Biotropica
May 2015, Volume 47 Issue 3 Pages 286-291
http://dx.doi.org/10.1111/btp.12220
http://archimer.ifremer.fr/doc/00266/37731/

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.
[2] Royal Netherlands Inst Sea Res NIOZ, Spatial Ecol, Yerseke, Netherlands.
[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

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 (1-2). In nutrient limited conditions (3-4), 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 (5-7). Given their large standing biomass and high productivity, mangrove and seagrass POM could be an important nutrient source to adjacent ecosystems (8-9). 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 (10-12). 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

63 Province in Southern Thailand (7°54'28. 26"N, 98°35'12. 47"E) (Fig. 1). Incubation experiments were completed in the marine
64 research station, also located on the island. Seagrass and mangrove leaves, sediment and water for the degradation and

65 incubation experiments were taken from Chong Lat Noi bay during July 2011. Mean temperature during sampling was 29°C and
66 salinity was 32 PSU.
67 We compared degradation rates in three habitat types: (1) the edge of the mangrove forest (MF); (2) the tidal flat (TF) at
68 approximately 300 m from the mangroves; and (3) a seagrass bed (SB), located approximately 600 m from the mangrove forests
69 (Fig 1). The mangrove forest was composed of fringing Rhizophora sp, Ceriops sp and Xylocarpus sp. The seagrass beds
70 comprised Enhalus sp, Haladule sp, Halophila sp and Thalassia sp, with Enhalus sp being the climax species with highest biomass.
71 For the experiments we used leaves from Rhizophora sp and Enhalus sp. The seagrass, tidal flat and fringing mangrove were
72 exposed at low tide for between 1-4 hours.
73
74 3. Methods
75 3.1 Incubations to measure release rates of dissolved nitrogen from seagrass and mangrove leaves
76 Sediment and mangrove/seagrass leaf samples were collected at low tide. Care was taken to pick leaf samples similar length
77 (mangrove leaves: 0.1 m, seagrass leaves: 0.45 m) and physical state (whole green leaves with no imperfections in the leaf
78 structure). Water samples were collected in the bay at high tide and transported to the marine laboratory in an icebox. Salinity and
79 temperature was recorded during sampling. Water samples were filtered to remove large particles (>2 mm). Three dark -incubations
80 with mangrove leaves were completed in parallel over a 24-hour period. The first incubation contained only seawater collected at

81 the mangrove site (control treatment); the second, mangrove sediment/soil plus seawater (soil treatment); and the third, fres h
82 mangrove leaves plus sediment plus seawater from mangroves (leaves treatment). Three replicates of all treatments were
83 performed.
84 Samples were incubated in the dark in 19.2-L chambers (radius: 142 mm, height: 303 mm). For the sediment and leaf
85 treatments, a 0.1 m thick sediment layer was placed on the bottom; and 12.9 L seawater was added. The temperature was kept
86 constant by placing the chambers in a water bath in which the temperature was maintained manually. Temperature (27-30 °C) and
87 salinity (28-33 ppt) were held within narrow ranges that corresponded with the sampling conditions. A magnetic stirrer was used to
88 maintain thorough mixing during the 24-hour incubations. Water samples (25 ml), were taken every 6 hours (at times 0, 6, 12, 18,
89 24 hours); temperature and salinity were recorded at the times of sampling. The water in the incubation chamber was replaced by
90 seawater from the site that had been kept at the sample temperature and salinity. Samples were immediately frozen for analysi s at
91 a later date. After transporting to NIOZ, the samples were analyzed for dissolved organic and inorganic nitrogen (DON & DIN). For
92 determining seagrass release of DON and DIN, we followed the same protocol described

above for mangroves. Nitrogen release
93 from mangroves or seagrass leaves was calculated as the subtraction of N contents (DON & DIN) of the soil treatment (seawater +
94 sediment incubation) from those of the leaves treatment (leaves + sediment + seawater incubation).
95 3.2 Transportation rate of seagrass and mangrove leaves -Field experiment

