant were sampled in October 1994 at a depth of 5 m.

Zandkreek Bay in the SW Netherlands is a largely intertidal bay in a tidal inlet of the North Sea. *Zostera marina* L. was sampled

Table 1 List of the locations where seagrasses were collected to investigate nutrient resorption from senescent leaves. Name of site and geographic position followed by a brief description of site, sediment type and inorganic N- and P-concentrations (μM) in the water column and pore water (*bdl* below detection limits; *nd* not determined; *a* ammonium; *n* nitrate and nitrite; *an* total inorganic nitrogen)

Site	Description	Sediment	Water column		Pore water		Source
			N	P	N	P	
Indonesia							
Barang Lompo (5°03′S; 119°20′E)	Intertidal reef flat	Coarse carbonate sand and coral rubble (98% $CaCO_3$)	0.8–5.3 a	bdl–1.2	20–80 a	2–13	Erftemeijer (1994) Stapel et al. (1996a)
Gusung Tallang (5°04′S; 119°27′E)	Intertidal coastal area	Terregenous mud (12% $CaCO_3$)	0.6–5.4 a	0.3–1.1	30–220 a	0.5–1.5	
Bira (5°38′S; 120°27′E)	Coastal reef flat	Fine carbonate sand and coral rubble (100% $CaCO_3$)	nd	nd	nd	nd	
Kenya							
Gazi Bay (4°25′S; 39°30′E)	Subtidal bay	Mostly carbonate sediment					Hemminga et al. (1994b) Hemminga et al. (1995)
MM	On edge of mangroves	(39% $CaCO_3$)	0.7–1.0 an	0.3–0.4	nd	nd	
MS	500 m from mangroves	(43% $CaCO_3$)	1.0 an	0.4	nd	nd	
CS	2 km from mangroves	(28% $CaCO_3$)	0.8 n	0.3	nd	nd	
Spain							
Medes Islands (42°03′N; 3°14′E)	Subtidal slope	Coarse sand	0.5–4.3 n	0.08–0.41	200–875 an	0–62	Romero (1985) Alcoverro et al. (1995) López et al. (1995)
Netherlands							
Veerse Meer (51°33′N; 3°45′E)	Brackish eutrophic lake	Silty sediment	3–200 an	4–23	10–180 a	4–57	Hemminga et al. (1994a) Van Lent and Verschuure (1994b)
Zandkreek (51°34′N; 3°54′E)	Intertidal flat	Fine sand	2–70 an	1–7	10–240 a	bdl–15	

(July 1994) from an annual population on the intertidal flats on the northern side of the bay. Lake Veere is a brackish eutrophic lake in the SW Netherlands. Part of the lake is covered by a perennial population of *Z. marina*. Shoots of this species were collected in August 1994.

Shoots of seagrass plants were collected from three replicate plots at each location and transported to the laboratory in containers or plastic bags filled with sea water. Epiphytes were gently wiped off the leaves using tissue paper. Intact leaves of the same age category, numbered from 1 (youngest leaf, >1 cm) to *j* (oldest leaf), were pooled until the samples contained enough material for carbon (C), nitrogen (N) and phosphorus (P) analysis (at least 5 g fresh weight, with 20 leaves or more per sample). Dead, brown leaves were discarded. The samples of the same leaf number, species and location were treated as triplicates. The samples were briefly rinsed in demineralised water and immediately dried to constant dry weight at 80 °C and stored for later analysis of C, N and P. C- and N-concentrations of the samples were analysed with a Fisons NA 1500 CN-analyzer. If necessary, epiphytic carbonate was first removed from the leaves according to the method described by Nieuwenhuize et al. (1995). Total P was analysed colorimetrically (Allen 1974), after oxidising acid digestion using a microwave furnace (Nieuwenhuize et al. 1991). Other leaf samples were collected to establish the average dry weight of successive leaf numbers. The samples were treated as described above, but individual intact leaves (15 to 45 per leaf number) were dried separately and weighed.

Using the weight data of the leaves, the biomass development of the intact leaves was modelled using nonlinear least square regression according to:

$$B_i = B_j(1 - e^{-ai}) \ , \tag{1}$$

in which i is the leaf number, B_i the biomass (dry weight) of the ith leaf, B_j the dry weight of the oldest leaf, and a the rate constant of biomass development.

