Particulate Matter in Mangrove Forests and Seagrass Beds as a Nitrogen Source in Tropical Coastal Ecosystems

Gillis Lucy G. ¹, *, Bouma Tjeerd J. ², Cathalot Cecile ³, Ziegler Alan D. ⁴, Herman Peter M. ²

¹ Leibniz Ctr Trop Marine Ecol GmbH, Mangrove Ecol, Bremen, Germany.
³ Ctr Brest, IFREMER, LEP, Brest, France.
⁴ Natl Univ Singapore, Dept Geog, Singapore 117548, Singapore.

* Corresponding author: Lucy G. Gillis, email address: lucy.gillis@zmt-bremen.de

Abstract:

We show in laboratory and field investigations that in the short-term seagrasses obtain most of their required nitrogen from the degradation of seagrass leaves, rather than degradation of leaves exported from adjacent mangroves. Mangrove forests at our Thailand site retain the majority of their nutrients, and therefore potentially buffer seagrasses from nutrients.

Keywords: buffering, mangrove forests, nitrogen, outwelling, particulate organic material, seagrass beds
Toward understanding the roles of mangrove and seagrass particulate matter as a nitrogen source in tropical coastal ecosystems.

L.G. Gillis1,2, T.J. Bouma1, A.D. Ziegler2 C. Cathalot3 and P.M.J. Herman1.

1 Spatial Ecology, Royal Netherlands Institute for Sea Research (NIOZ), Yerseke, The Netherlands.
2 Geography Department, National University of Singapore, Singapore
3 Laboratoire Environmentnement Profond (LEP), IFREMER, Centre de Brest, Brest, France

Abstract
The location of tropical mangrove forests and seagrass beds along coastlines and shallow water areas enables them both to receive and outwell particulate organic matter (POM), as well as inorganic and organic nitrogen in dissolved forms. Little is known about the potential importance of POM transfer between mangrove forests and seagrass beds as a nutrient source. Transportation experiments showed mangrove leaves were the dominant POM source exported to seagrass beds, but there was little difference between the POM forms (seagrass/mangrove leaves) exported to the coastal ocean. Seagrass leaves and mangrove leaves show differential degradation patterns. The slow degradation of mangrove leaves could potentially contribute to the nitrogen demand of seagrass beds but this will strongly depend on the size of the ecosystems donating and receiving the nitrogen. In contrast, the quick degradation of seagrass may form a more important nitrogen source for dissolved organic nitrogen into the water column, even within the seagrass beds. However, because of the rapid timescales involved in the degradation processes and resultant nitrogen release, seagrass leaves may not be an important nitrogen source for other ecosystems unless local hydrodynamics promote their quick transfer. These results indicate that mangrove forests and seagrass beds retain most of their nutrients allowing them to buffer adjacent nutrient sensitive ecosystems such as coral reefs.

1 Introduction
Tropical coasts contain highly productive ecosystems, such as mangrove forests and seagrass beds, which can be a sink and a source of significant amounts of particulate organic matter (POM) and associated nutrients (carbon and nitrogen) to neighboring ecosystems. In nutrient limited conditions, POM originating from adjacent ecosystems may form an important source of nutrients for both keystone organisms such as stony corals and seagrass plants, and their associated species. Given their large standing biomass and high productivity, mangrove and seagrass POM could be an important nutrient source to adjacent ecosystems. Mangroves may even contribute to positive interactions between adjacent ecosystems at the tropical seascape scale, but experimental evidence is very limited to date. Mangrove nutrient recycling is thought to occur predominantly in situ within the forest, with unused nutrients exported to coastal waters, in part via leaves and other types of POM. Decaying leaves...
release both organic and inorganic forms of dissolved nitrogen. Leaves are also utilized by organisms, such as crabs that process nitrogen to more palatable forms, ultimately providing it to other organisms (8, 13). Mangroves with high nutrient inputs may therefore export considerable amounts of nutrients in their exported leaves. Seagrass beds typically have high productivity, even within nutrient-poor environments (9, 14). One explanation for the ability to flourish in such conditions is internal recycling of nutrients released by senescent leaves or those shed by hydrodynamic forces—provided that degradation starts before leaves are exported from the beds (9, 14-15). Alternatively, some of the nutrients may come from the import of POM from adjacent sources, including mangroves. It has previously been observed that plant material from seagrasses and mangrove trees can form an important source of particulate organic matter in the water column (16-18). However, there is a lack of experimental studies addressing the importance of POM transfer as nutrient source to adjacent ecosystems. In order to understand the potential role of POM originating from mangrove forests and seagrass beds as nitrogen sources for adjacent ecosystems, one must first understand the rates of tidal export of POM from mangroves and seagrasses, as well as nutrient release rates from degrading leaves. In this study, we investigate if, and how, the degradation rate depends on the location within the ecosystem, for example, in the sediment or in suspension in the water column. We also investigate the difference between mangrove and seagrass leaves. Seagrass leaves are thought to break down easily and release nutrients much quicker than mangrove leaves, which have lower nutrient ratios and higher fiber content (20). Mangrove leaves generally depend on organisms like crabs and bacteria for breakdown (21-22).

