

Nutrient dynamics of seagrass ecosystems: ¹⁵N evidence for the importance of particulate organic matter and root systems

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ABSTRACT: The availability of nitrogen in sediment phytodetritus to seagrass was investigated in 5 tropical species (*Thalassia hemprichii*, *Halodule uninervis*, *H. pinifolia*, *Halophila ovalis/ovata* and *Syringodium isoetifolium*) from Indonesia. ¹⁵N-labeled phytodetritus was injected into the sediment and the appearance of ¹⁵N in the roots, the rhizomes and the leaves of the plants were measured after 1, 2, 4 and 8 d. The transfer of ¹⁵N from sediment phytodetritus to the plant tissues was very rapid (within 1 d) and continued over the 8 d period, indicating an efficient retention of the phytodetritus and a net mineralization of nitrogen rather than an immobilisation by bacteria. Relative enrichment of roots versus leaves indicated that ¹⁵N was taken up by the roots and then transferred to the leaves. The combined efficiency of seagrass canopy-induced trapping and retention of sestonic particles and root-uptake, results in the acquisition of nutrients released upon mineralization of particulate organic matter (POM), giving them a competitive advantage over other primary producers in oligotrophic environments.

KEY WORDS: Tropical seagrass · Nutrient uptake · Canopy · ¹⁵N · Mineralization · Phytodetritus

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INTRODUCTION

Seagrass meadows are among the most efficient ecosystems in terms of the value-added benefits of the services they provide. Their ecosystem's services are estimated at about \$19000 ha⁻¹ yr⁻¹ (Costanza et al. 1997) and they contribute about 12 % of the net ecosystem production (Duarte & Cebrian 1996), about 5 % of respiration (Middelburg et al. 2005) and about 25 % of carbon burial (Duarte et al. 2005) in coastal areas. Despite the obvious importance of the high productivity of seagrass meadows, current knowledge of their nutrient dynamics remains poor. Compared to most angiosperms, seagrasses are rather inefficient in re-using their internal nutrient pool (Hemminga et al. 1999); that is, seagrasses living in a physical dynamic environment lose a lot of nutrients when senescent leaves are ripped off from their meadow. Inefficient internal recycling is a typical trait of plants from nutri-

ent-rich environments. This raises the question as to how seagrass meadows are able to maintain such a high level of productivity in oligotrophic environments.

Seagrasses can take up nutrients through both their leaves and roots. The relative importance of roots and leaves for nutrient uptake depends on a number of factors including the concentrations and availability in the water column and sediment reservoirs, and can vary from leaf-dominated to root uptake-dominated (Carignan & Kalff 1980). Foliar uptake supplies around 50 % of the overall N requirement of *Thalassia testudinum* (Lee & Dunton 1999) and *T. hemprichii* (Stapel et al. 1996); between 30 to 90 % of the overall N requirement of *Zostera marina* (Iizumi & Hattori 1982, Short & McRoy 1984, Pedersen & Borum 1992, 1993); and in extreme cases, the complete N requirement of *Phyllospadix torreyi* (Terrados & Williams 1997). The assumed minor importance of roots for nutrient acqui-

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sition is remarkable considering that below-ground biomass is a major carbon investment with respect to tissue construction and maintenance. Below-ground carbon investments have even been identified as an important factor in the vulnerability of seagrasses to low-light conditions, which is one of the main reasons for the world-wide decline of seagrass meadows (Hemminga 1998). The relatively high carbon costs associated with seagrass roots combined with carbon and nutrient mass balance constraints (Erftemeijer & Middelburg 1995) raises the question as to whether the current understanding of the importance of seagrass roots for nutrient acquisition is correct.