96 We estimated the residence time of mangrove and seagrass leaves deposited on the sediment within the mangrove forest (MF),
97 tidal flat (TF) and seagrass bed (SB). In each of these habitat types, three replicates of marked fresh mang rove and seagrass
98 leaves were placed at low tide at edge (< 10 m from the ocean) and interior (100 m from the ocean) locations. The sites were
99 monitored every tidal cycle to determine the time when leaves were transported from their initial locations.
100 We measured the import/export rates of leaves from each ecosystem with 50 (length) x 1 (height) m nets, mesh size 0.05 m,
101 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
102 the seaward edge of the seagrass bed (3 in Fig. 1). We collected particulate matter during low tide for five tidal cycles, separating
103 the mangrove and seagrass leaves. Dry mass (g) was determined after drying for at least 48 hours at 60 °C.
104 Particulate organic material transportation (POMtransport; mg m-2 day -1) per unit area of each ecosystem was estimated as the
105 following (Fig. 2):
106 POMtransport= 2 x POMnet x (Leco/Lnet) /Aeco (1)
107 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)
108 and Leco the total length of the fringe edge of the ecosystem which is donating the POM (~900 m for mangrove, 560 m for
109 shoreward seagrass bed, 680 m for seaward seagrass bed); Aeco (m2) is the surface area of the entire donating ecosystem
110 (mangrove forest 2093775 m2 and seagrass bed 960000 m2); and the constant 2 converts the transportation rate from per tide to
111 per day.

112 We also calculated the total nitrogen exported per unit area (TNtransport; . mole m-2 day -1) as:
113 TNtransport= POMtransport * TNleaf (2)
114 where TNleaf (%) is the total leaf N determined from the fresh mangrove/seagrass leaves used in the degradatio n experiments (see
115 section 3.3). Collectively, these calculations provide a rough estimate of POM exchanged between ecosystems and the ocean, as
116 we assume all trapped leaves contribute to the total POM exported/imported.
117 3.3 In situ seagrass and mangrove leaf degradation experiment
118 Fresh seagrass (Enhalus sp) and mangrove (Rhizophora sp) leaves of similar length (mangrove leaves: 0.1 m, seagrass leaves:
119 0.45 m) and physical state (whole green leaves with no imperfections in the leaf structure) were used in the degradation
120 experiments. Leaves were collected at low tide and epiphytes were removed. Subsequently, leaves were separated into 180 piles;
121 90 piles of seagrass and 90 piles of mangrove leaves which were weighted (approxinatly10 g wet weight each). Each pile was then
122 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
125 three parallel transects (mid point symbolized by solid circle: Fig. 1). At each replicate, sets of 5 poles were driven into the
126 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
127 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
129 degradation rates and changes in C: N ratios. Following collection, the samples were dried in an oven for 48 hours at 60°C. They
130 were then weighed and placed in labeled sealed plastic bags for transp ortation to NIOZ, where they were further analyzed for C: N
131 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
134 needs we completed an approximate calculation of these requirements. The nitrogen requirements of seagrass plants Enhalus sp
135 and Halophila sp (NR; . mole m-2 day -1) was calculated as follows:
136 NR=TNleaf*B/LT (3)
137 where TNleaf (. mole gleaf
-1) for Enhalus sp is the total leaf N determined from the fresh seagrass leaves used in the degradation
138 experiment (1143 . mole gleaf
-1). For Halophila sp we used total N leaf content data of 34-54 . mole gleaf
-1 (23). Standing biomass
139 of the seagrass per m2 is represented as B, which was calculated by determining the above ground weight of Enhalus sp and
140 Halophila sp per m 2. 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 per cent
143 of C, N & CN ratios in dried leaves were determined using a using a Flash EA 1112 Elemental Analyzer (Thermo Finnigan).

