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INSIGHTS

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

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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.

Key words: buffering; mangrove forests; nitrogen; outwelling; particulate organic material; seagrass beds.

MANGROVES AND SEAGRASS BEDS OCCUPY UNIQUE LOCATIONS ALONG COASTLINES, WHERE THEY EXCHANGE PARTICULATE ORGANIC MATTER (POM) and dissolved nutrients with adjacent ecosystems on daily cycles (Alongi 1990, Lee 1995, Hemminga *et al.* 1999, Granek *et al.* 2009). Much internal nutrient recycling also occurs in mangrove forests, with excess nutrients outwelled in dissolved forms or retained in the mangrove as particulate material (Boto & Wellington 1988, Ewel *et al.* 1998, Adame & Lovelock 2011). Recycling is also a mechanism for seagrass beds to remain viable in nutrient-poor conditions (Hemminga *et al.* 1999, Koch & Verduin 2001, Infantes *et al.* 2009). Seagrass beds may receive nutrients outwelled from mangroves or terrestrial sources (Valiela & Cole 2002, Gillis *et al.* 2014). However, the extent they retain nutrients via internal recycling is still not thoroughly understood.

In this study, we attempt to determine: (1) the rate of export/import of POM between an adjacent mangrove forest and seagrass bed; and (2) the rate of breakdown of POM into usable forms of nitrogen in each ecosystem. While most studies typically focus on one of these aspects (Hemminga *et al.* 1991, 1995, Kristensen *et al.* 1998, Holmer & Olsen 2002, Bouillon *et al.* 2007), we compare the ability of each ecosystem to retain nutrients through internal recycling (degradation of its own leaves) versus the import of nutrients from adjacent sources (*e.g.*, degradation of leaves transported from the adjacent ecosystem). This approach has limitations, as we do not determine degradation rates for all types of imported organic matter in all substrate conditions. Nevertheless, our experiment produces a valuable first-order nutrient budget with respect to internal versus external sources.

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The study site was located in Koh Chong Lat Noi bay, on the island of Koh Yao Yai in Southern Thailand (7°54′28″ N, 98°35′12″ E) (Fig. 1). The mangrove forest area was 2,093,775 m^2 and the seagrass bed area was 960,000 m^2. The forest receives no discharge from a major river, and therefore receives the bulk of its fresh water from rainfall or land runoff (Fig. 1). The direction of the current is from south to north; and during low tide the whole seagrass bed is exposed. The mangrove forest was composed of fringing *Rhizophora apiculata, Ceriops tagel* and *Xylocarpus granatum/moluccensis.* The seagrass beds was composed of *Enhalus acorodies*, *Halodule pinifolia*, *Halophila beccarii* and *Cymodocea serrulata,* with *Enhalus acorodies* being the climax species with highest biomass.

For the experiments, we used leaves of *Rhizophora apiculata* and *Enhalus acorodies*, hereafter referred to as mangrove and seagrass leaves, respectively. For incubation and degradation experiments, we only used fresh seagrass and mangrove leaves of similar length (mangrove leaves: 0.1 m; seagrass leaves: 0.45 m), weight (approximately 10 g DW of both leaves) and physical state (whole green leaves with no apparent imperfections). All leaves were collected at low tide.

Water samples for the incubations were collected at high tide; and salinity and temperature were measured (28–33 PSU and 27–30°C). Samples were incubated in dark 19.2-l chambers (radius: 0.1 m, height: 0.3 m) over a 24-h period. The first incubation contained only sea water (control treatment). In the second, a 0.1-m thick sediment layer was covered with sea water (sediment treatment). The third incubation (leaf treatment) was similar to the second treatment (sediment) except that whole seagrass or mangrove leaves were added on top of the sediment layer. Three replicate experiments per treatment were performed. Water samples (25 ml) were taken at 0, 6, 12, 18, 24 h after incubation began. Samples were immediately frozen for later analysis.

