Temporally dependent C, N, and P dynamics associated with the decay of *Rhizophora mangle* L. leaf litter in oligotrophic mangrove wetlands of the Southern Everglades

Stephen E. Davis, III[ac], Carlos Coronado-Molina[bd], Daniel L. Childers[a], and John W. Day, Jr.[b]

[a] Southeast Environmental Research Center, Florida International University, University Park Campus, Miami, Florida 33199, U.S.A.

[b] Dept. of Oceanography & Coastal Sciences, Louisiana State University, Baton Rouge, Louisiana 70803, U.S.A.

[c] Author for correspondence. Current address: Dept. of Wildlife and Fisheries Sciences, 210 Nagle Hall, Texas A&M University, College Station, Texas 77843, U.S.A.

[d] Current address: Everglades Division, South Florida Water Management District, 3301 Gun Club Road, West Palm Beach, Florida 33416, U.S.A.

Abstract

We performed two litter decomposition experiments using nearly-senesced red mangrove (Rhizophora mangle L.) leaves collected from an Everglades dwarf mangrove wetland to understand the short-term (3 weeks) and long-term (1 year) changes in mass, as well as carbon, nitrogen, and phosphorus contents of decomposing leaf litter. We expected that leaves decomposing in this oligotrophic environment would be short-term sources of C, N, and P, but potential long-term sinks for N and P. In May 1998, we conducted a 3-week leaching experiment, incubating fresh, individual leaves in seawater for up to 21 days. From May 1997 to May 1998, leaf litter in mesh bags decomposed on the forest floor at two dwarf mangrove sites. Leaching accounted for about 33% loss of dry mass from R. mangle leaves after 3 weeks. Leaching losses were rapid, peaking by Day 2, and large, with leachate concentrations of total organic carbon (TOC) and total phosphorus (TP) increasing by more than an order of magnitude after 3 weeks. Mean leaf C:N increased from 105 to 115 and N:P increased from a mean of 74 to 95 after 21 days, reflecting the relatively large leaching losses of N and P. Loss of mass in the litterbags leveled off after 4 months, with roughly 60% dry mass remaining after nearly one year of decomposition. The mass of carbon in each litterbag declined significantly after 361 days, but the mass of nitrogen and phosphorus doubled, indicating long-term accumulation of these constituents into the detritus. Subsequently, the leaf C:N ratio dropped significantly from 90 to 34 after 361 days. Following an initial 44-day increase, leaf N:P decreased from 222 to 144, reflecting high accumulation of P relative to N. A review of several estuarine macrophyte decomposition studies reveals a trend in nitrogen accumulation through time regardless of site, but suggests no clear pattern for C and P. We believe that the increase in litter P observed in this study was indicative of the P-limited status of the greater Everglades ecosystem and that decomposing mangrove litter may represent a substantial phosphorus pool in the system.

Keywords: leaves; leaching; decomposition; carbon; nitrogen; phosphorus

1. Introduction

Litterfall from deciduous and evergreen trees is a primary mechanism by which nutrients are returned to the forest floor. Accounting for roughly 70% of the dry mass of all aboveground litter in forested ecosystems, leaves are usually the most important litter component (O'Neill and DeAngelis, 1981). In estuarine mangrove forests, leaf litter can account for 40-95% of the total pool of litterfall (e.g. Day et al., 1996; Wafar et al., 1997). This fraction of mangrove litter represents a relatively large, potentially labile source of organic matter to decomposer communities (Benner and Hodson, 1985; Benner et al., 1986).

Resorption of materials prior to leaf abscission can be an effective means of conserving vital elements in many mangrove species (Untawale et al., 1977; Karmarkar, 1982; Lin and Wang, 2001). However, there is still a substantial turnover of organic and inorganic materials in the system via leaf litter decomposition (Twilley et al., 1986a; Moran et al., 1991; Wafar et al., 1997). These materials can be an important source of energy and nutrition to heterotrophic communities, especially in oligotrophic wetland systems such as the Everglades.