144 Dissolved inorganic (NH_4^+, NO_3^- & NO_2^-) nitrogen (DIN) accumulated in the incubation water were filtered onto a GFF filter
145 (Whatman) and determined calorimetrically using a SK12 nutrient analyser, Skalar & Seal (24). Total nitrogen (TN) was determined
146 from a GFF filter (Whatman) after an alkaline persulphate destruction using the same instrument for dissolved nutrient
147 concentrations (25). Dissolved organic nitrogen was calculated from the difference between dissolved organic nitrogen (DIN) and
148 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
151 seagrass leaf export to other ecosystems and to the ocean, we used a Kruskal-wallis

test (K-W test) because the data were not
152 normally distributed. Three-way analysis of variance (ANOVA) with replication was used to test for differences in the following: i)
153 decomposition of detritus related to habitat type (MF, TF, SB) versus time period (2, 4, 6, 20 and 30 days) for each environment
154 (sediment and water column); and ii) C:N ratios of mangrove and seagrass leaves between habitat type (MF, TF, SB) versus time
155 period (2, 4, 6, 20 and 30 days) for each environment (sediment and water column). Three-way ANOVA was also used to compare
156 nitrogen release from both mangrove/seagrass leaves (DIN & DON) and time in the incubations. A Kruskal-wallis test was used to
157 compare changes in DIN & DON release from mangrove and seagrass leaves at 24 hours in the incubation; to prevent serial
158 correlation we used the final concentrations of DIN & DON. Least squares difference (LSD) post-hoc testing was performed

159 following ANOVA and Kruskal-wallis test. Probabilities (p) were expressed at $p < 0.01$ & 0.1, and are referred to in the text as
160 significant. All statistical testing was completed in an R programming platform.
161 4. Results
162 4.1 Incubation experiment
163 There was no apparent release of DIN from either Rhizophora sp. and Enhalus sp. leaves in the incubation experiments, the
164 amount did not significantly differ from zero (Fig. 2). In contrast, DON-amounts increased during 24-h of seagrass leaf
165 decomposition, with the maximum of the mean values of 93 . mole DON g-1. DON-release from decomposing mangrove leaves
166 was negligible (Fig. 2). A significant (K-W test: $p = 0.04$) difference was seen between DON release from seagrass versus
167 mangrove leaves at 24 hours (Fig. 2). In addition, DON amounts for seagrass increased significantly (Three-way ANOVA: $p = 0.05$),
168 then stabilized after 6 hours until the end of the experiment. Negative values originate from the calculation of the nitrogen release
169 from mangroves or seagrass leaves (subtraction of the N values of the “seawater + sediment” incubation from the “leaves +
170 sediment + seawater” incubation) (Tab.S1).
171 4.2 POM and TN exchange calculations
172 All tagged leaves that were deposited at positions within the mangrove forest, tidal flat and seagrass bed were transpor ted away
173 from their original location within one tidal cycle (data not shown). However , it is not known if they were transported out of the
174 system, or simply mobilized by the tide.

175 Our flux measurements using nets across the bay indicated that the export of mangrove leaves moving into seagrass beds
176 was significantly higher than the biomass of seagrass leaves moving inland toward the mangrove (K-W test, $p = 0.01$; net 3; Fig. 3).
177 The daily area-weighted mass of mangrove leaves transported toward the seagrass beds (3.7 mg m-2 day-1) was approximately six178
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
179 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
180 mangroves and seagrass (Fig. 3; nets 3 and 4). The total nitrogen in seagrass leaves conveyed to mangrove forests was
181 approximately half of that transferred to seagrass beds from mangroves (K-W test, p =