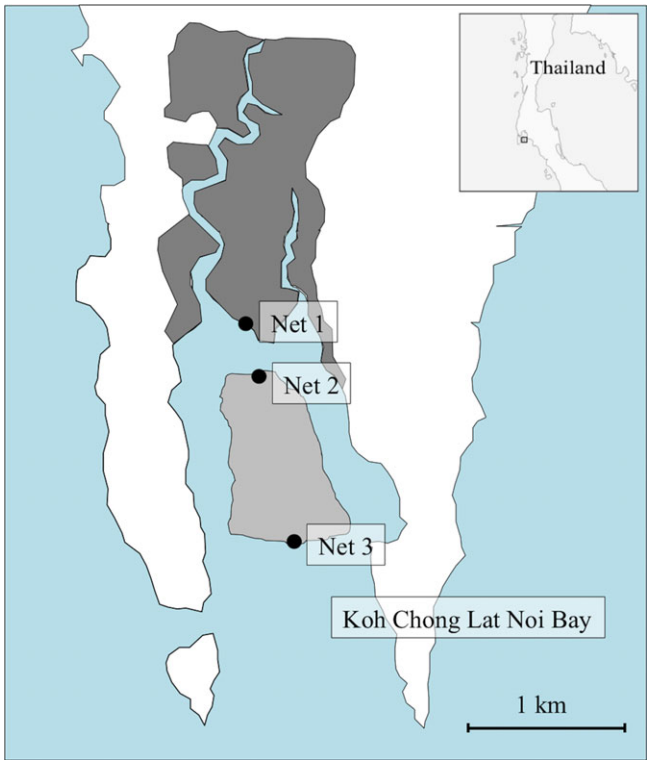

FIGURE 1. Study site for shallow water environments on the island of Koh Yao Yai, Phang Nga bay, southwest coast of Thailand (inset). The dark gray area shows the extent of the mangrove forest; and the light gray area indicates the seagrass bed. Black filled circles indicate the location of the POM flux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

Dissolved inorganic and total nitrogen (DIN and TN, respectively) was determined using a Skaler and Seal nutrient analyser, SK12 model (Seal Analytical) (Grasshoff *et al.* 1999) at the Royal Netherlands Institute for Sea Research (NIOZ). Dissolved Organic Nitrogen (DON) was computed as TN minus DIN. Nitrogen release rate per 6 h (DON and DIN) was obtained by subtracting the values of DON and DIN of the sediment and sea water treatment from the values of the leaf treatment (Table S1). We calculated the potential DON and DIN release rate per every 6 h (μ moles/g) using the DIN/DON concentration from the incubation samples and the mass of the seagrass and mangrove leaves (Table S1).

For the leaf degradation experiment, three adjacent habitats were targeted: (1) mangrove forest (MF); (2) tidal flat (TF) at approximately 300 m from the mangrove forest; (3) seagrass bed (SB) located approximately 600 m from the mangrove forest (Fig. 1). For each habitat, three equidistance points were established 50 m apart (Fig. 1). At each point, five reinforced steel poles (length 0.15 m) were driven into the substrate to a depth of 0.1 m allowing for 0.05 m of pole above the ground. Each pole supported two pairs of mesh bags (<0.5 mm) filled, respectively, with mangrove and seagrass leaves. Prior to the experiment, we collected 450 separate sets of approximately 10 g DW of seagrass and mangrove leaves and epiphytes were removed prior to experimentation. Each individual set was placed into the mesh bags (N = 900) that only allowed for small organisms to pass freely, but dispelled larger marine animals. The length (0.5 m) and width (0.05 m) of the mesh bags allowed us to introduce the leaves without folding or cutting them. Two bags (containing one species per bag) were attached to the pole 0.05 m above the sediment surface (five pairs of bags per point above the sediment); and another pair were buried 0.05 m in the sediment (five pairs of bags per point buried) giving us a total of 20 bags per point; ten buried, and ten suspended. Additional seagrass and mangrove leaf samples (three replicates each) were used to determine initial wet mass and dry mass. The samples were collected by selecting, at random, one buried and one suspended bag at each point. The samples were collected at 2, 4, 6, 20 and 30 d to determine leaf degradation rates.