Our aim is to determine the process rates that are needed for understanding nutrient exchange via POM between mangrove and seagrass. We address the following questions: 1) To what extent are mangrove & seagrass leaves exchanged under normal tidal conditions; 2) What is the rate of degradation of mangrove and seagrass leaves; (3) How do C:N ratios change with degradation; (4) How does leaf degradation affect dissolved organic and inorganic nitrogen in the water column; (5) How much nitrogen exchange potentially occurs between mangrove forests and seagrass beds as a result of the interchange of particulate organic matter and (6) Is the exchange of mangrove POM sufficient for seagrass plant nitrogen requirements. These questions are addressed through several field-and lab-based experiments.

2. Study Area
2.1 Ethics statement
The fieldwork was completed in collaboration with Rajabhat University (Phuket), which gained permission from the Ministry of Natural Resources and Environment.
2.2 Study site
The study site for all field-based experiments was located in Koh Chong Lat Noi bay, on the island of Koh Yao Yai, in Pang Nga.
Incubation experiments were completed in the marine research station, also located on the island. Seagrass and mangrove leaves, sediment and water for the degradation and incubation experiments were taken from Chong Lat Noi bay during July 2011. Mean temperature during sampling was 29°C and salinity was 32 PSU.

We compared degradation rates in three habitat types: (1) the edge of the mangrove forest (MF); (2) the tidal flat (TF) at approximately 300 m from the mangroves; and (3) a seagrass bed (SB), located approximately 600 m from the mangrove forests (Fig 1). The mangrove forest was composed of fringing Rhizophora sp, Ceriops sp and Xylocarpus sp. The seagrass beds comprised Enhalus sp, Halodule sp, Halophila sp and Thalassia sp, with Enhalus sp being the climax species with highest biomass.

For the experiments we used leaves from Rhizophora sp and Enhalus sp. The seagrass, tidal flat and fringing mangrove were exposed at low tide for between 1-4 hours.

### 3. Methods

#### 3.1 Incubations to measure release rates of dissolved nitrogen from seagrass and mangrove leaves

Sediment and mangrove/seagrass leaf samples were collected at low tide. Care was taken to pick leaf samples similar length (mangrove leaves: 0.1 m, seagrass leaves: 0.45 m) and physical state (whole green leaves with no imperfections in the leaf structure). Water samples were collected in the bay at high tide and transported to the marine laboratory in an icebox. Salinity and temperature was recorded during sampling. Water samples were filtered to remove large particles (>2 mm). Three dark incubations with mangrove leaves were completed in parallel over a 24-hour period. The first incubation contained only seawater collected at the mangrove site (control treatment); the second, mangrove sediment/soil plus seawater (soil treatment); and the third, fresh mangrove leaves plus sediment plus seawater from mangroves (leaves treatment). Three replicates of all treatments were performed.

Samples were incubated in the dark in 19.2-L chambers (radius: 142 mm, height: 303 mm). For the sediment and leaf treatments, a 0.1 m thick sediment layer was placed on the bottom; and 12.9 L seawater was added. The temperature was kept constant by placing the chambers in a water bath in which the temperature was maintained manually. Temperature (27-30 °C) and salinity (28-33 ppt) were held within narrow ranges that corresponded with the sampling conditions. A magnetic stirrer was used to maintain thorough mixing during the 24-hour incubations. Water samples (25 ml), were taken every 6 hours (at times 0, 6, 12, 18, 24 hours); temperature and salinity were recorded at the times of sampling. The water in the incubation chamber was replaced by seawater from the site that had been kept at the sample temperature and salinity. Samples were immediately frozen for analysis at a later date. After transporting to NIOZ, the samples were analyzed for dissolved organic and inorganic nitrogen (DON & DIN). For determining seagrass release of DON and DIN, we followed the same protocol described...
Nitrogen release from mangroves or seagrass leaves was calculated as the subtraction of N contents (DON & DIN) of the soil treatment (seawater + sediment incubation) from those of the leaves treatment (leaves + sediment + seawater incubation).