0.001; Fig. 3). There was no detectable
182 difference in TN exported to the ocean by mangrove and seagrass leaves.
183 4.3 Degradation experiments
184 Enhalus leaves followed an exponential decay pattern where loss of mass showed a 50-75% decrease within 6 days in the water
185 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
186 sediment, only 10-50 % of the initial mass of seagrass leaves remained (Fig.4B&D). Thereafter, little change in seagrass leaves
187 mass occurred until the end of the 30-days experiment (Fig. 4B&D). The degradation pattern of Enhalus leaves was in direct
188 contrast to Rhizophora leaves, which showed only a 25% loss in mass after 6 days, both in the water column and sediment
189 (Fig.4A&C). Rhizophora leaf mass were still around 50% of their initial weight after 30 days (Fig.4A&C). A significant relationship for
190 mangrove leaf mass loss was seen between the water column and the sediment in the different environments (water column &

191 sediment) ($p = 0.01$; Tab. 2). Changes in seagrass leaf mass over time were significant at the level $p = 0.1$ (Tab.1). Both mangrove
192 and seagrass leaves also indicated an interaction between time and the environment (water column vs. sediment) at $p = 0.01$ and p
193 $= 0.1$ respectively (Tab.1). No other mass changes were significant (Tab.1).
194 The C:N-ratio of Enhalus leaves in the water column gradually increased from a mean of 18 (0 days) to 26 (30 days)
195 (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
196 (Fig.5D). A highly significant ($p = 0.01$) difference was seen for C:N ratios of seagrass leaves between the water column and the
197 sediment and these differences in the water column changed over time (Tab.1). The C:N-ratio of Rhizophora leaves decreased
198 from mean values of 37 (6 days) to 32 (30 days) during degradation (Fig. 5A&C). Mangrove leaves showed a highly significant
199 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).
200
201 5. Discussion
202 Mangrove leaves were the dominant POM source transported between adjacent seagrass beds and mangrove forests, but had
203 similar POM transport rates to the open ocean as seagrass beds (Fig. 3). However, our results show faster degradation rates of
204 seagrass leaves than mangrove leaves (Fig. 4), with higher DON releases from the seagrass leaves (Fig.2). Thus on a short time
205 scale, seagrass leaves may be an important nitrogen source for the tropical coastal seascape due to their fast turnover rates and
206 the associated nitrogen release, but such process will strongly depend on local hydrodynamics. In contrast mangrove leaves are

207 the dominant particulate organic matter in the coastal area and they cannot be discarded as another potential source for dissolved
208 nitrogen. Importantly our study provides results, which could be used to quantify N processe s and pathways in the tropical coastal
209 seascape.
210 5.1 Leaf litter nitrogen release from seagrass & mangrove leaves
211 It has been thought that seagrass and mangrove detritus enhance nitrification and denitrification processes in the water

212 column (26-27). Detritus is a DIN/DON source through leaching and bacterial degradation. Fresh seagrass leaves had a much
213 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
214 incubations indicate that initially (first 24 hours) seagrass leaves are a more important source of DON in the coastal zone. The C:N
215 ratios in the degradation experiments indicated that overall seagrass leaves release d nitrogen, whereas mangrove leaves retained
216 it, in agreement with previous studies (26-27). Our incubations also verify this result for a very short initial time period.
217 5.2 Leaf litter transportation
218 Although rough estimates, the results of our POM transportation experiment across ecosystems showed that significant amounts of
219 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
220 transport a substantial amount of POM to seagrass beds compared to the fluxes from mangrove forest to the ocean and the fluxes
221 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
222 transported from the seagrass bed to the ocean (Fig 3). We therefore can estimate that 92 % of the mangrove leaves remained in