There are 2 reasons to re-assess the current view on nutrient cycling in seagrass meadows. Firstly, most studies on nutrient uptake by seagrass plants focus solely on inorganic nutrients and very little is known about uptake of organic nutrients (McRoy & Goering 1974, Bird et al. 1998). Consequently, we lack insight into the role of (1) dissolved organic nutrients that are usually more abundant than dissolved inorganic nutrients in oligotrophic environments and (2) nutrient recycling within seagrass meadows via microbial decomposition of POM in the water column and/or in the sediment. The organic matter that is mineralised in seagrass meadows may either be produced in the meadow (recycled production) or be imported from adjacent ecosystems (new production). A number of studies have focused on the complex biogeochemical interactions in sediments inhabited by seagrasses (e.g. Holmer et al. 1999, 2001). Secondly, seagrasses often grow on sandy sediments and Huettel and co-workers (Huettel & Gust 1992a,b, Huettel & Rusch 2000, Rusch & Huettel 2000) have reported high rates of water exchange between permeable, sandy sediments and overlying water. These enhanced rates of water exchange relieve diffusive limitations of nutrient transport into the sediment towards seagrass roots and result in the transfer of small particles (including algae and bacteria) from the water column to the sediment. In the sediment, these particles may be trapped and retained depending on the relative sizes of pore spaces and particles but also on the topography of the sediment. Consequently, POM transported and trapped into sandy sediments and the subsequent regeneration and release of dissolved nutrients may be a pathway of nutrient supply to seagrasses.

The objective of our study was to assess whether seagrasses may derive nutrients from organic nutrient sources such as POM that are transported into sandy sediments. Using an *in situ* isotopic enrichment experiment, we demonstrate for 5 tropical species that seagrass roots enable a rapid transfer of nutrients from degrading phytodetritus trapped in the sediment to the seagrass shoots.

MATERIALS AND METHODS

Study site. The experiment was carried out at Derawan Island (2° 16' 40" N, 118° 16' 40" E), situated in the Berau delta in East Kalimantan, Indonesia. The area closer to the Berau is strongly influenced by the river discharge, which can transport substantial amounts of terrigenous organic materials, sediment and nutrient loads. More outward in the estuary, the river influence is limited, and oligotrophic tropical coral islands are present. The vegetative cover at the experimental site at Derawan Island is a heterogeneous and sparse mix of *Thalassia hemprichii*, *Cymodocea rotundifolia*, *Halodule uninervis*, *H. piniifolia*, *Halophila ovalis/ovata* and *Syringodium isoetifolium*. The meadow was short due to grazing by the green sea turtle *Chelonia mydas*.

In situ labelling. The experiment was carried out in a shallow, but continuously submerged, seagrass meadow. Within this meadow, a 3 × 3 m square research area was protected against turtle grazing by a 3 m high cage made out of white (i.e. visible to the turtles) fishing net (50 mm mesh size). The subtidal location allowed us to work in the cage without causing any damage to the vegetation or disrupting the sediment. Within the turtle enclosure, we equally subdivided 3 plots: 2 replicate plots for labelling and 1 plot as a control. In each plot, 6 flagged bamboo sticks were sparsely distributed.

An axenic clone of the diatom *Amphora coffeaeformis* (UTCC 58) was cultured at 16°C under 32 W incandescent lights. The artificial seawater (F2 medium) contained 50% ¹⁵N-enriched nitrate (98% ¹⁵N, Isotech) to label the diatoms. After 3 wk, the labelled diatoms were concentrated by centrifugation, washed several times to remove adhering ¹⁵N-NO₃ and subsequently freeze-dried. The axenic state of the diatom culture was verified microscopically. The freeze-dried phytodetritus was subsequently distributed to 12 Eppendorf tubes (2 ml) containing 35 mg of dried material each. At the field site, the diatoms were re-suspended in 2 ml of seawater and gently homogenized by sucking the solution in and out 3 times with a syringe. At low tide, the re-suspended solution was injected in the upper 50 mm of sediment, at 4 equidistant points 50 mm around each bamboo stick of the 2 replicate labelling plots (Day 0).

Sample collection and analysis. Seagrass samples (2 replicates and 1 control) were retrieved during low tide at 1, 2, 4 and 8 d after label addition. Each flagged subplot was sampled digging a deep groove (150 mm deep) with a long blade knife. A 150 × 150 mm square clump of seagrass around the bamboo stick was extracted from the sediment and poured into a plastic bag. Seagrass samples were first sorted by species

present at each subplot. Due to the sparse and heterogeneous seagrass cover, it was not always possible to recover all different species (e.g. *Halodule pinifolia* and *Halophila ovalis*). Subsequently and respectively to their subplot (the 2 replicates and the control), plants were dissected to isolate their roots, rhizomes and leaves. In the case of *Thalassia hemprichii*, we also isolated the sheath. Epiphytes were carefully removed from the leaves scraping them clean with a razor blade and all of the samples were rinsed twice in seawater. All separated parts were placed into 20 ml glass vials and dried in a stove at 60°C for 72 h. Dried samples were ground using an agate mortar.