3.2 Transportation rate of seagrass and mangrove leaves - Field experiment

We estimated the residence time of mangrove and seagrass leaves deposited on the sediment within the mangrove forest (MF), tidal flat (TF) and seagrass bed (SB). In each of these habitat types, three replicates of marked fresh mangrove and seagrass leaves were placed at low tide at edge (< 10 m from the ocean) and interior (100 m from the ocean) locations. The sites were monitored every tidal cycle to determine the time when leaves were transported from their initial locations.

We measured the import/export rates of leaves from each ecosystem with 50 (length) x 1 (height) m nets, mesh size 0.05 m, stretched across the seaward edge of the mangrove forest (1 in Fig. 1), the landward edge of the seagrass bed (2 in Fig. 1), and the seaward edge of the seagrass bed (3 in Fig. 1). We collected particulate matter during low tide for five tidal cycles, separating the mangrove and seagrass leaves. Dry mass (g) was determined after drying for at least 48 hours at 60 °C.

Particulate organic material transportation (POMtransport; mg m-2 day -1) per unit area of each ecosystem was estimated as the following (Fig. 2):

POMtransport = 2 x POMnet x (Leco/Lnet) /Aeco (1)

where POMnet (mg tide-1) is the total POM captured in the 50 m long net during one tidal cycle; Lnet is the length of the net (50 m); Leco the total length of the fringe edge of the ecosystem which is donating the POM (~900 m for mangrove, 560 m for shoreward seagrass bed); and Aeco (m2) is the surface area of the entire donating ecosystem.

Collectively, these calculations provide a rough estimate of POM exchanged between ecosystems and the ocean, as we assume all trapped leaves contribute to the total POM exported/imported.

3.3 In situ seagrass and mangrove leaf degradation experiment

Fresh seagrass (Enhalus sp) and mangrove (Rhizophora sp) leaves of similar length (mangrove leaves: 0.1 m, seagrass leaves: 0.45 m) and physical state (whole green leaves with no imperfections in the leaf structure) were used in the degradation experiments. Leaves were collected at low tide and epiphytes were removed. Subsequently, leaves were separated into 180 piles; 90 piles of seagrass and 90 piles of mangrove leaves which were weighted (approximately 10 g wet weight each). Each pile was then placed into a net bag of mesh size < 0.5 mm that allowed for small organisms to migrate in and out, but dispelled larger marine.
123 animals such as crabs. Additional seagrass and mangrove leaf samples (3 replicates each) were used to determine initial wet mass.

124 (Mwet), dry mass (Mdry), and C:N ratios. At each habitat type (MF, TF, SB), three replicates 50 m apart were established, creating three parallel transects (mid point symbolized by solid circle: Fig. 1). At each replicate, sets of 5 poles were driven into the substrate. The poles were the support of 2 sets of bags: one attached 0.05 m above the surface, and one buried 0.05 m in the sediment. Each set of bags consisted of a bag with mangrove leaves (approx. 10 g) and a second bag with seagrass leaves

128 (approx. 10 g). We collected one set of randomly chosen bags after periods of 2, 4, 6, 20 and 30 days to determine the leaf degradation rates and changes in C: N ratios. Following collection, the samples were dried in an oven for 48 hours at 60°C. They were then weighed and placed in labeled sealed plastic bags for transportation to NIOZ, where they were further analyzed for C: N ratios.

132 3.4 Nitrogen requirements of seagrass beds

133 To quantify if nitrogen in mangrove POM exported to seagrass ecosystems could provide the seagrass plants with their nitrogen needs we completed an approximate calculation of these requirements. The nitrogen requirements of seagrass plants Enhalus sp and Halophila sp (NR; . mole m-2 day -1) was calculated as follows:

\[ NR = TN_{leaf} \times B / LT \]

134 where \( TN_{leaf} \) (mole gleaf -1) for Enhalus sp is the total leaf N determined from the fresh seagrass leaves used in the degradation experiment (1143 mole gleaf -1). For Halophila sp we used total N leaf content data of 34-54 mole gleaf -1 (23). Standing biomass of the seagrass per m2 is represented as B, which was calculated by determining the above ground weight of Enhalus sp and Halophila sp per m2. The leaf turnover (LT; days) for Enhalus sp is 100 days and for Halophila sp 30 days.

141 3.5 Analytical analyses

142 Following drying, leaf samples were ground to ensure homogenization using a mixer mill (Retsch, type MM301). The total percent of C, N & CN ratios in dried leaves were determined using a Flash EA 1112 Elemental Analyzer (Thermo Finnigan).

144 Dissolved inorganic (NH4 +, NO3 -& NO2 -) nitrogen (DIN) accumulated in the incubation water were filtered onto a GFF filter (Whatman) and determined calorimetrically using a SK12 nutrient analyser, Skalar & Seal (24). Total nitrogen (TN) was determined from a GFF filter (Whatman) after an alkaline persulphate destruction using the same instrument for dissolved nutrient concentrations (25). Dissolved organic nitrogen was calculated from the difference between dissolved organic nitrogen (DIN) and total nitrogen (TN).