The nutrient contents of leaves of a given age category were calculated by multiplying the %C, N or P of the ith leaf with its corresponding modelled biomass. The proportion of nutrient resorption (resorption efficiency; Shaver and Melillo 1984) was calculated by:

$$\%R = \frac{K_{\max} - K_j}{K_{\max}} \cdot 100\ \% \ , \tag{2}$$

in which $\%R$ is the percentage of the maximum leaf nutrient content that is resorbed (resorption efficiency), $K_{\max}$ the nutrient content (mg C, N or P) of the leaf number with the highest total nutrient content and K_j the C, N or P content (mg) of the oldest leaf. We thus assume that the decline in the absolute nutrient content of ageing leaves reflects nutrient resorption. The remaining nutrient content of the oldest leaf, furthermore, is assumed to be lost by detachment or death of the leaf. Leaching of nutrients from senescent seagrass leaves is considered to be a process with an insignificant contribution to nutrient loss (Borum et al. 1989) and was therefore disregarded. By the above given calculation, a figure of the *maximum* physiological nutrient resorption efficiency is obtained, because only intact leaves were examined. This, however, may represent a rare situation. Often leaves fragment at the tip during ageing, or they are (partially) consumed by herbivores or are detached from the plant before they have reached their maximum life span. From these lost leaves or leaf fragments, nutrients cannot be resorbed. To gain insight in the quantitative importance of this premature nutrient loss, we investigated the Indonesian seagrasses in more detail. In order to do so, we now included also the incomplete leaves of the seagrass shoots that were first left out when the average dry weight of the *intact* leaves of successive age categories was established in our calculations (see above). If a leaf number was missing because it had been detached completely, we substituted 0 g as a value for its dry weight when calculating the average biomass for that specific age category. Because we do not know when a leaf fragment or entire leaf was lost from a shoot, we cannot be sure of the amount of nutrients resorbed from this leaf (fragment). It may have been lost before any resorption had occurred, or at the moment that the resorption process already had been completed. In this last case, the resorption equals the maximum possible (physiological) resorption. We therefore calculated a new resorption value which takes incomplete resorption due to premature loss of leaf material into account by assuming that the physiological resorption (R) had occurred to its full extent from the remaining biomass fraction of the oldest leaf, and that 50% of the physiological resorption had occurred from the biomass fraction that was prematurely lost from the oldest leaf (i.e. the average of minimal and maximal possible resorption). If this is expressed mathematically, we obtain the formula:

$$\%R' = \frac{R(B_{j,\mathrm{obs}} + B_j)}{2B_j K_{\max}} \cdot 100\% \quad , \tag{3}$$

in which $\%R'$ is the corrected resorption efficiency, R the absolute physiological resorption ($K_{\max} - K_j$ in mg C, N or P), $B_{j,\mathrm{obs}}$ the observed biomass (mg dry weight) of the oldest leaf, B_j the modelled biomass (mg dry weight) of the (intact) oldest leaves and $K_{\max}$ the C, N or P content (mg) of the leaf number with the highest absolute C, N or P content (mg), calculated using the modelled biomass.

Results

The C, N and P concentrations (percentage of dry weight) in the different age categories (leaf numbers) of seagrass leaves are shown in Table 2. Changes in nutrient concentration in the course of leaf development were tested using one-way ANOVA followed by a Tukey post-hoc comparison. The carbon concentration showed the smallest changes. A decline occurred in *Thalassia hemprichii* (Barang Lompo and Gusung Tallang) and in *Enhalus acoroides* (Gusung Tallang), varying between 11 and 24% (Table 2). In the other cases, no significant change was observed. Apart from *Thalassodendron ciliatum* (Gazi MM) and *Zostera marina* (Veerse Meer), the nitrogen concentration declined significantly, varying between 19 and 58% (Table 2). The phosphorus concentration did not change significantly in *T. ciliatum* (Gazi MM and MS); in all other investigated situations a significant decline was observed, varying between 34 and 66% (Table 2).

The biomass development of intact leaves of the different seagrass species is presented in Fig. 1. In addition, Fig. 1A–F (Indonesian species) also show the biomass of successive leaf numbers when natural fragmentation and detachment are taken into account. Using the fitted biomass curves shown in Fig. 1 and the data on C, N and P concentrations shown in Table 2, we calculated the total C, N and P content in the different age categories of the leaves of each species (Table 3). The results were used to calculate the physiological resorption (%R), according to Eq. 2. Significant carbon resorption apparently did not occur in any one of the investigated seagrass species, not even in cases of a significant decline in the carbon concentration during leaf development (Tables 2, 3). This may be expected as a major part of the carbon will have been fixed in cell wall structures, from which resorption does not occur. The resorption of nitrogen ranged between 3.8 and 29%, and the resorption of phosphorus ranged between 0 and 51% (Table 3). However, the re-

Table 2 Carbon, nitrogen and phosphorus concentrations (percentage of dry weight) in the successive leaf numbers of each of the investigated seagrass species. Values represent averages of three replicate pooled leaf samples. A difference in nutrient concentration between leaf numbers was tested using one-way ANOVA followed by a Tukey post-hoc comparison of all age categories. Values designated with the same letter within each row are not significantly different (0.05 probability level). If a significant difference in nutrient concentration between the last leaf number and a preceding number existed, % change was calculated between the oldest leaf and the leaf number with the highest concentration (marked with *) (*ns* not significant; *na* not analysed)