We measured the import and export rates of leaf particles from each ecosystem with 50 m (length) × 1 m (height) nets (mesh size 0.05 m) stretched across three locations where the mangrove forest is separated from the ocean by a seagrass bed: (1) the seawards edge of the mangrove forest (net 1); (2) the landward edge of the seagrass bed (net 2); (3) the seaward edge of the seagrass bed (net 3) (Fig. 1). We collected mangrove and seagrass leaves trapped in the nets over five consecutive tidal cycles. Only leaf material trapped on the side of the net facing the ecosystem (either the mangrove forest or the seagrass bed) was collected to represent exported material. Dry mass (g) was determined after drying for 48 h at 60°C. Leaf samples were then ground to ensure homogenization. Daily POM transportation rate per unit area of each ecosystem ($POM_{transport}$; mg/m^2/d) was determined (see equation 1 in the Supporting Information). We subsequently calculated the total nitrogen exported per unit area ($TN_{transport}$; μ mole/m^2/d) (see equation 2, Supporting Information). To investigate the extent that POM exported to seagrass ecosystems contributes (potentially) to the nitrogen needs of the seagrass plants, we estimated the nitrogen requirements of *Enhalus acorodies* and *Halophila beccarii* meadows (N_R; μ mole/m^2/d) (equation 3; see Supporting Information).

Data were analyzed using analysis of variance (ANOVA) if normally distributed (based on *D'Agostino–Pearson* test), or the *Kruskal–Wallis* (*K–W*) test if not normally distributed. Three-way ANOVA was used to test for differences in the degradation state of leaves related to habitat type (MF, TF, SB) versus time period (2, 4, 6, 20 and 30 d) for each milieu (sediment or water column). Repeated measures ANOVA (rmANOVA) was also used to compare nitrogen release rate per 6 h from mangrove and seagrass leaves (DIN and DON) over time in the incubation experiments. The *K–W* test was used in two experiments: (1) comparison of changes in DIN and DON release rate from leaves at 24 h in the incubation; (2) comparison of leaf export rates of the two ecosystems. Least squares difference (LSD) *post-hoc* testing was performed following ANOVA and *K–W* tests. Differences were considered significant when probabilities $P < 0.05$. All analyses were conducted in the R programming platform.

In the incubation experiments, only the DON release rate per 6 h increased following decomposition of the seagrass (Fig. 2, panel A). In contrast, DON released from mangrove leaves and DIN for both seagrass and mangrove leaves did not increase. The DON in the seagrass chamber reached a mean of 93 μ mole DON/g (Fig. 2, panel A), which was significantly greater than the DON release from mangrove leaves (*K–W* test: $P = 0.04$). The DON for seagrass increased significantly (rmANOVA: $P = 0.002$), then stabilized after 6 h until the end of the experiment. Negative values originate from the calculation of the nitrogen release rate per 6 h from mangroves or seagrass leaves.

In the field-based leaf degradation experiment, seagrass leaves lost about half of their initial masses over the first 6 d in both the water column and in the sediment (Fig. 2, panel C and E). After 20–30 d, the mass of the seagrass leaves in the water column was reduced to about 25–30 percent at all three locations mangrove forest, mudflats, and seagrass beds (Fig. 2, panel C). In contrast, the remaining mass of seagrass leaves in the