The stable isotope measurements were made using a Finnigan Delta S isotope ratio mass spectrometer coupled on-line via a conflo interface with a Carlo Erba/Fisons/Interscience elemental analyser. The nitrogen isotopic composition was expressed in the delta notation using the equation:

$$\delta^{15}\text{N}(\%) = \left(\frac{R_{\text{sam}}}{R_{\text{air}}} - 1 \right) \times 1000$$

where $R_{\text{sam}} = {}^{15}\text{N}/{}^{14}\text{N}$ (ratio of the sample) and $\delta^{15}\text{N}$ expressed relative to the atmospheric nitrogen ratio ($R_{\text{air}} = 0.0036765$).

$\delta^{15}\text{N}$ values were averaged between the 2 replicate subplots for the different seagrass fractions isolated for each species. Background values were obtained by averaging the control $\delta^{15}\text{N}$ values over the 4 sampling days.

RESULTS

Transfer of ${}^{15}\text{N}$ from the labelled phytodetritus to seagrass plants was very rapid (Table 1, Fig. 1). Within 24 h after injecting the ${}^{15}\text{N}$ -labelled phytodetritus in the sediment, all exposed seagrass plants showed a significant increase in $\delta^{15}\text{N}$ values, despite differences in turnover, size and standing biomass between species. The response of the relatively large *Thalassia hemprichii* plants seems somewhat slower than that of the relatively small *Halophila ovalis* plants, which we

ascribe to differences in biomass and biomass turnover rates. The relatively low $\delta^{15}\text{N}$ values of *T. hemprichii* leaves is partly due to the separation of leaves and sheaths, which were not separated for the other species. As the sheath contains the growing part of the leaves, it may be expected that labelling would be greater there. Although the sheaths were indeed labelled to a greater extent than the leaves (Fig. 1a), *T. hemprichii* was labelled to a smaller extent the other species.

For all species except *Halophila ovalis*, the roots were initially labelled to a much greater extent than the rest of the plant (Table 1). This suggests that the rapid nutrient transfer from phytodetritus in the sediment to seagrass rhizomes and shoots occurred via the roots. This nutrient transfer pathway is further confirmed by calculating the ratio of $\delta^{15}\text{N}$ in the leaves to $\delta^{15}\text{N}$ in the roots from the time series (Fig. 2). For all the seagrass species except for *H. ovalis*, this ratio increased with time, indicating that, over time, leaves became enriched relative to the roots.

DISCUSSION

The *in situ* deliberate tracer experiment convincingly demonstrated the potential role of sediment POM as a nutrient source for seagrass productivity in oligotrophic systems. In addition, we demonstrated that seagrass roots can play a major role in nutrient uptake once POM is trapped in the sediment. Before discussing in detail the results and their implications, it is instructive to evaluate the experimental approach. The pulse-chase experiment was performed *in situ* rather than in the laboratory or mesocosms in order to minimise disturbances and deviations from field conditions. Particle transport to seagrass sediment was simulated by injecting algae into the upper 50 mm of sediment. Although the resulting depth distributions within the sediment may differ from natural particle trapping depth distributions, the retention and subsequent fate of this material was similar to particles

Table 1. Natural $\delta^{15}\text{N}$ abundance (i.e. background value) and $\delta^{15}\text{N}$ values as measured 1 d after label addition; mean \pm SD (n). Natural ${}^{15}\text{N}$ abundance in seagrass leaves agreed well with literature values for a wide range of species (Udy et al. 1999, Marba et al. 2002, Anderson & Fourqurean 2003, Yamamuro et al. 2003)