Nutrient, site	Species	Leaf number								% change
		1	2	3	4	5	6	7	8	
Carbon										
Barang Lompo	*Thalassia hemprichii*	38.67 a*	35.88 ab	34.20 b	34.25 b*	na				−11
	Enhalus acoroides	35.52 a	33.49 a	32.69 a	36.06 a	33.87 a				ns
	Cymodocea rotundata	39.33 a	39.46 a	37.74 a	34.03 a					ns
Gusung Tallang	*Thalassia hemprichii*	37.65 a*	34.75 b	30.67 c	28.70 d*					−24
	Enhalus acoroides	35.18 a*	32.96 b	31.78 bc	29.86 c	29.97 c*				−15
Bira	*Thalassodendron ciliatum*	38.76 a	38.69 a	39.01 a	39.50 a	37.23 a	39.19 a	38.36 a	35.35 a	ns
Gazi MM	*Thalassodendron ciliatum*	39.24 a	38.75 a	38.41 a	41.55 a	42.10 a	41.52 a	42.51 a	45.26 a	ns
Gazi MS	*Thalassodendron ciliatum*	39.45 a	40.58 a	40.49 a	40.70 a	41.55 a	40.14 a	40.81 a	43.58 a	ns
Gazi CS	*Thalassodendron ciliatum*	39.10 a	41.51 a	41.23 a	39.04 a	38.84 a	39.35 a	38.25 a	37.92 a	ns
Medes Islands	*Posidonia oceanica*	41.65 a	38.28 a	38.49 a	36.94 a	37.82 a				ns
Zandkreek	*Zostera marina*	36.29 a	36.03 a	36.04 a	36.06 a	35.91 a	35.44 a	35.43 a	35.05 a	ns
Veerse Meer	*Zostera marina*	35.73 a	35.66 a	35.51 a	34.60 a	35.23 a	34.33 a			ns
Nitrogen										
Barang Lompo	*Thalassia hemprichii*	3.20 a*	2.49 b	1.99 c	1.78 c	1.34 d*				−58
	Enhalus acoroides	2.37 a*	2.04 a	1.95 ab	1.94 ab	1.47 b				−38
	Cymodocea rotundata	2.33 a	2.45 a*	1.94 b	1.63 c*					−33
Gusung Tallang	*Thalassia hemprichii*	3.47 a*	2.71 b	1.99 c	1.54 d*					−56
	Enhalus acoroides	4.35 a*	3.59 b	3.23 bc	2.70 cd	2.21 d*				−49
Bira	*Thalassodendron ciliatum*	1.79 a*	1.69 a	1.59 ab	1.47 bc	1.32 cd	1.26 de	1.20 de	1.10 e*	−39
Gazi MM	*Thalassodendron ciliatum*	1.55 a	1.57 a	1.70 a	1.75 a	1.72 a	1.59 a	1.48 a	1.40 a	ns
Gazi MS	*Thalassodendron ciliatum*	1.68 ab	1.87 a	1.91 a*	1.78 ab	1.81 ab	1.69 ab	1.66 ab	1.51 b*	−21
Gazi CS	*Thalassodendron ciliatum*	1.85 ab	2.11 a*	2.08 a	1.93 ac	1.85 ab	1.71 bc	1.51 bd	1.25 d*	−41
Medes Islands	*Posidonia oceanica*	1.86 a*	1.53 b	1.39 bc	1.21 bc	1.11 c*				−40
Zandkreek	*Zostera marina*	3.21 a*	3.13 ab	2.94 ac	2.89 ac	2.79 bc	2.80 bc	2.59 c	2.61 c*	−19
Veerse Meer	*Zostera marina*	2.36 a	2.18 a	2.01 a	1.89 a	1.92 a	1.80 a			ns
Phosphorus										
Barang Lompo	*Thalassia hemprichii*	0.33 a*	0.23 b	0.18 b	0.17 b*	na				−48
	Enhalus acoroides	0.31 a*	0.25 ab	0.20 bc	0.17 bc	0.13 c*				−58
	Cymodocea rotundata	0.26 a*	0.22 ab	0.16 bc	0.09 c*					−65
Gusung Tallang	*Thalassia hemprichii*	0.38 a*	0.24 b	0.16 c	0.13 c*					−66
	Enhalus acoroides	0.47 a*	0.42 ab	0.37 b	0.27 c	0.22 c*				−53
Bira	*Thalassodendron ciliatum*	0.27 a*	0.25 a	0.23 a	0.18 b	0.14 bc	0.15 bc	0.12 c	0.13 c*	−52
Gazi MM	*Thalassodendron ciliatum*	0.16 a	0.17 a	0.15 a	0.14 a	0.13 a	0.12 a	0.11 a	0.11 a	ns
Gazi MS	*Thalassodendron ciliatum*	0.15 a	0.16 a	0.15 a	0.13 a	0.13 a	0.11 a	0.10 a	0.10 a	ns
Gazi CS	*Thalassodendron ciliatum*	0.19 a*	0.18 a	0.16 ab	0.14 bc	0.13 bcd	0.12 cd	0.10 cd	0.09 d*	−53
Medes Islands	*Posidonia oceanica*	0.14 a*	0.12 ab	0.08 ab	0.07 b	0.07 b*				−50
Zandkreek	*Zostera marina*	0.38 a*	0.33 ab	0.28 c	0.26 c	0.25 c	0.26 c	0.25 cb*		−34
Veerse Meer	*Zostera marina*	0.40 a*	0.31 b	0.25 c	0.23 c	0.23 c*				−43