The decomposition of plants typically occurs in three, often simultaneous phases: 1) leaching of soluble components, 2) microbial oxidation of refractory components such as cellulose and lignin, and 3) physical and biological fragmentation (Valiela et al. 1985). The leaching phase of mangrove leaf decomposition, as with most other litter types, is characterized by a rapid loss of soluble organic compounds (sugars, organic acids, proteins, phenolics, etc.) and inorganic minerals (K, Ca, Mg, Mn, etc.). Regardless of vegetation type, this phase lasts anywhere from a few days to a few weeks and can be responsible for substantial losses of mass, carbon, nitrogen, and phosphorus (Valiela et al., 1985; Parsons et al., 1990; Chale, 1993; Steinke et al., 1993; Taylor and Barlocher, 1996; France et al., 1997). The biotic contributions in this early stage of decomposition are usually minimal and are most often limited to microbial conditioning of the litter (Nykvist, 1959; Cundell et al., 1979; France et al., 1997).

The second and third phases of leaf litter decomposition are characterized by microbially mediated breakdown of labile organic material and refractory structural components, all of which is enhanced by physical and biological fragmentation of the litter (Harrison and Mann, 1975). Since refractory compounds make up the bulk of leaf mass, these latter stages of decay operate over longer time scales than leaching, resulting in a gradual loss of reduced carbon over time. However, relative to carbon, there is often a considerable amount of nutrient accumulation associated with increasing microbial biomass in the detritus complex. Studies on the decay of a variety of estuarine macrophytes have shown significant accumulation of N and P relative to carbon on temporal

scales of a few weeks to several months (Rice and Tenore, 1981; Day et al., 1982; Twilley et al., 1986a; Twilley et al., 1986b).

There are a number of studies that have focused on the decomposition of estuarine macrophytes (e.g. Harrison and Mann, 1975; White et al., 1978; Rice and Tenore, 1981; Tam et al., 1990). Many of these have addressed temporal changes in the nutritional content of the litter. However, only a few have considered the time-dependence of such dynamics by focusing on both the rapid (hours—days) decay component and the long-term (weeks—months), more refractory components of decomposition (Twilley et al., 1986a; Chale, 1993). In the present study, we report the findings of simultaneous experiments that addressed both the short-term (3 week) and long-term (one year) dynamics of carbon, nitrogen, and phosphorus associated with the decay of leaves from a dwarf red mangrove (Rhizophora mangle L.) forest in the oligotrophic Southern Everglades.

As others have previously shown, we anticipated high leaching losses of carbon, nitrogen, and phosphorus from the leaves over the first few weeks of decomposition. We also expected that the low availability of N and P in this oligotrophic wetland would result in the long-term accumulation of these nutrients into the detritus matrix, as has been shown for nitrogen in many other systems. Finally, we compared our results with data synthesized from numerous estuarine macrophyte decomposition studies to reveal any temporal trends in litter C, N, and P dynamics. Given the trophic state of the Everglades and concerns about anthropogenic inputs of nutrients to the Everglades and Florida Bay, there is a need to understand the importance of mangrove leaf detritus as temporally dependent sources or sinks of nitrogen and phosphorus.

2. Site Description

The Southern Everglades mangrove zone is part of a highly oligotrophic estuarine system. Roughly 6,000 ha of this area are composed primarily of the dwarf form (1-2 m canopy height) of the red mangrove (Rhizophora mangle L.; Lin and Sternberg, 1992). Leaf litter comprises about 87% ± 4% of total litterfall in this area and productivity and standing crop values are among the lowest recorded for any mangrove forest (Corronado-Molina, 2000). Phosphate concentrations in the surface water and soil pore water are low and often below the limit of detection (0.01 μM), reflecting the P-limited nature of this region (Koch, 1997; Koch and Snedaker, 1997; Davis et al., 2001). Rates of herbivory on dwarf red mangrove vegetation are also low, as herbivory has been linked to

nutrient status (Onuf et al., 1977; Feller, 1995). As a result, much of the annual litter production (and associated nutrients) is made available to higher trophic levels only through detrital pathways.