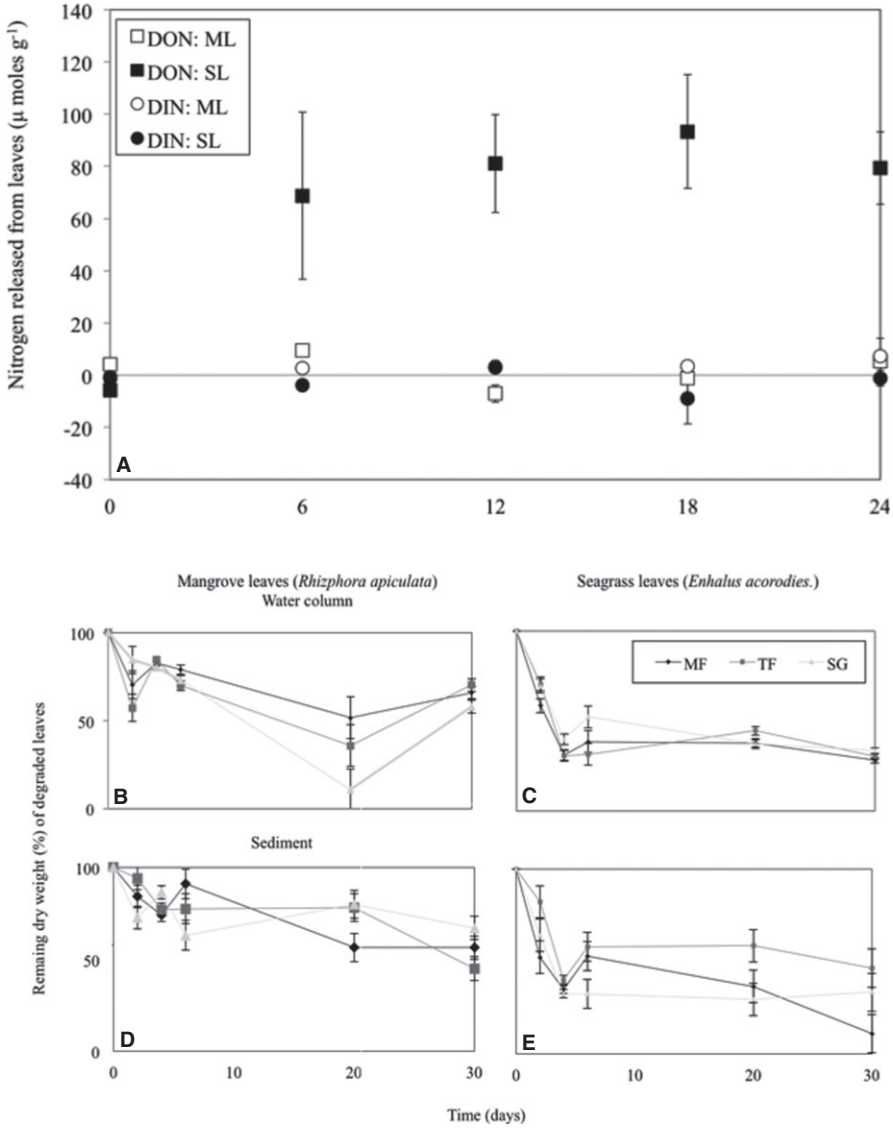

FIGURE 2. Panel (A) Nitrogen release every 6 h (24-h incubation experiments) from fresh mangrove leaves (clear symbols) and seagrass leaves (black symbols) for the following variables: dissolved inorganic nitrogen (DIN, circles) and dissolved organic nitrogen (DON, squares). Values are means ± one standard 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).

sediment varied greatly (remaining mass 1–56%) between locations (Fig. 2, panel E). For mangrove leaves 75 percent remained of mass after 6 d in both the water column and the sediment (Fig. 2, panel B and D). In the sediment, the mass of the mangrove leaves decreased at a near-constant rate over the 20-d period. In contrast, the mass of the leaves in the water column showed substantial variability after 6 d, before reaching a final mass of about 40–50 percent of their initial mass at 20 d for all three treatments (Fig. 2, panel D). The interaction between time and the environment (water column vs. sediment) was significant at 20 d for mangrove leaves (3-way ANOVA, $P = 0.01$, Table S2). No other mass changes were significant (Table S2).