	Roots		Rhizomes		Leaves	
	Background	After 1 d	Background	After 1 d	Background	After 1 d
<i>Thalassia hemprichii</i>	4.47 \pm 2.02 (2)	346.8 \pm 242.7 (2)	2.9 \pm 0.4 (2)	17.5 \pm 1.5 (2)	4.6 \pm 0.6 (2)	19.6 \pm 22.5 (2)
<i>Syringodium isoetifolium</i>	5 \pm 2.4 (4)	238 \pm 239.8 (2)	3.9 \pm 1 (4)	65.7 \pm 65 (2)	3.4 \pm 0.5 (4)	49.1 \pm 47.5 (2)
<i>Halodule uninervis</i>	6.9 \pm 3.4 (4)	278.6 \pm 347.9 (2)	3.8 \pm 1.3 (4)	107.2 \pm 83.2 (2)	3.8 \pm 1.3 (4)	106 \pm 55.5 (2)
<i>Halodule pinifolia</i>	5	720 \pm 417.2 (2)	5.1	417.6 \pm 13.3 (2)	5.9	583.1 \pm 143.2 (2)
<i>Halophila ovalis</i>	3	676	5.3	774.3	4.8	913.2

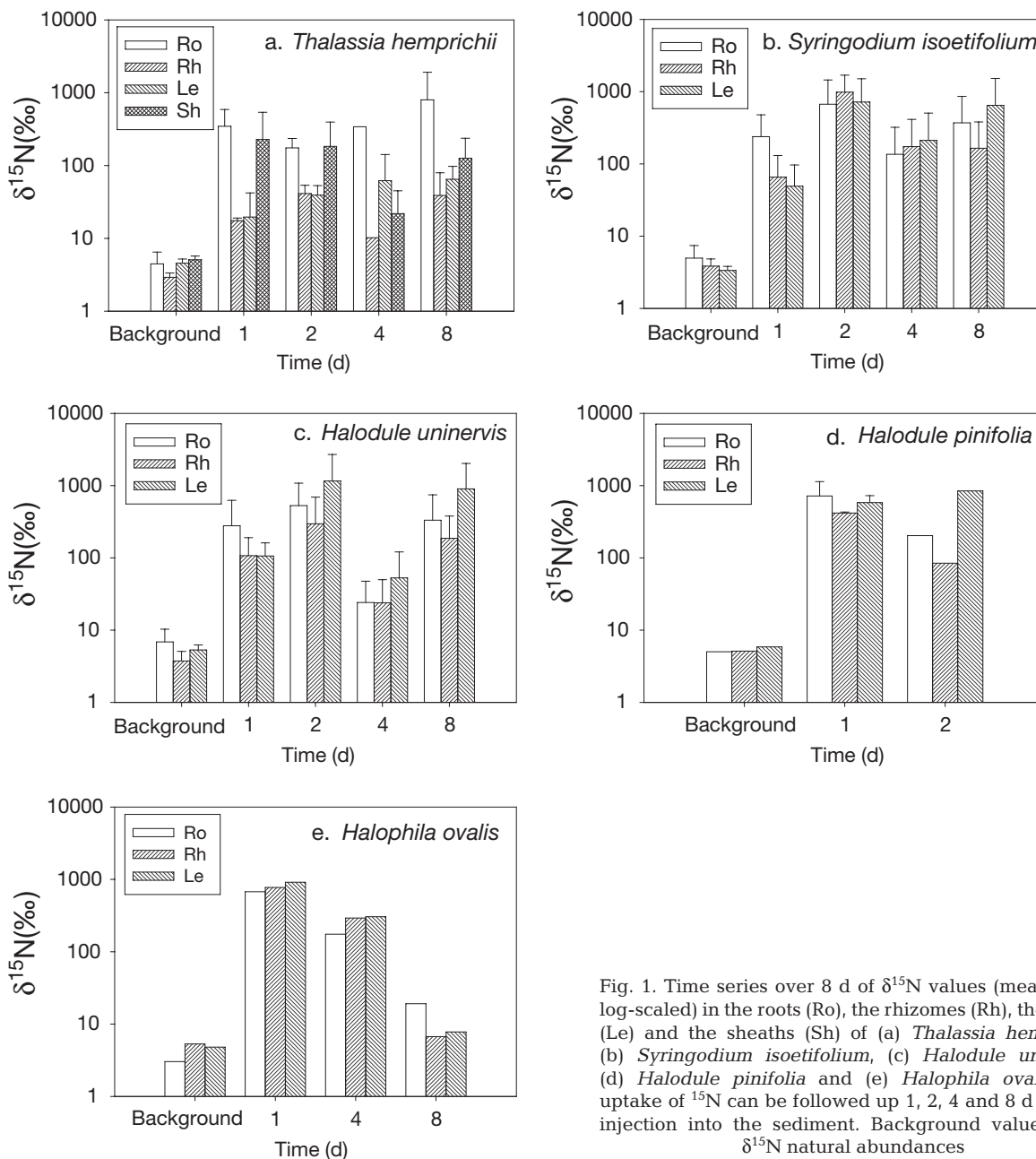


Fig. 1. Time series over 8 d of $\delta^{15}\text{N}$ values (mean + SD, log-scaled) in the roots (Ro), the rhizomes (Rh), the leaves (Le) and the sheaths (Sh) of (a) *Thalassia hemprichii*, (b) *Syringodium isoetifolium*, (c) *Halodule uninervis*, (d) *Halodule pinifolia* and (e) *Halophila ovalis*. The uptake of ^{15}N can be followed up 1, 2, 4 and 8 d after its injection into the sediment. Background values show $\delta^{15}\text{N}$ natural abundances

delivered by natural processes. As with most tracer studies, the labelled phytodetritus material added may not have been the same as that in the field in terms of size and degradability. *In situ* deliberate tracer experiments provide essential and unequivocal information on nitrogen flows, even though interpretation may be somewhat complicated by heterogeneity as reflected in the relatively