The hydrology of the Southern Everglades mangrove zone is micro-tidal (< 5 cm tidal range) and seasonal in rainfall and discharge (wet and dry seasons). Therefore, the direction and velocity of flow and salinity patterns in mangrove creeks such as Taylor River are driven by the interaction of precipitation, upland runoff, and wind, the combination of which leads to a net southerly flow and oligohaline/fresh conditions throughout much of the wet season (usually from June – November) and no net flow and mesohaline/polyhaline conditions throughout the dry season (Sutula, 1999). Furthermore, dwarf mangrove wetlands in this area are characterized by persistent standing water throughout most of the year, and the soils are completely exposed to the atmosphere only during an extended drought (S. Davis, pers. observ.).

3. Materials and Methods

For both experiments, we collected nearly-senesced, yellow leaves from dwarf red mangrove trees along the lower Taylor River in the southern portion of Everglades National Park (Figure 1). We report the carbon, nitrogen, and phosphorus content of leaf material from the leaching and litterbag studies as relative (% or mass of constituent g dry weight^{-1} of tissue) or absolute (mass of constituent per leaf or litterbag). Single-factor analyses of variance were used to determine a significant ($p<0.05$) change in leaf mass, C, N, or P content of leachate or leaves over time. Tukey tests were used to determine significant ($p<0.05$) differences among treatment means.

3.1 Leaching Study

In May 1998, we incubated individual, fresh leaves in 250 ml, clear, glass bottles containing filtered (GF/F) seawater (32 ppt) for up to 21 days. The experimental leaves were not pre-dried, as drying has been shown to modify rates of leaching in many species (Taylor and Barlocher, 1997; Taylor, 1998). Bottles were incubated in the field under ambient temperature and sunlight conditions. In order to determine the abiotic contributions (leaching) to mass and nutrient loss from each individual leaf, we added 2 ml of a 1% NaN_3 solution to half of the experimental units as an inhibitor of aerobic respiration. We collected 3 replicate bottles of each treatment after 1, 2, 5, 10, and 21 days of decomposition. Following incubation, leaves were removed from the bottles and rinsed with de-ionized water and dried to a constant weight at 60 °C (final dry mass = DM_t).

Since we chose to use fresh material, an accurate means of estimating initial dry weight was needed in order to determine change in mass over the period of decay. We used a batch of initial control leaves (n=75) to develop a simple linear regression model that could be used to estimate initial dry weight (DM_0) of each experimental leaf from its initial fresh mass. This model—with no y-intercept—indicated that dry mass was consistently34% of initial fresh mass ($p<0.0001$; adjusted $r^2=0.99$).

Water samples collected from each bottle were stored at 4° C until analyzed for total phosphorus (TP)—according to a modification of the dry ashing, acid-hydrolysis technique of Solorzano and Sharp (1980)—total nitrogen (TN)—using an Antec 7000N total nitrogen analyzer—and total organic carbon (TOC)—using a hot platinum catalyst, direct injection analyzer; Shimadzu model TOC-5000. After final dry weight measurements were taken, all leaves were ground to a fine powder and analyzed for carbon and nitrogen content—using a Carlo Erba 1500-N CHN analyzer—and TP content, as described above.

At the conclusion of the 21-day experiment, we calculated percent dry mass remaining (% DMR) for each leaf by dividing DM_t by DM_0. To ensure that changes in water nutrients were due to the presence of the leaves, we also incubated "control" bottles containing only filtered seawater or seawater + NaN_3 for the entire 21-day length of the leaching experiment. We compared TOC, TN, and TP concentrations from these control bottles with initial values to determine changes associated with water column or photochemical processes. Paired t-tests were used to determine significant differences between initial and final concentrations ($\alpha=0.05$). Leaching rates (i.e. fluxes) of TOC, TN, and TP were calculated from concentrations in the water as moles g DW $leaf^{-1}$ and averaged over the number of days between each sampling interval.