In the other field-based experiment, export of mangrove leaves (3.7 mg/m^2/d) into seagrass beds was significantly higher than that for seagrass leaves (0.6 mg/m^2/d) moving into the mangrove forest (K–W test, $P = 0.01$; Fig. 3). The transport of both mangrove (0.3 mg/m^2/d) and seagrass leaves (0.1 mg/m^2/d) to the ocean was much lower than the exchange between mangroves and seagrasses (Fig. 3). The total nitrogen in seagrass leaves conveyed to mangrove forests was approximately half of that transferred to seagrass beds from mangroves (K–W test, $P = 0.001$; Fig. 3). There was no detectable difference in TN exported to the ocean by mangrove and seagrass leaves.

Our data support the idea that seagrass sediment is a sink for water column DIN. Negative values for DIN from seagrass leaves (Fig. 2, panel A) originate from an influx of DIN into the seagrass sediment (Table S1). This may result from enhanced denitrification (nitrate reduction) from organic material derived ammonium (Holmer & Olsen 2002). Seagrass leaves had a higher DON release rate per 6 h compared to the bare seagrass sediment, indicating that DON mainly comes from the degrading leaves. The rapid initial degradation of the seagrass leaves (Fig. 2, C–E), also suggest that once trapped, seagrass leaves will release DON to the surrounding water column quickly (24 h). The differences in degradation rates are due firstly to lignocelluloses, which are found in mangrove particulate matter and have a greater resilience to microbial degradation than seagrass leaves and secondly to tanins in mangrove leaves which are known enzymatic and bacteria inhibitor (Cundell *et al.* 1979, Alongi 1990, Kristensen *et al.* 2008). Although it is clear that mangrove leaf degradation rates are low, exact degradation rates of these leaves are likely to differ from those observed in our experiments. For instance, we did not include large organisms such as crabs, which are known to accelerate the degradation time of mangrove litter (D'Croz *et al.* 1989, Twilley *et al.* 1997). Nor did we incorporate different species of mangrove leaves in the experiment, which could also correspond with dissimilar N release from the leaves (Ake-Castillo *et al.* 2006, Hossain *et al.* 2014). If we included these other biotic factors that speed up degradation, then the potential N release from mangrove leaves will be greater.

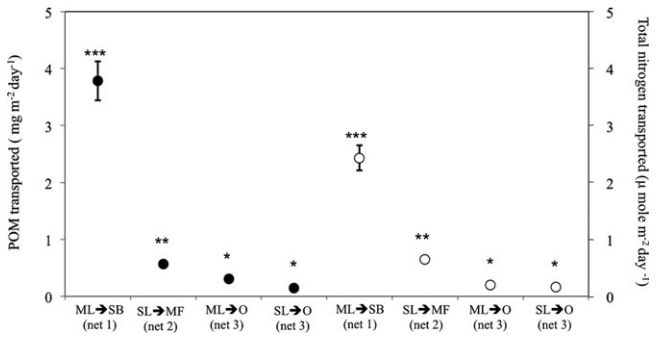

FIGURE 3. Transportation of total organic matter and nitrogen, contained in *Rhizophora apiculata* mangrove leaves (ML) and *Enhalus acorodies* seagrass leaves (SL), between mangrove forests (MF), seagrass beds (SB), and the ocean (O). Nets refer to the location of nets between the ecosystems (Fig. 1). 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).

Assuming our transect POM trapping rates are representative of the entire bay, about 90 percent of the mangrove leaves leaving the forest were transferred to the seagrass bed at a rate of approximately 3.5 mg/m^2/d. Mangrove leaves therefore constitute a substantial input of POM to seagrass beds compared with the comparatively small flux (0.3 mg/m^2/d) to the ocean (Fig. 3). We have previously also found a high trapping capacity in mimic seagrass canopies, possibly because the canopy retained desiccated seagrass leaves (Gillis *et al.* 2014). High trapping capacity partially explains why few seagrass leaves were transported to the mangrove forest flux (0.6 mg/m^2/d, Fig. 3). Waves acting on mangrove roots also decrease their trapping capacity by physically releasing sequestered particulate matter (Gillis *et al.* 2014). Due to the physical nature of mangrove forests where wave forcing will be mainly on the seaward edge of the forest, we speculate that leaves transported will come from this area and not from the landward side, as waves in this area would be smaller. Wherever the leaves are trapped (*e.g.,* mangrove roots, seagrass canopy), organisms and the plants themselves in the vicinity would benefit from the quick N released into the water column (Holmer *et al.* 1999, Van Engeland *et al.* 2011). In addition trapped leaves will be removed by crabs into their burrows and converted into more palatable forms of nutrients for other organisms within the system. Crabs have been found to transport 24–82 percent of leaves from the sediment surface to their burrows where the leaves are processed (Robertson & Daniel 1989, Twilley *et al.* 1997). Therefore, the slow degradation rate of mangrove leaves (and associated release of nutrients), combined with enhanced trapping by forest roots, may make mangroves an important source of nutrients for the mangrove ecosystem itself, but not necessarily for adjacent systems.