149 3.6 Statistical analysis

150 Prior to testing, normality in the data was tested using a D'Agostino-Pearson test. To test the differences between mangrove and seagrass leaf export to other ecosystems and to the ocean, we used a Kruskal-wallis...
test (K-W test) because the data were not normally distributed. Three-way analysis of variance (ANOVA) with replication was used to test for differences in the following: i) decomposition of detritus related to habitat type (MF, TF, SB) versus time period (2, 4, 6, 20 and 30 days) for each environment; and ii) C:N ratios of mangrove and seagrass leaves between habitat type (MF, TF, SB) versus time period (2, 4, 6, 20 and 30 days) for each environment (sediment and water column). Three-way ANOVA was also used to compare nitrogen release from both mangrove/seagrass leaves (DIN & DON) and time in the incubations. A Kruskal-wallis test was used to compare changes in DIN & DON release from mangrove and seagrass leaves at 24 hours in the incubation; to prevent serial correlation we used the final concentrations of DIN & DON. Least squares difference (LSD) post-hoc testing was performed following ANOVA and Kruskal-wallis test. Probabilities (p) were expressed at p < 0.01 & 0.1, and are referred to in the text as significant. All statistical testing was completed in an R programming platform.

4. Results

4.1 Incubation experiment

There was no apparent release of DIN from either Rhizophora sp. and Enhalus sp. leaves in the incubation experiments, the amount did not significantly differ from zero (Fig. 2). In contrast, DON-amounts increased during 24-h of seagrass leaf decomposition, with the maximum of the mean values of 93. mole DON g-1. DON-release from decomposing mangrove leaves was negligible (Fig. 2). A significant (K-W test: p = 0.04) difference was seen between DON release from seagrass versus mangrove leaves at 24 hours (Fig. 2). In addition, DON amounts for seagrass increased significantly (Three-way ANOVA: p = 0.05), then stabilized after 6 hours until the end of the experiment. Negative values originate from the calculation of the nitrogen release from mangroves or seagrass leaves (subtraction of the N values of the “seawater + sediment” incubation from the “leaves + sediment + seawater” incubation) (Tab.S1).

4.2 POM and TN exchange calculations

All tagged leaves that were deposited at positions within the mangrove forest, tidal flat and seagrass bed were transported away from their original location within one tidal cycle (data not shown). However, it is not known if they were transported out of the system, or simply mobilized by the tide.

Our flux measurements using nets across the bay indicated that the export of mangrove leaves moving into seagrass beds was significantly higher than the biomass of seagrass leaves moving inland toward the mangrove (K-W test, p = 0.01; net 3; Fig. 3). The daily area-weighted mass of mangrove leaves transported toward the seagrass beds (3.7 mg m-2 day-1) was approximately six times higher than for seagrass material transported toward the mangroves (0.6 mg m-2 day-1; Fig. 3; nets 1 and 2). The transport to the ocean of both mangrove (0.3 mg m-2 day-1) and seagrass leaves (0.1 mg m-2 day-1) was much lower than the exchange between mangroves and seagrass (Fig. 3; nets 3 and 4). The total nitrogen in seagrass leaves conveyed to mangrove forests was approximately half of that transferred to seagrass beds from mangroves (K-W test, p =
There was no detectable difference in TN exported to the ocean by mangrove and seagrass leaves.

4.3 Degradation experiments

Enhalus leaves followed an exponential decay pattern where loss of mass showed a 50-75% decrease within 6 days in the water column or in the sediment (Fig. 4B&D). The leaves plateaued in mass loss from 20-30 days in the water column, whilst in the sediment, only 10-50% of the initial mass of seagrass leaves remained (Fig. 4B&D). Thereafter, little change in seagrass leaves mass occurred until the end of the 30-days experiment (Fig. 4B&D). The degradation pattern of Enhalus leaves was in direct contrast to Rhizophora leaves, which showed only a 25% loss in mass after 6 days, both in the water column and sediment.

The degradation pattern of Enhalus leaves was in direct contrast to Rhizophora leaves, which showed only a 25% loss in mass after 6 days, both in the water column and sediment.

Thereafter, little change in seagrass leaves mass occurred until the end of the 30-days experiment (Fig. 4B&D). The degradation pattern of Enhalus leaves was in direct contrast to Rhizophora leaves, which showed only a 25% loss in mass after 6 days, both in the water column and sediment.