3.2 Litterbag Study

We dried the leaves for the litterbag study at 60 °C for 48 hours and partitioned the pooled mass into replicates, each weighing approximately 5 g. We then placed samples into mesh bags fashioned from fiberglass window screen (approx. 1-2 mm mesh size). Sixteen litterbags were distributed on the forest floor at each of two sites (Sites A and B) each approximately 5 m from creek channel in the dwarf mangrove forest (Figure 1). These two sites were randomly selected to account for some of the variability in the dwarf mangrove forest along lower Taylor River. The litterbag experiment lasted from May 1997 to May 1998. At the beginning of the experiment

(time = 0), two bags were retained to determine relative and absolute C, N, and P content. Thereafter, duplicate samples were retrieved from each site after 13, 31, 44, 87, 128, 184, 304, and 361 days of decomposition in the field.

After collection, litterbags were immediately taken to the laboratory and prepared for analysis. Leaves were removed from each bag, gently washed to remove sediment and then oven-dried to constant weight at 60 °C. We calculated % DMR by dividing DM_t by DM_0 and multiplying by 100. A sub-sample of dried tissue from each litterbag was ground to a fine powder and analyzed for C, N, and P content using the same procedures as described for the leaching experiment.

4. Results

4.1 Leaching study

There was no significant inhibitor effect on % DMR over the 21-day leaching experiment (Figure 2a), and all leaves lost a significant amount of mass (ANOVA, $p<0.0001$). After 24 hours of decomposition in the bottles, red mangrove leaves had lost 17% ± 2% (std dev) of the initial dry mass. The majority of these losses were attributable to leaching rather than microbially mediated processes, as aerobic respiration was inhibited with sodium azide in half of the experimental units (Figure 2a). For the next 9 days, all leaves lost approximately the same amount of dry mass per day (1.3% d^{-1}). However, from day 10 to day 21, leaching losses seemed to subside while microbial activity (bottles without NaN_3) appeared to increase, as the difference between poisoned and non-poisoned bottles became more noticeable (Figure 2a). At the conclusion of the experiment, poisoned and non-poisoned leaves had lost 33% ± 6% and 41% ± 17% of their initial dry mass, respectively, but these did not differ significantly.

The C, N, and P content of the leaves in the leaching experiment showed little inhibitor effect (poison vs. no poison) over the 3-week experiment. In addition, we were unable to detect any statistically significant change in relative and absolute C, N, and P content of the leaves over time. Nevertheless, mean relative C of leaves increased slightly after three weeks (Figure 2b), but absolute values decreased noticeably from Day 0 to Day 21(Figure 2c), reflecting the large losses of mass. Similarly, the mean relative N content of all leaves remained fairly steady at about 0.6% (Figure 2b), but they showed a decrease in the absolute N content after three weeks (Figure 2c). Mean % P content of leaves also declined—especially over the first few days in the presence of azide (Figure 2b). Initial values of relative P (0.021±0.001%) were nearly double those after 3 weeks (0.011±0.001%). As with C and N, absolute P content decreased throughout the 3-week study period (Figure 2c).