large standard errors (Figs. 1 & 2, Table 1). Heterogeneity is related to a number of causes, including differences in the quantity and depth distribution of tracer injection, variability in sediment grain size (causing differences in tracer retention after

injection) and heterogeneity of the seagrass meadow in terms of plant, zoobenthos and micro-organism biomass. While *in situ* tracer experiments can unequivocally identify the flows of ^{15}N from sediment POM to seagrass tissues, they do not provide any resolution if dissolved inorganic or organic nitrogen is assimilated.

Solute exchange between the water column and sediments has been studied extensively. Hydrodynamics play a critical role in the advective transport and the degradation of organic matter in sediment, as was shown for permeable bare sediments in the field, in flumes and in chamber experiments (Huettel & Gust

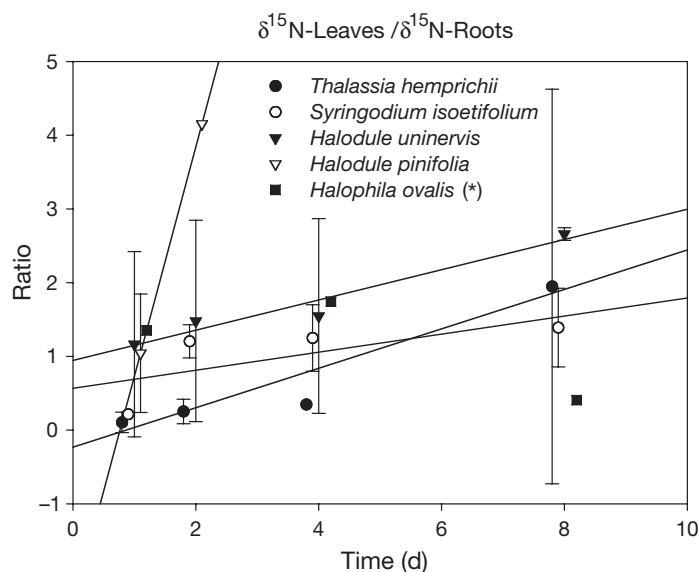


Fig. 2. Ratio (mean \pm SD and linear regression) of leaf to root $\delta^{15}\text{N}$ signatures over time. An increasing ratio indicates that there is a transfer of ^{15}N from the roots to the leaves. Points at each time step were slightly shifted to enhance readability. Coefficients of determination (r^2) for the regression lines are 0.91, 0.50 and 0.95 for *Thalassia hemprichii*, *Syringodium isoetifolium* and *Halodule uninervis*, respectively. **Halophila ovalis* linear regression is not represented here as the very low value of the last data point might be erroneous