sorption of these nutrients was not significant in all cases. Only for *Cymodocea rotundata*, *Thalassia hemprichii* (Barang Lompo and Gusung Tallang), *Enhalus acoroides* (Gusung Tallang), *Thalassodendron ciliatum* (Gazi CS) and *Posidonia oceanica* was N-resorption significant. Significant P-resorption was demonstrated for *C. rotundata*, the seagrasses at Gusung Tallang, *T. ciliatum* (Bira) and *T. ciliatum* (Gazi CS).

The values on resorption efficiency presented in Table 3 were calculated using modelled leaf biomasses, which were based on weight measurements of intact leaves. Although this approach gives a good indication of the physiological resorption capabilities of a seagrass species, it does not fully reflect the natural situation as premature leaf fragmentation and detachment is not taken into account. The calculation of nutrient resorption efficiency based on the biomasses of intact leaves includes resorption from a considerable part of the leaf biomass which, in the natural situation, may have been lost before the resorption process is completed. The more detailed study of the Indonesian seagrasses shows that natural mixtures of older leaves have a much lower average biomass than their modelled weight, which was calculated on the basis of intact leaves only (Fig. 1A–F). Consequently, the actual resorption efficiency (%R') is substantially lower than the physiological resorption efficiency (%R). We calculated that as a result of fragmentation and premature detachment only between 50 and 77% of the physiological resorption potential is actually realised (Table 4).