223 the seagrass bed, approximately 3.5 mg m-2 day-1 (Fig. 2). Other studies have shown that seagrass plants can trap mangrove
224 leaves from mangrove forests located up to 3 km away (Hemminga et al 1994). Exchanges of mangrove leaves (Rhizphora sp. &
225 Ceriops sp.) to seagrass (Thalassodendron sp.) and then back to mangroves have been reported previously in Gazi Bay, Kenya
226 (28).
227 Seagrass leaves were exported both to the mangrove forest and the ocean, with 80% transported to the forest (Fig. 3). The
228 movement of mangrove leaves to seagrass beds and vice versa indicates that the hydrodynamics between mangrove forests and
229 seagrass beds facilitates a back and forth exchange of POM. Thus, seagrass leaves transported to the mangrove forest could
230 return to the beds, but we have no data to support this. In our transportation experiment, leaves trapped in the nets were fresh;
231 degraded leaves were not present. Once leaves are degraded, they may be trapped in either the mangrove roots or seagrass
232 plants, ending their transport for normal hydrodynamic conditions. Such hypothesis is supported by other studies showing seagrass
233 leaves trapped within seagrass beds, where they represent a viable source of nutrients (29).
234 Likely, retention of mangrove and seagrass leaves within tropical coastal systems can be quite substantial, and constitute a
235 potentially important nutrient source, depending on the degradation timescales and nitrogen release. In the case of seagrass beds,
236 seagrass canopies have been found to retain half of the nitrogen released from leaf litter within a 27-175 m 2 radius (30).
237 Furthermore mangrove forests have been shown to export carbon and nutrients as particulate organic matter to the coastal ocean

238 and therefore seagrass beds (31). Furthermore they will also import dissolved nitrogen usually at high tides and high
239 concentrations, although further studies are required to form firm conclusions regarding nitrogen fluxes (31).

240 5.3 Leaf litter Decomposition
241 Enhalus sp. degraded much faster (75% decrease in mass) in the initial six days than Rhizophora sp. leaf samples, across all
242 habitat types (MF, TF, and SB) and both environments (sediment and water column). Our observations agree with past degradation
243 experiments with seagrass and mangrove litter (27, 32). Differences in degradation rates are due to the higher structural content of
244 mangrove leaves compared to seagrass leaves. Lignocelluloses have been found in mangrove particulate matter to have greater
245 resilience to microbial degradation than other marine macrophytes such as seagrass leaves (33). Over 30 days our degrading
246 mangrove leaves lost about 50% of their mass, which is comparable to other studies (Fig. 4) (34-37). The breakdown of the
247 physical structure of mangrove leaves indicates a gradual bacterial colonization, which is also verified by the decrease in C:N ratio
248 (Fig. 5).
249 Mangrove leaf C:N ratio showed little difference across both environments and habitat types, but they did show a decrease
250 over the course of a month (Fig. 5). A decrease in C:N ratios could be attributed to carbon being the preferentially respired whilst
251 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
252 tannin content in the mangrove leaves as well as the physical structure of the leaves (27). The C:N ratio of seagrass leaves buried
253 in the sediment plateaued in the mangrove forest, seagrass bed and tidal flat sediment, at approximately median value 15. The C:N

254 ratio in the water column increased, indicating a decrease in nitrogen content. This pattern agrees with past rates of the mass loss
255 of the seagrass leaves (28) (Fig. 4&5). Differences in the evolution of the C/N ratios of seagrass and mangrove le aves during
256 decomposition have been previously interpreted by the C:N differences of the starting material: the low C:N material of seagr ass
257 leaves have sufficient food quality to decompose rapidly, but microbes must accumulate N in order to degrade the hi gh C:N material
258 of mangrove leaves (39). Likely the increase in C:N ratio observed in seagrass leaves indicates a nitrogen release to the water
259 column that will be available for other organisms.
260
261 6 Exchange between Ecosystems: Facilitation potential?
262 We estimated maximum nitrogen requirements (. mole m -2 day-1) for Enhalus sp and Halophila sp (via equation 3) to be
263 approximately 21300 and 580-920 . moles m-2 day-1 respectively. Comparing these values with the mangrove derived total nitrogen
264 exported in POM to seagrass beds (2.4 . mole-1 m -2 day-1; Fig. 3) indicates that mangrove forests could provide a negligible amount
265 (0.01 %) of the N requirements for Enhalus sp patches via the export of leaves. For Halophile sp mangrove leaves could provide
266 approximately 0.3-0.4 % of nitrogen requirements of this species. It should be noted that in this particular site, these two
267 ecosystems area have a ratio of 2 (mangrove forest 2093775 m2 and seagrass bed 960000 m2). But in a site with a large mangrove
268 forest and small seagrass bed and thus a larger ratio between areas the potentially for mangrove forests to provide seagrass beds
269 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 man grove 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 mangroves forests and seagrass beds are primarily found to withhold nutrients within their own ecosystems. These mechanisms of trapping particulate organic material (and associated nutrients) m ay 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.