Thereafter, little change in seagrass leaves mass occurred until the end of the 30-days experiment (Fig. 4B&D). The degradation pattern of Enhalus leaves was in direct contrast to Rhizophora leaves, which showed only a 25% loss in mass after 6 days, both in the water column and sediment.

The C:N-ratio of Enhalus leaves in the water column gradually increased from a mean of 18 (0 days) to 26 (30 days) (Fig. 5B). In comparison, the C:N ratio of the Enhalus leaves in the sediment didn't change greatly from the initial mean value of 16 (Fig. 5D). A highly significant (p = 0.01) difference was seen for C:N ratios of seagrass leaves between the water column and the sediment and these differences in the water column changed over time (Tab. 1). The C:N-ratio of Rhizophora leaves decreased from mean values of 37 (6 days) to 32 (30 days) during degradation (Fig. 5A&C). Mangrove leaves showed a highly significant change (p = 0.01) between C:N ratios at 6 and 20-30 days and these were affected by the site (Tab. 1; LSD test).

5. Discussion

Mangrove leaves were the dominant POM source transported between adjacent seagrass beds and mangrove forests, but had similar POM transport rates to the open ocean as seagrass beds (Fig. 3). However, our results show faster degradation rates of seagrass leaves than mangrove leaves (Fig. 4), with higher DON releases from the seagrass leaves (Fig. 2). Thus on a short time scale, seagrass leaves may be an important nitrogen source for the tropical coastal seascape due to their fast turnover rates and the associated nitrogen release, but such process will strongly depend on local hydrodynamics. In contrast mangrove leaves are

the dominant particulate organic matter in the coastal area and they cannot be discarded as another potential source for dissolved nitrogen. Importantly our study provides results, which could be used to quantify N processes and pathways in the tropical coastal seascape.

5.1 Leaf litter nitrogen release from seagrass & mangrove leaves

It has been thought that seagrass and mangrove detritus enhance nitrification and denitrification processes in the water
Detritus is a DIN/DON source through leaching and bacterial degradation. Fresh seagrass leaves had a much higher concentration of TN (total nitrogen) in the leaf than mangroves leaves (SL: 2. mole N g⁻¹, ML: 1. mole N g⁻¹). Our incubations indicate that initially (first 24 hours) seagrass leaves are a more important source of DON in the coastal zone. The C:N ratios in the degradation experiments indicated that overall seagrass leaves release nitrogen, whereas mangrove leaves retained it, in agreement with previous studies (26-27). Our incubations also verify this result for a very short initial time period.

5.2 Leaf litter transportation

Although rough estimates, the results of our POM transportation experiment across ecosystems showed that significant amounts of mangrove leaves are exported to seagrass beds (ML 3.7 ± 0.8; SL 0.6 ± 0.04 mg m⁻² day⁻¹; Fig. 3). Via leaf export, mangroves transport a substantial amount of POM to seagrass beds compared to the fluxes from mangrove forest to the ocean and the fluxes of seagrass POM to the mangrove forest and the ocean. Only 8% (0.3 mg m⁻² day⁻¹) of the mobilized mangrove leaves were transported from the seagrass bed to the ocean (Fig 3). We therefore can estimate that 92% of the mangrove leaves remained in the seagrass bed, approximately 3.5 mg m⁻² day⁻¹ (Fig. 2). Other studies have shown that seagrass plants can trap mangrove leaves from mangrove forests located up to 3 km away (Hemminga et al 1994). Exchanges of mangrove leaves (Rhizophora sp. & Ceriops sp.) to seagrass (Thalassodendron sp.) and then back to mangroves have been reported previously in Gazi Bay, Kenya (28).

Seagrass leaves were exported both to the mangrove forest and the ocean, with 80% transported to the forest (Fig. 3). The movement of mangrove leaves to seagrass beds and vice versa indicates that the hydrodynamics between mangrove forests and seagrass beds facilitates a back and forth exchange of POM. Thus, seagrass leaves transported to the mangrove forest could return to the beds, but we have no data to support this. In our transportation experiment, leaves trapped in the nets were fresh; degraded leaves were not present. Once leaves are degraded, they may be trapped in either the mangrove roots or seagrass plants, ending their transport for normal hydrodynamic conditions. Such hypothesis is supported by other studies showing seagrass leaves trapped within seagrass beds, where they represent a viable source of nutrients (29). Likely, retention of mangrove and seagrass leaves within tropical coastal systems can be quite substantial, and constitute a potentially important nutrient source, depending on the degradation timescales and nitrogen release. In the case of seagrass beds, seagrass canopies have been found to retain half of the nitrogen released from leaf litter within a 27-175 m² radius (30). Furthermore mangrove forests have been shown to export carbon and nutrients as particulate organic matter to the coastal ocean and therefore seagrass beds (31). Furthermore they will also import dissolved nitrogen usually at high tides and high concentrations, although further studies are required to form firm conclusions regarding nitrogen fluxes (31).
5.3 Leaf litter Decomposition