We found no statistical difference in C:N ratios between poisoned and non-poisoned leaves after 21 days of immersion. After 24 hours, leaves exhibited a decline in C:N from 105 to an overall mean of 96 (Figure 3). Thereafter, the C:N of poisoned leaves increased above initial levels, fluctuating between a mean of 110 and 115 throughout the remainder of the experiment (Figure 3). The C:N of the non-poisoned leaves showed an overall decline over the first 10 days, and then increased from a mean of 82 to 105 after 21 days (Figure 3). The ratios of N:P in these same leaves showed overall increases from 74±8 (std dev) at Day 0 to Day 21 levels of 95±18 (non-poisoned) and 104±10 (poisoned; Figure 3). The only significant difference in N:P between treatment levels was at Day 1, when N:P of the non-poisoned leaves decreased below initial levels to 53±10 while poisoned leaves remained unchanged at 76±7 (ANOVA; $p=0.03$). From Day 1 to Day 2, the N:P of non-poisoned leaves nearly doubled to a mean of 94 (Figure 3).

We observed substantial changes in water chemistry throughout the leaching study. Bottles with leaves showed significant increases in TOC, TN, and TP over the 3-week study (Table 1). In either treatment, mean TOC and TP concentrations increased by more than an order of magnitude after 21 days, and average concentrations of TN more than doubled in the "no azide" treatment (Table 1). Given the high N-content of our poison (NaN_3) relative to ambient water concentrations, we did not analyze poisoned samples for TN content. Fluxes for all constituents were generally highest after 1 or 2 days, then declined considerably over the next 19 to 20 days of incubation (Table 1). We found no significant change in the TOC, TN, or TP content of the water in the control bottles without leaves.

4.2 Litterbag study

We observed a significant decrease in the % DMR over time using the litterbag technique (ANOVA; $p<0.0001$; Figure 4a). Although there appeared to be a difference in the loss of dry mass between sites after 128 days of decay, there was no significant difference in % DMR between sites (ANOVA; $p>0.05$; Figure 4a). The percentage of dry mass loss in individual litterbags was quite variable after 13 days of decomposition in the field, ranging from 2% to 35%. High losses of mass continued for about 3 months at Site A and 4 months at Site B, but then appeared to level off (Figure 4a). At the conclusion of the litterbag experiment, leaves decomposing at both sites had lost an average of 40±7% of their initial dry mass.

The C, N, and P contents of the litterbag leaves were consistent between sites. The relative carbon content of litterbag leaves increased from about 44% to as much as 55% over the first 3 months of the study, but then declined, approaching initial levels by the end of the study (Figure 4b). Normalized to dry mass of tissue, this pattern was not evident, as the absolute concentration of carbon decreased over the course of the entire experiment (Figure 4c). Patterns for nitrogen and phosphorus in these leaves were comparable with significant increases in the relative and absolute content occurring over the entire year of this study (Figures 4b and 4c). Mean relative nitrogen increased from 0.6% to 1.7% and absolute values nearly doubled (0.03 to 0.05 g). Long-term increases in phosphorus were somewhat similar, with relative P increasing from a mean of 0.009% to 0.029% and absolute P increasing from an initial average of 0.4 mg to 0.9 after 1 year (Figures 4b and 4c).

Molar ratios of C:N and N:P in leaf tissue were also quite similar in the two sites. Leaf C:N decreased significantly from a mean of 90 to 34 after 361 days in the field, reflecting the losses in absolute C and increases in absolute N (Figure 5). The pattern for leaf N:P was different, with large increases up through Day 44 followed by decreases to near initial levels by Day 128 (mean=144; Figure 5). At its highest, the N:P ratio of our mangrove litter averaged 222±41.

5. Discussion

Leaching has been shown to be a major pathway for loss of mass and materials from senesced estuarine vegetation. In our bottle experiment, leaching accounted for more than a third of the mass lost after three weeks, and short-term leaching losses were nearly as great as the mass lost from leaves after one year in the litterbag study (Figures 2 & 4). This was remarkable given that past studies using the litterbag methodology have shown a 60%–90% loss of mangrove leaf mass in 6 months or less (Steinke et al., 1983; Twilley et al., 1986a; Tam et al., 1990; Mackey and Smail, 1996). As anticipated, leaching losses translated to substantial fluxes of TOC, TN, and TP to the water column, with highest flux rates occurring during the first few days of leaf submergence (Table 1).