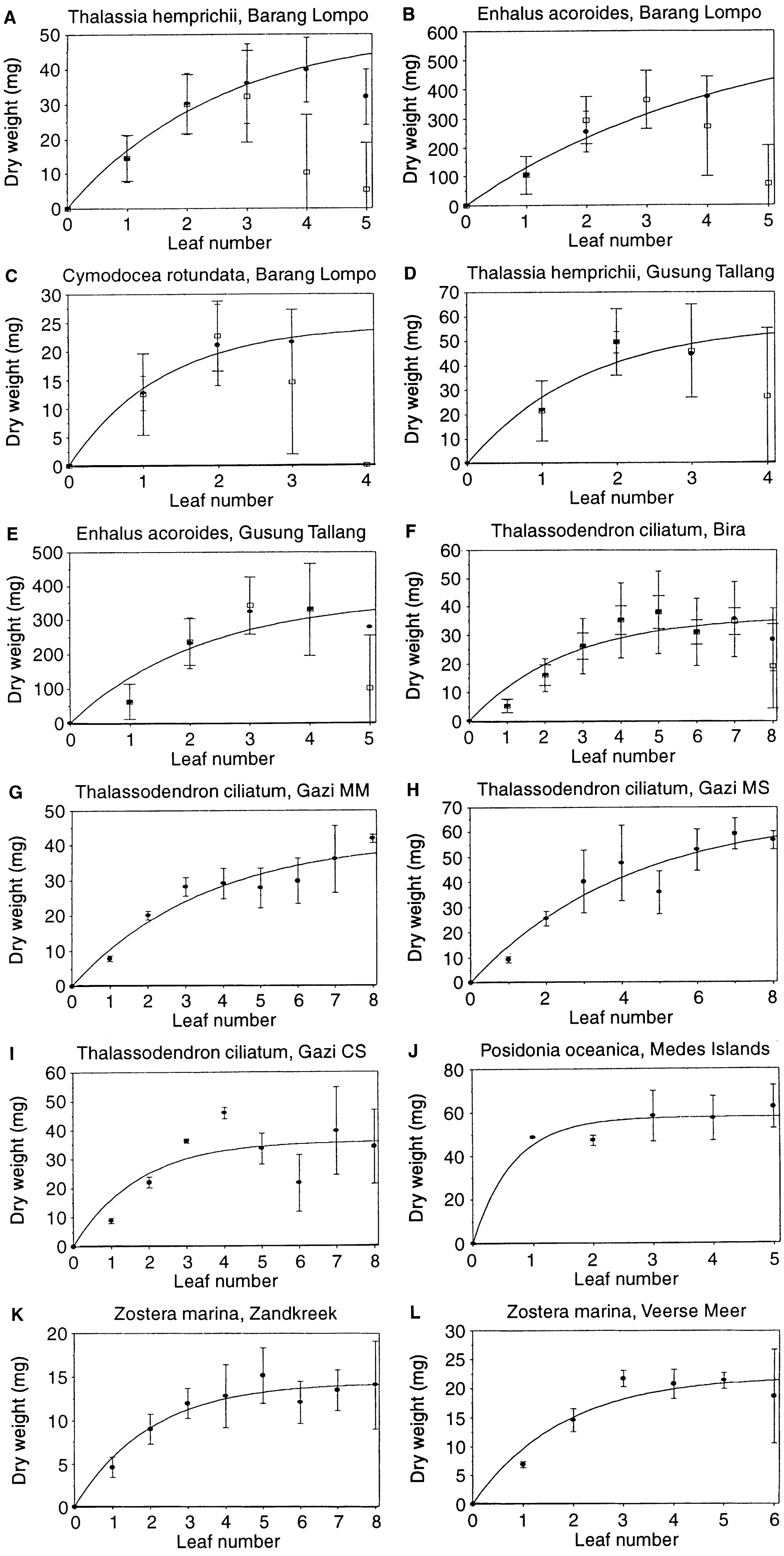

Fig. 1 Biomass (dry weight; mg leaf^{-1}) of the successive leaf numbers of the investigated seagrasses. *Closed circles* represent the average biomass of intact leaves; *error bars*: ± 1 SD (n = 15 to 45). The model for leaf biomass development (Eq. 1) is fitted to all replicates of these data. *Open squares* (species from Indonesia) represent the average biomass of a natural mixture of both intact and fragmented leaves; prematurely detached leaves were included as leaves having a zero biomass; *error bars*: ± 1 SD (n = 15 to 45)

Table 3 Total average carbon, nitrogen and phosphorus content of the successive leaf numbers of each of the investigated seagrass species (mg leaf^{-1}). Values based on the C-, N- and P-concentrations of three replicate pooled leaf samples and fitted biomasses of intact leaves. Resorption efficiency (%*R*) was calculated as described in "Materials and methods", using model (Eq. 2). Where appropriate, resorption efficiency was statistically tested for each nutrient and each species using the data of all age categories in a one-way ANOVA followed by a Tukey post-hoc comparison between the nutrient content of the leaf number with the highest nutrient content and the nutrient content of the oldest leaf (marked with *). If the difference was significant ($p < 0.05$), the *p*-value is given (*ns* not significant; *na* not analysed)

Nutrient, site	Species	Leaf number								%*R*	*p*
		1	2	3	4	5	6	7	8		
Carbon											
Barang Lompo	*Thalassia hemprichii*	6.47	10.03	12.15	13.91	na				na	–
	Enhalus acoroides	45.90	77.65	102.4	136.3	145.4				0	–
	Cymodocea rotundata	5.33	7.74	8.43 *	8.01 *					5.0	ns
Gusung Tallang	*Thalassia hemprichii*	10.13	14.31	14.94	15.13					0	–
	Enhalus acoroides	46.68	71.58	86.13	91.18	98.07				0	–
Bira	*Thalassodendron ciliatum*	4.58	7.66	9.84	11.42	11.69	12.97	13.13	13.42	0	–
Gazi MM	*Thalassodendron ciliatum*	4.09	7.06	9.25	11.83	13.37	14.21	15.34	16.96	0	–
Gazi MS	*Thalassodendron ciliatum*	5.70	10.48	14.08	17.02	19.68	20.76	22.50	25.21	0	–
Gazi CS	*Thalassodendron ciliatum*	6.29	10.39	12.37	12.79	13.33	13.84*	13.64	13.62*	1.6	ns
Medes Islands	*Posidonia oceanica*	18.60	21.15	22.10*	21.39	21.93*				0.8	ns
Zandkreek	*Zostera marina*	2.09	3.32	4.06	4.50	4.75	4.84	4.94	4.94	0	–
Veerse Meer	*Zostera marina*	3.45	5.38	6.45	6.88	7.34	7.34			0	–
Nitrogen											
Barang Lompo	*Thalassia hemprichii*	0.54	0.70	0.71	0.72*	0.59*				18	0.044
	Enhalus acoroides	3.06	4.73	6.12	7.31*	6.30*				14	ns
	Cymodocea rotundata	0.32	0.48*	0.43	0.38*					20	0.002
Gusung Tallang	*Thalassia hemprichii*	0.93	0.12*	0.97	0.81*					28	0.001
	Enhalus acoroides	5.77	7.79	8.75*	8.25	7.23*				17	0.023
Bira	*Thalassodendron ciliatum*	0.21	0.33	0.40	0.43	0.41	0.42*	0.41	0.38*	9.8	ns
Gazi MM	*Thalassodendron ciliatum*	0.16	0.29	0.41	0.50	0.55*	0.54	0.54	0.52*	4.1	ns
Gazi MS	*Thalassodendron ciliatum*	0.24	0.48	0.66	0.75	0.86	0.87	0.91*	0.87*	4.1	ns
Gazi CS	*Thalassodendron ciliatum*	0.30	0.53	0.62	0.63	0.63*	0.60	0.54	0.45*	29	0.001
Medes Islands	*Posidonia oceanica*	0.84	0.85*	0.80	0.71	0.64*				24	0.023
Zandkreek	*Zostera marina*	0.18	0.29	0.33	0.36	0.37	0.38*	0.36	0.37*	3.8	ns
Veerse Meer	*Zostera marina*	0.23	0.33	0.36	0.37	0.40*	0.38*			3.8	ns
Phosphorus											
Barang Lompo	*Thalassia hemprichii*	0.055	0.063	0.065	0.067	na				na	–
	Enhalus acoroides	0.41	0.57	0.62	0.64*	0.56*				12	ns
	Cymodocea rotundata	0.036	0.044*	0.035	0.021*					51	0.013
Gusung Tallang	*Thalassia hemprichii*	0.10	0.099*	0.076	0.069*					31	0.003
	Enhalus acoroides	0.62	0.91	0.99*	0.83	0.71*				29	0.017
Bira	*Thalassodendron ciliatum*	0.032	0.050	0.058*	0.052	0.045	0.048	0.042	0.040*	30	0.004
Gazi MM	*Thalassodendron ciliatum*	0.016	0.033	0.037	0.041	0.043*	0.041	0.040	0.042*	2.3	ns
Gazi MS	*Thalassodendron ciliatum*	0.022	0.042	0.053	0.054	0.061*	0.056	0.055	0.058*	5.7	ns
Gazi CS	*Thalassodendron ciliatum*	0.030	0.046	0.049*	0.045	0.043	0.041	0.034	0.033*	33	0.005
Medes Islands	*Posidonia oceanica*	0.061	0.067*	0.049	0.043	0.043*				35	ns
Zandkreek	*Zostera marina*	0.022	0.033	0.031	0.032	0.034	0.035	0.035		0	–
Veerse Meer	*Zostera marina*	0.039	0.046	0.045	0.047	0.048				0	–