Enhalus sp. degraded much faster (75% decrease in mass) in the initial six days than Rhizophora sp. leaf samples, across all habitat types (MF, TF, and SB) and both environments (sediment and water column). Our observations agree with past degradation experiments with seagrass and mangrove litter (27, 32). Differences in degradation rates are due to the higher structural content of mangrove leaves compared to seagrass leaves. Lignocelluloses have been found in mangrove particulate matter to have greater resilience to microbial degradation than other marine macrophytes such as seagrass leaves (33). Over 30 days our degrading mangrove leaves lost about 50% of their mass, which is comparable to other studies (Fig. 4) (34-37). The breakdown of the physical structure of mangrove leaves indicates a gradual bacterial colonization, which is also verified by the decrease in C:N ratio (Fig. 5).

Mangrove leaf C:N ratio showed little difference across both environments and habitat types, but they did show a decrease over the course of a month (Fig. 5). A decrease in C:N ratios could be attributed to carbon being the preferentially respired whilst nitrogen remains in the in the biomass (27, 38). However the rate of bacteria use of carbon is slow over 30 days, possibly due to tannin content in the mangrove leaves as well as the physical structure of the leaves (27). The C:N ratio of seagrass leaves buried in the sediment plateaued in the mangrove forest, seagrass bed and tidal flat sediment, at approximately median value 15. The C:N ratio in the water column increased, indicating a decrease in nitrogen content. This pattern agrees with past rates of the mass loss of seagrass leaves (28) (Fig. 4&5). Differences in the evolution of the C/N ratios of seagrass and mangrove leaves during decomposition have been previously interpreted by the C:N differences of the starting material: the low C:N material of seagrass leaves have sufficient food quality to decompose rapidly, but microbes must accumulate N in order to degrade the high C:N material of mangrove leaves (39). Likely the increase in C:N ratio observed in seagrass leaves indicates a nitrogen release to the water column that will be available for other organisms.

6 Exchange between Ecosystems: Facilitation potential?

We estimated maximum nitrogen requirements (μ mole m⁻² day⁻¹) for Enhalus sp and Halophila sp (via equation 3) to be approximately 21300 and 580-920 μ moles m⁻² day⁻¹ respectively. Comparing these values with the mangrove derived total nitrogen exported in POM to seagrass beds (2.4 μ mole-1 m⁻² day⁻¹; Fig. 3) indicates that mangrove forests could provide a negligible amount of N requirements for Enhalus sp patches via the export of leaves. For Halophile sp mangrove leaves could provide approximately 0.3-0.4 % of nitrogen requirements of this species. It should be noted that in this particular site, these two ecosystems area have a ratio of 2 (mangrove forest 2093775 m² and seagrass bed 960000 m²). But in a site with a large mangrove forest and small seagrass bed and thus a larger ratio between areas the potentially for mangrove forests to provide seagrass beds with their nitrogen requirements will be greater. Given that seagrass beds are found in oligotrophic water and consequently have
developed effective nutrient retention and recycling, mangrove leaves therefore may provide a small addition of nitrogen to seagrass beds.

7 Conclusion

In-situ transportation experiments showed that POM in tidal waters was mainly comprised of mangrove leaves. Seagrass leaves degraded quicker across all habitat types, both in sediment and water column, than mangrove leaves. Furthermore, incubations indicated that DON released from seagrass leaves was higher than mangrove leaves. Depending on the specific hydrodynamics of a site (i.e. if leaves are transported quickly) seagrass leaves may be an important source of TN for some coastal ecosystems. Their quicker degradation will allow palatable nitrogen to become immediately available. These findings are useful for quantifying nitrogen processes and pathways in the tropical coastal seascape.

To improve insight into nitrogen interactions via particulate organic matter exchange between mangrove forests and seagrasses beds, further information should be obtained regarding the changes of DIN and DON release from degraded leaves over longer timescales (>1 month). Data are also required on the productivity of the mangrove forest and seagrass ecosystems, potentially providing information on nitrogen dynamics, especially nutrient requirements within the ecosystem. Furthermore, the trapping capacity of mangrove roots and seagrass plants would support approximations of how much POM is outwelled from each system.