We estimated maximum nitrogen requirements (μ mole/m^2/d) for *Enhalus acorodies* and *Halophila beccarii* to be ~21,300 and 580–920 μ mole/m^2/d, respectively. The difference in nitrogen requirements results from *Enhalus acorodies* being a large climax plant, whilst *Halophila beccarii* is a small pioneer species. The

mangrove-derived TN exported to seagrass beds as leaves (2.4 μ mole/m^2/d; Fig. 3), would not fulfill these requirements. This estimation suggests that *Rhizophora apiculata* mangrove leaves provide only a negligible amount of the TN seagrass requirement via mangrove leaf export (0.01%; *Enhalus acorodies* and 0.3–0.4 percent; *Halophila beccarii*) in this bay. However, this estimation is based on the short-time N dynamics in mangrove leaves and does not consider changes in their N content. Changes in N content can come from microbial fixation. Tremblay and Benner (2006) estimated that exogenous N input in mangrove leaves caused by microbial fixation and colonization could be 50–75 percent of the N. In contrast for degraded seagrass leaves it would be no more than 50 percent, due to a higher amount of refractory material in mangrove leaves than seagrass leaves (Vonk & Stapel 2008). Another potential error may be that for the experiments we used fresh green leaves and not senescent leaves. Senescent leaves have lower amounts of N, for example fresh mangrove leaves can have 80 percent more N than senescent leaves (Wang *et al.* 2011). Senescent leaves are likely to be the main source of particulate nutrients from the trees and plants within these ecosystems (Strother & Vatta 1986, Lin & Wang 2001, Wang *et al.* 2003, Hansen & Reidenbach 2013). Therefore, our approximation of available N will be an over estimation because of the difference between N in senescent and fresh green leaves. We do not take this potential error into account, as our study only provides an initial short-term estimation of N content of degrading leaves. Longer term studies are required to establish the importance of these processes for N fluxes.

Our initial results show that, in the short-term, our study site of seagrass beds probably obtains most of their (POM-derived) nitrogen requirements from degradation of their own leaves and not from POM imported from the mangrove. This finding is in agreement with other publications regarding the trapping capacity of seagrass canopies (Terrados & Duarte 2000, Gillis *et al.* 2014) and the internal recycling within seagrass ecosystems (Touchette & Burkholder 2000, Vonk *et al.* 2008, Van Engeland *et al.* 2011). This runs counter to the outwelling hypothesis (Odum 1968, Lee 1995), which suggests that mangrove-derived nutrients are important for other coastal organisms and ecosystems. Here we recognize the status of mangrove forest outwelling will strongly depend on the physical conditions of the ecosystem (*i.e.,* enclosed basin or fringing mangroves) (Lee 1995, Adame & Lovelock 2011). Our results also indicate that the mangrove forest at our study site retains the majority of its nutrients, and therefore, buffer seagrass beds from receiving nutrients.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Concentrations of dissolved inorganic and organic nitrogen from seagrass and mangrove leaf incubation over 24 hours.*

TABLE S2. *Statistical summary of the 3-way ANOVA analysis of mangrove leaf and seagrass leaf degradation experiments of leaf mass.*

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