Table 4 Comparison of the physiological resorption efficiency (%*R*, see Table 3) and the actual resorption efficiency calculated taking fragmentation and premature detachment of leaves into consideration (%*R′*, calculated using model Eq. 3), for the Indonesian seagrass species. Percentage (physiological) resorption realized is calculated as $100\ \% \cdot \frac{\%R'}{\%R}$ (*na* not analysed)

Site	Species	%*R*		%*R′*		% resorption realized
		N	P	N	P	
Barang Lompo	*Thalassia hemprichii*	18	na	10	na	56
	Enhalus acoroides	14	12	8.1	7.3	57
	Cymodocea rotundata	20	51	10	26	50
Gusung Tallang	*Thalassia hemprichii*	28	31	20	24	76
	Enhalus acoroides	17	29	11	19	65
Bira	*Thalassodendron ciliatum*	9.8	30	7.6	23	77

Discussion

Nutrient resorption

The present results show that the concentrations of nitrogen and phosphorus in the leaves of all of the investigated seagrass species decrease with increasing leaf age. There is, however, a considerable variation in this decline, both within as well as among species. The significant declines we found for the leaf nitrogen concentration (19 to 58%) are lower than the 70% decline reported for *Thalassia testudinum* (Patriquin 1972), but in the same range as earlier reported for *Zostera marina* (20 to 25%: Harrison and Mann 1975; 21%: Thayer et al. 1977; 20 to 80%, depending on the season: Pedersen and Borum 1993) and *Posidonia oceanica* (25 to 40%: Alcoverro 1995). In the present study, the decline in the leaf phosphorus concentration was between 34 and 66%. The 40% P-concentration decline in *Amphibolis antarctica* (derived from Walker and McComb 1988) and the 30 to 40% decline found for *P. oceanica* (Alcoverro 1995) are within this range. The contribution of carbon to total leaf weight remains more stable during the development and ageing of the leaves. Changes in the %C were only significant in three cases and varied up to 24% decline, which is not much different from literature values for *Z. marina* (20 to 25% decline: Harrison and Mann 1975; 36% decline: Thayer et al. 1977) and *P. oceanica* (5 to 17% decline: Alcoverro 1995). Fixed to an important degree in structural components, carbon is expected to be less mobile in senescent leaves than other elements, which may explain the relatively constant tissue concentration (Dawes and Lawrence 1979; Thayer et al. 1984).