1992a, Huettel & Rusch 2000, Rusch & Huettel 2000, Ehrenhauss et al. 2004a,b). Permeable sediments act as biocatalytic filters where algal material, flocs and detritus are trapped. In the ecosystem we studied (seagrass meadow behind coral reef), particle trapping can be considerably enhanced, as exuded coral mucus traps POM in the water column and concentrates it in the lagoon with tidal currents (Wild et al. 2004). Moreover, seagrass canopies strongly enhance sedimentation by reducing current velocity and wave energy. Canopy trapping has been demonstrated in temperate areas (Koch 1999, Koch & Gust 1999, Terrados & Duarte 2000, Gacia & Duarte 2001, Granata et al. 2001, Gacia et al. 2002) as well as in tropical ones (Agawin & Duarte 2002, Gacia et al. 2003). In a seagrass meadow dominated by *Thalassia hemprichii*, Agawin & Duarte (2002) showed that particle loss is 4 times higher than in unvegetated areas, suggesting an important transfer of planktonic production to the seagrass meadow. Even though one may show that, in extreme conditions, seagrass meadows become a source of suspended particulate matter (Koch 1999), particle resuspension is generally limited (Terrados & Duarte 2000, Gacia & Duarte 2001, Granata et al. 2001); thus, the literature suggests that POM will be transported to and trapped in sediments, as was mimicked by the label addition applied in this experiment.

The POM trapped in seagrass sediments enters the benthic food web as a resource for macrofauna, meiofauna and bacteria. The rapid appearance of ^{15}N in the seagrass plants following the addition of the labelled material suggests that bacterial mineralisation dominates over bacterial immobilisation in our system. While in temperate zones or sparse vegetations bacterial growth may not be linked directly to seagrass production (Boschker et al. 2000), it seems to be the opposite in tropical zones or dense vegetations where bacterial growth can be enhanced in seagrass sediments (Holmer et al. 1999, Jones et al. 2003). For instance, Blaabjerg et al. (1998) reported diurnal cycles in sulphate reduction in sediments with dense cover of *Zostera marina*. In our experiment, the bacterial community immediately responded to the addition of phytodetritus and thus regenerated nutrients which were then taken up by the plants. The steady increase in $\delta^{15}\text{N}$ over the 8 d period reveals persistent retention and mineralisation of the labelled material and excludes the possibility that the entire ^{15}N uptake is due to the assimilation of an early release of residual dissolved nitrogen that might have been inadvertently added with the introduced phytodetritus. Moreover, the steady increase in $\delta^{15}\text{N}$ of leaves relative to roots indicates that the majority of uptake occurs via the roots (Fig. 2).

Recycling internal nutrient pools (nutrient resorption) through the remobilisation of older senescent parts was shown to have a rather low efficiency of about 15% (Stapel & Hemminga 1997, Hemminga et al. 1999). Perhaps nutrient resorption can be more efficient under specific conditions, but it is unlikely to be sufficient enough to maintain the high productivities observed in oligotrophic tropical offshore coral islands. It appears that POM trapped in the sediment offers an important nutrient source that seagrasses take-up via their roots. These findings corroborate the results of a nutrient mass balance model that underlined the importance of organic matter mineralisation for nutrient supply and seagrass roots for nutrient uptake (Ertfemeijer & Middelburg 1995).

In this paper, we identified that phytodetritus and POM trapping in the sediment, either by advective transport or due to canopy friction, in combination with root nutrient uptake are among the key processes involved in sustaining nutrient supply to seagrass meadows in oligotrophic environments. Although our *in situ* experiment does not allow us to derive a precise nutrient budget, it clearly demonstrates that the roots provide seagrasses with a competitive advantage over other primary producers because additional nutrients, i.e. those in particulate organic form in the sediments, can be utilised. This issue needs further assessment for a better understanding of systems where seagrass meadows dominate over other primary producers.