Importantly, the major findings of this study indicate that mangrove forests and seagrass beds are primarily found to withhold nutrients within their own ecosystems. These mechanisms of trapping particulate organic material (and associated nutrients) may be related to the oligotrophic conditions which seagrass beds and mangroves forests can be found in. Coral reefs, which can be an adjacent ecosystem to mangrove forests and seagrass beds, are thought to be nutrient sensitive. In fact they can easily alter due to nutrient enrichment from a coral, dominated system to macro algae dominated. In this view we suggest that mangrove forests and seagrass beds through retaining nutrients may buffer coral reefs from excess nitrogen.

Acknowledgments

Our thanks go to Kalaya Kantawong, Nam Wani, Boonchai Phrathaan, Bedeen Phrathaan and Mairi Fenton for their logistic help with the fieldwork in Thailand and to the NIOZ analysts for the laboratory measurements.

References


307 5. Alongi DM (1990) Effect of mangrove detrital outwelling on nutrient regeneration and oxygen fluxes in coastal sediments of
308 the central Great barrier reef lagoon. Estuar Coast Shelf Sci 31(5): 581-598.
312 Ecosystems 12:462-472.
315 systems. Aquat Bot 65: 141-158.

319 Ecology and Biogeography 7: 83-94.
327 15. Koch EW & Verduin JJ (2001) Measurements of physical parameters in seagrass habitats. In Frederick TS, Catherine AS,

331 17. Goni MA, Ruttenberg KC, Eglinton TI (1997) Source and contribution of terrigenous organic carbon to surface sediments in
332 the Gulf of Mexico. Nature 389: 275-278.
the importance of detritus C-N-P content. Oecologia 94: 457-471.


36. Silva C, Oliveira SR, Rego RDP, Mozeto AA (2007) Dynamics of phosphorus and nitrogen through litter fall and
373
374
375
376
377

378 Figures Legends
379
380 Figure 1. Study site location for shallow water environments on the island of Koh Yao Yai, Phang Nga bay, southwest coast of
381 Thailand (inset). The black area shows the extent of the mangrove forest (grey lines are channels) and the white area indicates the
382 seagrass bed. Solid circles indicate the location of the POM flux nets and mid point of transects. The dotted lines refer to the widths
383 of the mangrove forest (900 m) and the seagrass beds (landward 560 m and seaward 680 m) used in Equation 1.
384
385 Figure 2. Incubations of fresh mangrove leaves (circles) and seagrass leaves
386 (squares). Indicated here are dissolved inorganic nitrogen (DIN) release (clear markers) and dissolved organic nitrogen (DON) release
387 (filled markers) over 24 hours. Three-way ANOVA indicated seagrass DON concentrations varied over time (p = 0.05). The seagrass
388 leaf DON response was significantly different from that for mangrove leaves (Kruskal-Wallis test: p = 0.04). Values are
389 means of 3 replicates.
390
391 Figure 3. Transportation of total organic matter and nitrogen contained in Rhizophora
392 sp and Enhalus sp leaves, between mangrove forests, seagrass beds, and the coastal ocean. X-axis labels represent the movement of
393 leaf material between ecosystems. 394 ML=>SB shows mangrove leaf (ML: grey) transportation from the mangrove forest (MF) to
395 the seagrass bed (SB); SL=>MF, 396 seagrass leaf (SL: white) from the seagrass bed (SB) to the mangrove forest (MF). The
397 last two columns indicate leaf movement to the ocean (O). The top panel indicates the total dry mass transported from each
398 ecosystem per day (POMtransport; mg m-2 day-1), which was calculated using equation (1). Letters denote significant differences
399 between total leaf mass transported (mg m-2 day-1), 400 with different letters indicating a difference (K-W test; LSD test). The lower panel
401 shows total nitrogen transportation in leaf content 402 of Rhizophora and Enhalus. Letters denote significant differences between total
403 nitrogen transported (mole m-2 day-1) where different letters indicate a difference (K-W test; LSD test). Values are means (± SE, n=5).
404
405 Figure 4. Remaining dry mass (%) of Rhizophora (A & C) and Enhalus (B & D) leaves
406 during 2, 4, 6, 20 and 30-days degradation experiments conducted in different ecosystems: mangrove forest (MF: black diamonds),
mud-flat (MD: dark grey squares) and seagrass bed (SG: light grey triangles). Top graphs represent incubations in the water column (A and B); bottom graphs, within the sediment (C and D). The change in mangrove (p = 0.01) and seagrass leaf (p = 0.1) mass over time was highly significant (p = 0.01; Tab. 1), an interaction was also seen between the environment and time for mangrove (p = 0.01) and seagrass (p = 0.1) leaves (Tab. 1). Values are means (±SE, n=3).