A decline in the tissue nutrient concentration does not necessarily imply that nutrients are actually resorbed. The tissue concentration may decline during the development of leaves, but if leaves are still growing, the total nutrient content of a leaf (the resultant of tissue concentration and leaf biomass) may still increase. The nutrient resorption efficiency in seagrasses in this study is up to 28% (average 15%) for nitrogen and up to 51% (average 21%) for phosphorus. Compared to terrestrial plants, these values are remarkably low; in a review, Chapin and Kedrowski (1983) reported values of up to 79% (average 52%) for nitrogen and up to 90% (average 43%) for phosphorus.

Effective nutrient resorption could be an important mechanism to decrease the plants' dependence on external input of nutrients in nutrient-poor environments (Chapin 1980). Several studies of terrestrial and salt marsh plants have reported a negative relation between resorption efficiency and environmental nutrient levels (Broerner 1984; Shaver and Melillo 1984; Lajtha 1987; Chapin and Moilanen 1991; Li et al. 1992). In general, nutrient resorption in terrestrial plants is proportionally larger in less fertile environments than in fertile soils (Chapin 1988). The nutrient concentrations in seagrass leaves are usually positively correlated with environmental nutrient levels (e.g. Fourqurean et al. 1992). Duarte (1990) reviewed the literature data on N- and P-concentrations in seagrass leaves and reported 1.8% N and 0.20% P (% dry weight) as median values for these nutrients. We divided the seagrasses investigated in the present study according to these reference concentrations (total plant averages). There was no evidence for a difference in resorption efficiency between seagrasses with a low (<1.8% N and <0.20% P) and seagrasses with a high (>1.8% N and >0.20% P) leaf nutrient concentration (ANOVA; $p = 0.788$ and 0.342 for N and P, respectively). When individual species are considered, however, in some cases a *positive* relation between the nutrient concentration of leaves and the percentage resorption is found, which (assuming that the higher nutrient levels in the leaves coincide with higher environmental nutrient levels) is in contradiction with the observations that in terrestrial plants the resorption efficiency is larger in less fertile environments. The average N- and P-concentrations in leaves of *Enhalus acoroides* and the average N-concentration in leaves of *Thalassia hemprichii* are significantly higher at Gusung Tallang than at Barang Lompo, which coincides with a higher resorption efficiency (Table 5). The explanation may be that a large internal nutrient pool may coincide with a smaller fraction of nutrients being fixed in structural cell components that are less accessible to hydrolysis and resorption (Lajtha 1987; Pedersen and Borum 1993; Pugnaire and Chapin 1993). However, not in all cases was a positive relationship between leaf nutrient concentrations and resorption efficiency found. Although the average nitrogen concentration in leaves of *Zostera marina* is significantly higher in the Zandkreek population than in the Lake Veere population, there is virtually no difference in resorption efficiency. Similarly, the relation between the average N- and P-concentrations in leaves of *Thalassodendron ciliatum* and the resorption efficiency is not straightforward. A lack of consistency seems a common phenomenon in terrestrial studies as well. Chapin (1980, 1988) indicated that terrestrial plants of nutrient-poor environments have several other effective strategies to overcome periods of nutrient stress, such as luxury consumption, reduced growth rates, increased leaf longevity, reduced leaching and nutrient uptake by leaves. Often, one or more of these strategies co-occur with nutrient resorption (Chapin 1980; Li et al. 1992; Reich et al. 1992). It is likely that different species make use of different strategies, or that a species switches between strategies, which could coincide with variations in the resorption efficiency between species. Comparison between species, and even within species, are therefore best made with caution.

Data evaluation

We calculated the physiological resorption efficiency based on the tissue nutrient concentrations of the oldest

Table 5 Average nitrogen and phosphorus concentrations (± 1 SD, $n = 3$) in seagrass leaves in relation to nutrient resorption efficiency. Concentrations calculated as the sum of N- or P-contents in all leaf classes, divided by the summed biomass (g dry weight) of those leaf classes, for each species. Seagrasses are sorted according to decreasing %R within each species

Nutrient, site	Species	Average concentration	% R
Nitrogen			
Gusung Tallang	*Thalassia hemprichii*	2.26 ± 0.07	28
Barang Lompo	*Thalassia hemprichii*	1.97 ± 0.12	18
Gusung Tallang	*Enhalus acoroides*	3.02 ± 0.09	17
Barang Lompo	*Enhalus acoroides*	1.86 ± 0.09	14
Gazi CS	*Thalassodendron ciliatum*	1.76 ± 0.05	29
Bira	*Thalassodendron ciliatum*	1.37 ± 0.03	9.8
Gazi MS	*Thalassodendron ciliatum*	1.72 ± 0.05	4.1
Gazi MM	*Thalassodendron ciliatum*	1.59 ± 0.07	4.1
Zandkreek	*Zostera marina*	2.82 ± 0.07	3.8
Veerse Meer	*Zostera marina*	1.98 ± 0.11	3.8
Phosphorus			
Gusung Tallang	*Enhalus acoroides*	0.32 ± 0.02	29
Barang Lompo	*Enhalus acoroides*	0.19 ± 0.02	12
Gazi CS	*Thalassodendron ciliatum*	0.13 ± 0.01	33
Bira	*Thalassodendron ciliatum*	0.17 ± 0.01	30
Gazi MS	*Thalassodendron ciliatum*	0.12 ± 0.01	5.7
Gazi MM	*Thalassodendron ciliatum*	0.13 ± 0.01	2.3
Zandkreek	*Zostera marina*	0.28 ± 0.01	0
Veerse Meer	*Zostera marina*	0.27 ± 0.01	0