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LITERATURE CITED

- Agawin NSR, Duarte GM (2002) Evidence of direct particle trapping by a tropical seagrass meadow. *Estuaries* 25: 1205–1209
- Anderson WT, Fourqurean JW (2003) Intra- and interannual variability in seagrass carbon and nitrogen stable isotopes from south Florida, a preliminary study. *Org Geochem* 34: 185–194
- Bird KT, Johnson JR, Jewett-Smith J (1998) In vitro culture of the seagrass *Halophila decipiens*. *Aquat Bot* 60:377–387
- Blaabjerg V, Mouritsen KN, Finster K (1998) Diel cycles of sulphate reduction rates in sediments of a *Zostera marina* bed (Denmark). *Aquat Microb Ecol* 15:97–102
- Boschker HTS, Wielemaker A, Schaub BEM, Holmer M (2000) Limited coupling of macrophyte production and bacterial carbon cycling in the sediments of *Zostera* spp. meadows. *Mar Ecol Prog Ser* 203:181–189
- Carignan R, Kalff J (1980) Phosphorus sources for aquatic weeds: water or sediments? *Science* 207:987–989
- Costanza R, d'Arge R, de Groot R, Farber S and 9 others (1997) The value of the world's ecosystem services and natural capital. *Nature* 387:253–260
- Duarte CM, Cebrian J (1996) The fate of marine autotrophic production. *Limnol Oceanogr* 41:1758–1766
- Duarte CM, Middelburg JJ, Caraco N (2005) Major role of marine vegetation on the oceanic carbon cycle. *Biogeochemistry* 2:1–8
- Ehrenhauss S, Witte U, Bühring SI, Huettel M (2004a) Effect of advective pore water transport on distribution and degradation of diatoms in permeable North Sea sediments. *Mar Ecol Prog Ser* 271:99–111
- Ehrenhauss S, Witte U, Janssen F, Huettel M (2004b) Decomposition of diatoms and nutrient dynamics in permeable North Sea sediments. *Cont Shelf Res* 24:721–737
- Erfemeijer PLA, Middelburg JJ (1995) Mass balance constraints on nutrient cycling in tropical seagrass beds. *Aquat Bot* 50:21–36
- Gacia E, Duarte CM (2001) Sediment retention by a Mediterranean *Posidonia oceanica* meadow: the balance between deposition and resuspension. *Estuar Coast Shelf S* 52:505–514
- Gacia E, Duarte CM, Middelburg JJ (2002) Carbon and nutrient deposition in a Mediterranean seagrass (*Posidonia oceanica*) meadow. *Limnol Oceanogr* 47:23–32
- Gacia E, Duarte CM, Marba N, Terrados J, Kennedy H, Fortes MD, Tri NH (2003) Sediment deposition and production in SE-Asia seagrass meadows. *Estuar Coast Shelf Sci* 56: 909–919
- Granata TC, Serra T, Colomer J, Casamitjana X, Duarte CM, Gacia E (2001) Flow and particle distributions in a near-shore seagrass meadow before and after a storm. *Mar Ecol Prog Ser* 218:95–106
- Hemminga MA (1998) The root/rhizome system of seagrasses: an asset and a burden. *J Sea Res* 39:183–196
- Hemminga MA, Marba N, Stapel J (1999) Leaf nutrient resorption, leaf lifespan and the retention of nutrients in seagrass systems. *Aquat Bot* 65:141–158
- Holmer M, Andersen FO, Holmboe N, Kristensen E, Thongtham N (1999) Transformation and exchange processes in the Bangrong mangrove forest-seagrass bed system, Thailand: seasonal and spatial variations in benthic metabolism and sulfur biogeochemistry. *Aquat Microb Ecol* 20:203–212
- Holmer M, Andersen FO, Nielsen SL, Boschker HTS (2001) The importance of mineralization based on sulfate reduction for nutrient regeneration in tropical seagrass sediments. *Aquat Bot* 71:1–17
- Huettel M, Gust G (1992a) Impact of bioroughness on interfacial solute exchange in permeable sediments. *Mar Ecol Prog Ser* 89:253–267