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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 indica tes 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 (squares). Indicated here are dissolved inorganic
386 nitrogen (DIN) release (clear markers) and dissolved organic nitrogen (DON) release (filled markers) over 24 hours. Three -way
387 ANOVA indicated seagrass DON concentrations varied over time ($p = 0.05$). The seagrass leaf DON response was significantly
388 different from that for mangrove leaves (Kruskal-wallis test: $p= 0.04$). Values are means of 3 replicates.
389
390 Figure 3. Transportation of total organic matter and nitrogen contained in Rhizphora sp and Enhalus sp leaves, between mangrove
391 forests, seagrass beds, and the coastal ocean. X-axis labels represent the movement of leaf material between ecosystems.
392 ML=>SB shows mangrove leaf (ML: grey) transportation from the mangrove forest (MF) to the seagrass bed (SB); SL=>MF,
393 seagrass leaf (SL: white) from the seagrass bed (SB) to the mangrove forest (MF). The last two columns indicate leaf movement to

394 the ocean (O). The top panel indicates the total dry mass transported from each ecosystem p er day (POMtransport; mg m-2 day-1),
395 which was calculated using equation (1). Letters denote significant differences between total leaf mass transported (mg m -2 day-1),
396 with different letters indicating a difference (K-W test; LSD test). The lower panel shows total nitrogen transportation in leaf content
397 of Rhizphora and Enhalus. Letters denote significant differences between total nitrogen transported (. mole m -2 day-1) where
398 different letters indicate a difference (K-W test; LSD test). Values are means (± SE, n=5).
399
400 Figure 4. Remaining dry mass (%) of Rhizphora (A & C) and Enhalus (B & D) leaves during 2, 4, 6, 20 and 30-days degradation
401 experiments conducted in different ecosystems: mangrove forest (MF: black diamonds),

mud -flat (MD: dark grey squares) and
402 seagrass bed (SG: light grey triangles). Top graphs represent incubations in the water column (A and B); bottom graphs, withi n the
403 sediment (C and D). The change in mangrove (p = 0.01) and seagrass leaf (p = 0.1) mass over time was highly significant (p =
404 0.01; Tab. 1), an interaction was also seen between the environment and time for mangrove (p = 0.01) and seagrass (p = 0.1)
405 leaves (Tab.1). Values are means (±SE, n=3).
406
407 Figure 5. C:N ratios of Rhizphora (A & C) and Enhalus (B & D) leaves during 30 days of degradation in different ecosystems:
408 mangrove forest (MF: black diamonds), tidal-flat (TF: dark grey squares) and seagrass bed (SB: light grey triangles). Top graphs
409 represent incubations in the water column (A and B); bottom graphs in the sediment (C and D). The change in mangrove (p = 0.01)

410 and seagrass leaf (p = 0.1) mass over time was highly significant (p = 0.01; Tab. 1), an interaction was also seen between the
411 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
412 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
413 the water column also changed over time shown by the time interaction (Tab.1). Mangrove leaves showed a highly significant
414 relationship (p = 0.01) between C:N ratios for time and these were affected by the site (Tab.1; LSD test).
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and seagrass leaf (p = 0.1) mass over time was highly significant (p = 0.01; Tab. 1), an interaction was also seen between the
411 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
412 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
413 the water column also changed over time shown by the time interaction (Tab.1). Mangrove leaves showed a highly significant
414 relationship (p = 0.01) between C:N ratios for time and these were affected by the site (Tab.1; LSD test).
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425 Tables

426 Table 1. Statistical summary of the 3-way ANOVA analysis of mangrove leaf (ML) and seagrass leaf (SL) degradation experiments,
427 for leaf mass and C:N ratios variables. The data reflect statistically significant interactions between environment (water co lumn
428 versus buried in the sediment), site (seagrass bed versus mangrove forest), and time (0, 2, 4, 6, 30, 30 days) variables.