leaf. This leaf is, however, still attached to the plant, which may imply that the process of resorption has not been completed. As an alternative, we could have used the tissue contents of freshly detached detritus. However, in the early stages of decay, especially in the tropics, rapid changes in the nutrient contents occur. This can either be an initial accumulation, as has been repeatedly reported for nitrogen (Fenchel 1977; Godshalk and Wetzel 1978; Kenworthy et al. 1987), but also a rapid decline caused by increased leaching (Swift et al. 1979). Because of the questionable nutrient contents of detritus, we decided not to use this material, but we are aware of the fact that our data on physiological resorption efficiency may be slight underestimations.

Our data on nutrient resorption are based on single sampling campaigns. Due to seasonal changes in nutrient demand, especially in temperate regions (changing temperature and light conditions; Duarte 1989), the intra-annual variation in nutrient resorption may be considerable. We did not find evidence for nitrogen resorption in *Zostera marina*, while Borum et al. (1989) and Pedersen and Borum (1992, 1993) reported 12 to 27% resorption on an annual basis. They did, however, indicate that reclamation decreased dramatically in July and onwards, which coincides with the period when our samples were taken. Although the seasonal dynamics of seagrasses in tropical and subtropical areas is usually much less than in temperate regions (Duarte 1989), also our data on tropical species may not be representative as annual means. Extrapolations on the contribution of nutrient resorption in meeting annual requirements should therefore be made with caution.

Our results, furthermore, show that the calculation of resorption efficiency based on the biomasses of intact leaves was 23 to 50% larger than the actually realised resorption. Premature loss of leaves and leaf fragments may therefore substantially interfere with the resorption process, making it less effective. The magnitude of loss of leaves or leaf fragments is to a large extent determined by species' characteristics and the physical conditions of the habitat. Robust species show less fragmentation, as is also the case for species that are less favoured by herbivores (e.g. *Thalassodendron ciliatum*). Fragile, elongated leaves of fast-growing species are relatively easily detached (e.g. *Cymodocea rotundata*; Stapel et al. 1996b) and usually favoured by herbivores (Erftemeijer et al. 1993a; Preen 1995). Seagrasses growing in intertidal habitats, which frequently emerge, may also experience fragmentation as a result of desiccation stress (Van Lent et al. 1991; Erftemeijer and Herman 1994; De Iongh et al. 1995; Stapel et al. 1997).

In climax species such as *Thalassia hemprichii*, *Enhalus acoroides*, *Thalassodendron ciliatum* and *Posidonia oceanica*, leaf production accounts for 90 to 95% of the total nitrogen and phosphorus demand (Brouns 1985; Erftemeijer et al. 1993b; Pergent et al. 1994; Pergent-Martini et al. 1994). In these species, the resorption efficiency established in the leaves, therefore, is virtually equal to the percentage of the total plant nutrient demand which can be met by internal reclamation. In other species, such as *Cymodocea rotundata* and *Zostera marina*, below-ground production can be substantial in comparison to leaf production (Nienhuis and De Bree 1977; Erftemeijer et al. 1993b; Van Lent and Verschuure 1994a), which implies that the percentage of the total plant nutrient demand that can be met by internal reclamation from senescent leaves will be considerably lower than the resorption efficiency reported in this study. Obviously, it is true for all species that in expanding clones, the contribution of nutrient resorption to total plant demand will also be lower than the reported resorption efficiency.

Conclusion

We conclude that nutrient resorption from senescent leaves may play a role in the nutrient balance of seagrasses. However, our findings suggest that the contribution of internal reclamation to annual nutrient demands may be less important than previously assumed (Patriquin 1972; Hemminga et al. 1991; Pedersen and Borum 1993). On average, the seagrasses investigated in the present study are physiologically capable of resorbing 16 and 22% of their maximum nitrogen and phosphorus leaf content, respectively. Due to fragmentation and premature detachment of leaves, however, only part of this potential is actually realised under natural conditions (e.g. on average only 64% in Indonesian seagrass species). We estimate, therefore, that nutrient reclamation from senescent seagrass leaves reduces the nutrient requirements for seagrass leaf production by approximately 10% for nitrogen and 15% for phosphorus. In relation to total plant demands, these figures may even be lower, dependent on clonal expansion and the importance of below-ground production relative to leaf production.

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