- Huettel M, Gust G (1992b) Solute release mechanisms from confined sediment cores in stirred benthic chambers and flume flows. *Mar Ecol Prog Ser* 82:187–197
- Huettel M, Rusch A (2000) Transport and degradation of phytoplankton in permeable sediment. *Limnol Oceanogr* 45:534–549
- Iizumi H, Hattori A (1982) Growth and organic production of eelgrass (*Zostera marina* L.) in temperate waters of the Pacific coast of Japan. III. The kinetics of nitrogen uptake. *Aquat Bot* 12:245–256
- Jones WB, Cifuentes LA, Kaldy JE (2003) Stable carbon isotope evidence for coupling between sedimentary bacteria and seagrasses in a sub-tropical lagoon. *Mar Ecol Prog Ser* 255:15–25
- Koch EW (1999) Sediment resuspension in a shallow *Thalassia testudinum* banks ex König bed. *Aquat Bot* 65:269–280
- Koch EW, Gust G (1999) Water flow in tide- and wave-dominated beds of the seagrass *Thalassia testudinum*. *Mar Ecol Prog Ser* 184:63–72
- Lee KS, Dunton KH (1999) Inorganic nitrogen acquisition in the seagrass *Thalassia testudinum*: development of a whole-plant nitrogen budget. *Limnol Oceanogr* 44:1204–1215
- Marba N, Hemminga MA, Mateo MA, Duarte CM, Mass YEM, Terrados J, Gacia E (2002) Carbon and nitrogen translocation between seagrass ramets. *Mar Ecol Prog Ser* 226:287–300
- McRoy CP, Goering JJ (1974) Nutrient transfer between the seagrass *Zostera marina* and its epiphyte. *Nature* 248: 173–174
- Middelburg JJ, Duarte CM, JP Gattuso (2005) Respiration in coastal benthic communities. In: del Giorgio PA, Williams PJLeB (eds) *Respiration in aquatic ecosystems*. Oxford University Press, Oxford, p 206–224
- Pedersen MF, Borum J (1992) Nitrogen dynamics of eelgrass *Zostera marina* during a late summer period of high growth and low nutrient availability. *Mar Ecol Prog Ser* 80: 65–73
- Pedersen MF, Borum J (1993) An annual nitrogen budget for a seagrass *Zostera marina* population. *Mar Ecol Prog Ser* 101:169–177
- Rusch A, Huettel M (2000) Advective particle transport into permeable sediments — evidence from experiments in an intertidal sandflat. *Limnol Oceanogr* 45:525–533
- Short FT, McRoy CP (1984) Nitrogen uptake by leaves and roots of the seagrass *Zostera marina* L. *Bot Mar* 27:547–555
- Stapel J, Hemminga MA (1997) Nutrient resorption from seagrass leaves. *Mar Biol* 128:197–206
- Stapel J, Aarts TL, van Duynhoven BHM, de Groot JD, van den Hoogen PHW, Hemminga MA (1996) Nutrient uptake by leaves and roots of the seagrass *Thalassia hemprichii* in

- the Spermonde Archipelago, Indonesia. *Mar Ecol Prog Ser* 134:195–206
- Terrados J, Duarte CM (2000) Experimental evidence of reduced particle resuspension within a seagrass (*Posidonia oceanica* L.) meadow. *J Exp Mar Biol Ecol* 243:45–53
- Terrados J, Williams SL (1997) Leaf versus root nitrogen uptake by the surfgrass *Phyllospadix torreyi*. *Mar Ecol Prog Ser* 149:267–277
- Udy JW, Dennison WC, Long WJL, McKenzie LJ (1999) Responses of seagrass to nutrients in the Great Barrier Reef, Australia. *Mar Ecol Prog Ser* 185:257–271
- Wild C, Huettel M, Klueter A, Kremb SG, Rasheed MYM, Jorgensen BB (2004) Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. *Nature* 428:66–70
- Yamamuro M, Kayanne H, Yamano H (2003) Delta N-15 of seagrass leaves for monitoring anthropogenic nutrient increases in coral reef ecosystems. *Mar Pollut Bull* 46:452–458

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