Leaf type
SL
Experiment
mass
D'Agostino-Pearson
p>0.05
Environment
-
Site
-
Time
*
Environment*Site
-
Environment*Time
*
Site*Time
-
Environment*Site*Time
-
C:N ratios p>0.05 ** ---** --
ML mass p>0.05 --** -** --
C:N ratios p>0.05 --** --** -

429 * P-value < 0.10
430 **P-value<0.01
431 -Not significant

Figure 1

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Figure 2

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Figure 3

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Figure 4

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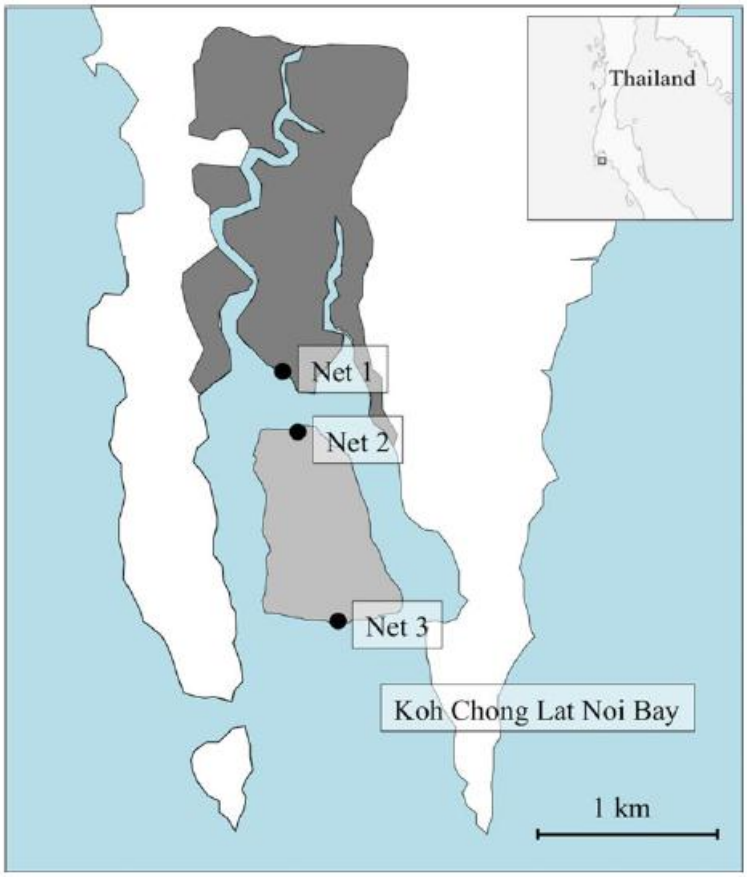

FIGURE 1. Study site for shallow water environments on the island of Koh Yao Yai, Phang Nga bay, southwest coast of Thailand (inset). The dark gray area shows the extent of the mangrove forest; and the light gray area indicates the seagrass bed. Black filled circles indicate the location of the POM flux nets.