Figure 5. C:N ratios of Rhizophora (A & C) and Enhalus (B & D) leaves during 30 days of degradation in different ecosystems: mangrove forest (MF: black diamonds), tidal-flat (TF: dark grey squares) and seagrass bed (SB: light grey triangles). Top graphs represent incubations in the water column (A and B); bottom graphs in the sediment (C and D). The change in mangrove (p = 0.01) and seagrass leaf (p = 0.1) mass over time was highly significant (p = 0.01; Tab. 1), an interaction was also seen between the environment and time for mangrove (p = 0.01) and seagrass (p = 0.1) leaves (Tab. 1). Values are means (±SE, n = 3). A change in C:N ratios of seagrass leaves was found to be highly significant (p = 0.01) between the environments (Tab. 1). Different C:N ratios in the water column also changed over time shown by the time interaction (Tab. 1). Mangrove leaves showed a highly significant relationship (p = 0.01) between C:N ratios for time and these were affected by the site (Tab. 1; LSD test).

and seagrass leaf (p = 0.1) mass over time was highly significant (p = 0.01; Tab. 1), an interaction was also seen between the environment and time for mangrove (p = 0.01) and seagrass (p = 0.1) leaves (Tab. 1). Values are means (±SE, n = 3). A change in C:N ratios of seagrass leaves was found to be highly significant (p = 0.01) between the environments (Tab. 1). Different C:N ratios in the water column also changed over time shown by the time interaction (Tab. 1). Mangrove leaves showed a highly significant relationship (p = 0.01) between C:N ratios for time and these were affected by the site (Tab. 1; LSD test).
Table 1. Statistical summary of the 3-way ANOVA analysis of mangrove leaf (ML) and seagrass leaf (SL) degradation experiments, for leaf mass and C:N ratios variables. The data reflect statistically significant interactions between environment (water column versus buried in the sediment), site (seagrass bed versus mangrove forest), and time (0, 2, 4, 6, 30, 30 days) variables.

<table>
<thead>
<tr>
<th>Leaf type</th>
<th>SL</th>
<th>Experiment mass</th>
<th>D'Agostino-Pearson p&gt;0.05</th>
<th>Environment</th>
<th>Site</th>
<th>Time</th>
<th>Environment*Site</th>
<th>Environment*Time</th>
<th>Site*Time</th>
<th>Environment<em>Site</em>Time</th>
<th>C:N ratios p&gt;0.05</th>
<th>ML mass p&gt;0.05</th>
<th>C:N ratios p&gt;0.05</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>**</td>
<td>--</td>
</tr>
</tbody>
</table>

* P-value < 0.10
** P-value < 0.01
--- Not significant

Figure 1

Click here to download high resolution image
FIGURE 1. Study site for shallow water environments on the island of Koh Yao Yai, Phang Nga bay, southwest coast of Thailand (inset). The dark gray area shows the extent of the mangrove forest, and the light gray area indicates the seagrass bed. Black filled circles indicate the location of the POM flux nets.
FIGURE 2. Panel (A) Nitrogen release every 6 h (24-h incubation experiment) from fresh mangrove leaves (clear symbols) and seagrass leaves (black symbols) for the following variables: dissolved inorganic nitrogen (DIN, circle) and dissolved organic nitrogen (DON, squares). Values are means ± one standard error. DON release rates in the seagrass leaf incubation varied significantly over time (two-way ANOVA, \( P = 0.05 \)). The seagrass leaf DON response was significantly higher than that for mangrove leaves (Kruskal–Wallis test: \( P = 0.04 \)). Panels (B-E) show the remaining dry mass (%) of Rhizophora apiculata (A & C) and Zostera cerata (B & D) leaves during 2, 4, 6, 20 and 30 d in the field-based degradation experiments conducted in different ecosystems: mangrove forest (MF: black diamonds), tidal-flat (TF: dark grey squares) and seagrass bed (SG: light grey triangles). Panels (B) and (C) represent degradation in the water column, while D and E figure are indicative of degradation within the sediment. The change in mangrove leaf mass over time was significant (\( P = 0.01 \); Table S1). A significant interaction was also seen between the environment and time for mangrove leaves at 20 d (Table S2).
FIGURE 3. Transportation of total organic matter and nitrogen, contained in Rhizophora apiculata mangrove leaves (ML) and Enhalus acoroides seagrass leaves (SL), between mangrove forests (MF), seagrass beds (SB), and the ocean (O). Nets refer to the location of nets between the ecosystems (Fig. 1). Means of POM transported from each ecosystem per day (POM$_{\text{transport}}$ mg/m$^2$/d) are shown in panel A. Means of total nitrogen transportation in leaf content of Rhizophora apiculata and Enhalus acoroides are shown in panel B. Stars denote significant differences between total leaf mass transported (mg/m$^2$/d), with 1, 2 and 3 stars indicating a difference (K–U test; LSD test).