We found no inhibitor effects on total fluxes of C, N, and P or on litter C, N, and P content throughout the study. This supported the notion that leaching was the principal process contributing to materials loss during the early phase of R. mangle leaf litter decay. After 361 days, the relative concentration of C in the litter was no different than % C in the leaching leaves. However, relative concentrations of N were significantly higher after long-term decomposition in the field (1.6±0.09) than after 21 days of leaching (0.53±0.08). In addition, relative P

was higher at the conclusion of the litterbag study (0.028±0.003 vs. 0.011±0.002) even though initial % P of the leaching leaves was double the initial content of the litterbag leaves (Figures 2 and 4). This N and P enrichment over time signifies the microbial contribution to the long-term control of red mangrove leaf litter quality.

The early decay of estuarine macrophytes often varies as a result of inundation period, with highest losses generally occurring in low inter-tidal zones (Kruczynski et al., 1978; Valiela et al., 1985; Twilley et al, 1986a; Mackey and Smail; 1996). Our short-term losses are similar to those (25% after 14 days) reported by Steinke et al. (1993) in their study of Avicennia marina leaves. Other work on A. marina indicated a 19% loss of mass after 24 hours of submergence and only an additional 11% loss after 6 weeks (Chale, 1993). Robertson (1988) determined that two species of mangrove leaves decomposed much more slowly on the exposed forest floor than when continuously submerged. In our leaching study, leaves were continually submerged for up to 3 weeks, perhaps enhancing the rate of loss. The inundation pattern at our litterbag sites was much more variable. Although we did not intensively monitor site inundation, we estimated that the litterbags at both dwarf mangrove sites were inundated at least 50% of the year.

The carbon content of our leaves showed little change over the first few weeks of decay. Given that the bulk of the carbon in these leaves is tied up in refractory structural tissues, this was not unexpected. Nevertheless, many estuarine macrophytes, including red mangrove leaves, are known to leach considerable amounts of labile DOC to the water column when submerged (Rice and Tenore, 1981; Benner et al., 1986; Twilley et al., 1986a; this study).

Early changes in N seem to be variable and may be related to soluble protein content in the leaf tissue (Table 2). Some have suggested that changes in leaf N are function of initial C:N (Harrison and Mann, 1975; Fell et al., 1984). However, initial C:N ratios alone do not seem to explain the differences we observed in early N dynamics. Cundell et al. (1979) and Fell et al. (1975) measured large, early increases in % N of submerged R. mangle leaves with initial C:N ranging from 90-110 (Table 2). We found a small, early decrease in leaf % N with initial C:N also ranging from 90-110 (Table 2). The difference, as described by Twilley et al. (1986b), may be controlled by the amount of N available to microbial decomposers. Perhaps the greater availability of N (relative to P) at our Southern Everglades sites accounted for the differences we observed in R. mangle leaf decomposition.

Early P dynamics in decomposing estuarine macrophytes appears more consistent, as a preponderance of the cases we reviewed showed substantial decreases in relative P in 3 weeks or less (Table 2). In this study, we

found a significant increase in the TP content of the leachate in the bottles that coincided with an apparent decrease in the mean % P content of the leaves. High P leaching from estuarine macrophytes is believed to be a result of the large inorganic fraction of P in leaf tissue, as opposed to N, which is mostly organic (Twilley et al., 1986b). Data in Table 2 suggest that estuarine macrophyte litter can be a rapid, short-term source of N and P to the environment, possibly enhancing the degradability and microbial conditioning of the plant litter. This may be particularly important to the degradation of litter in oligotrophic environments such as the dwarf mangrove wetlands of the Southern Everglades.