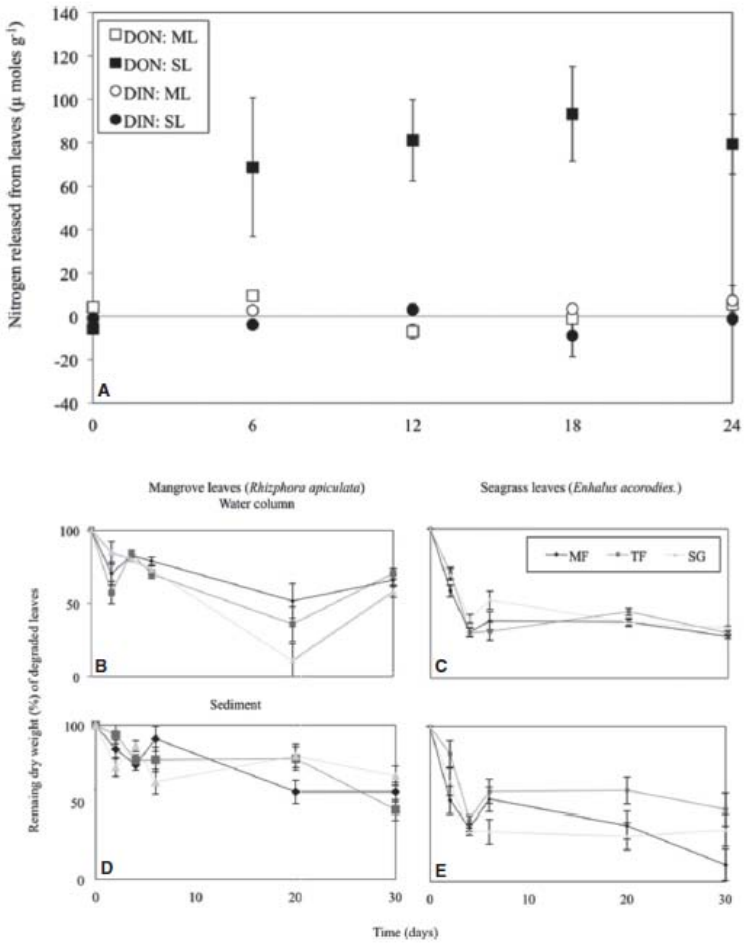

FIGURE 2. Panel (A) Nitrogen release every 6 h (24-h incubation experiments) from fresh mangrove leaves (clear symbols) and seagrass leaves (black symbols) for the following variables: dissolved inorganic nitrogen (DIN, circles) and dissolved organic nitrogen (DON, squares). Values are means ± one standard error. DON release rates in the seagrass leaf incubation varied significantly over time (rmANOVA; $P = 0.05$). 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 *Enhalus acorodies* (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 gray squares) and seagrass bed (SG: light gray 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).

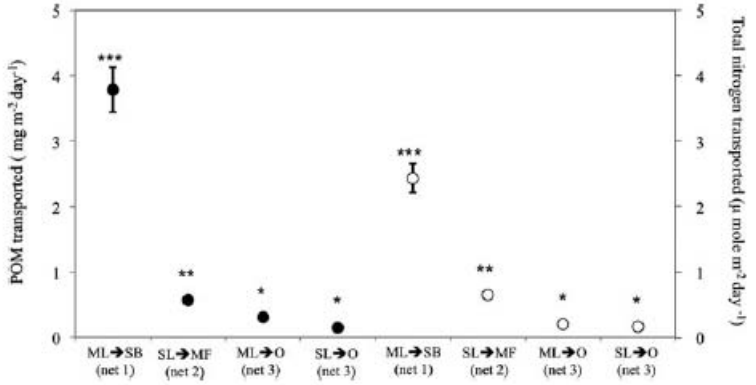

FIGURE 3. Transportation of total organic matter and nitrogen, contained in *Rhizophora apiculata* mangrove leaves (ML) and *Enhalus acorodies* seagrass leaves (SL), between mangrove forests (MF), seagrass beds (SB), and the ocean (O). Nets refer to the location of nets between the ecosystems (Fig. 1). Means of POM transported from each ecosystem per day ($POM_{transport}$; $mg/m^2/d$) are shown in panel A. Means of total nitrogen transportation in leaf content of *Rhizophora apiculata* and *Enhalus acorodies* 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–W* test; LSD test).