The long-term decay of the more refractory components of estuarine macrophyte litter is not as influenced by the inundation pattern of the site (Valiela et al., 1985). We observed a continuous loss of mass from our litterbag leaves until about Day 128, regardless of inundation pattern. From this point on, values stabilized at about 55-65% DMR for the remaining 200+ days of the study (Figure 2), suggesting that about half of the mass of these dwarf mangrove leaves is refractory. Johnson et al. (1993) demonstrated a similar trend for blades of S. patens in a mesohaline Louisiana coastal marsh with about 56% DMR after 320 days. Studies have shown that the breakdown of this recalcitrant fraction is more dependent on habitat characteristics such as the decomposer community, tidal energy, site fertility, tissue nutrient content, and air temperature (Cramer et al., 1981; Valiela et al., 1985; Robertson, 1986; Twilley et al. 1986a; Robertson, 1988; Mackey and Smail, 1996; Slim et al., 1997).

Long-term changes in the elemental content of litter tend to reflect the importance of biotic over abiotic processes. Our experiments revealed small increases in R. mangle leaf % C with considerable increases in both % N and % P after nearly one year (Figure 4; Table 2). Increases in the relative N content of R. mangle leaves overshadowed any change in C, resulting in a large decline in leaf C:N from 90 (initial average) to 34 (final average). However, N enrichment was surpassed by increases in % P of R. mangle leaf detritus after about 50 days of decomposition in the field. At this point, N:P began declining to a mean of 132 after 361 days—slightly less than initial N:P of 142 (Figure 5).

A review of estuarine macrophyte decomposition studies supports our findings for tissue N dynamics, with consistent increases in the % N content of leaves over time regardless of habitat type and climate (Figure 6). This accumulation of nitrogen through time has been linked to increases in bacterial and fungal protein on the surface of estuarine macrophyte detritus (Harrison and Mann, 1975; Fell et al., 1975; Cundell et al., 1979; Rice and Tenore, 1981). Nitrogen derived from the water column and soil accounts for a sizable fraction of this immobilized N, but

these combined sources do not always account for all accumulated nitrogen in estuarine detritus. It has been shown that this N budget deficit can be accounted for by nitrogen fixed from the atmosphere (Fell et al., 1975; Valiela et al., 1985; Twilley et al., 1986a).

While this concept may be useful in explaining the long-term increases in litter nitrogen in low N environments, it does not explain the long-term increases in phosphorus we observed in the P-limited dwarf mangrove wetland we studied. A few studies have noted long-term increases in litter P; however, they offered little or no explanation as to the sources or mechanisms for P-accumulation (Twilley et al., 1986b; Tam et al., 1990). In our litterbag study, the sources of immobilized phosphorus were likely limited to the water column (via direct precipitation or upland runoff) and soil.

Another potentially important source of phosphorus may have been from the leachate of freshly fallen leaves. When leaves abscise in this dwarf mangrove forest, they accumulate on the forest floor, as there is little particulate export in this system (S. Davis pers. observ.). It is likely that leachate from recently abscised leaves supplies a portion of the P accumulated in microbial biomass in older leaves, thus maintaining an efficient recycling of phosphorus in this system. We contend that the occurrence of P accumulation in dwarf mangrove detritus, despite extremely low phosphorus concentrations in the surrounding environment (water column TP≈0.5 µM; pore water SRP≈0.2 µM; and soil TP<25µg cm^{-3}; Koch, 1997; Davis et al. 2001), reflected the P-limited status of the Southern Everglades Ecosystem.

Acknowledgements

We want to acknowledge numerous individuals for their assistance in the field or in the lab. These include, S. Kelly, D. Rudnick, F. Sklar, C. Madden, C. Donovan, E. Reyes, M. Sutula, B. Perez, J. Davis, L. Romero, and D. Rondeau. Funding for this research was provided by the South Florida Water Management District (contract # C-E6608) and the Tropical Biology Program at Florida International University (FIU). This material is also based upon ongoing work in the Florida Coastal Everglades Long-Term Ecological Research (FCE-LTER) Program and supported by the National Science Foundation under Grant #9910514. This manuscript was greatly enhanced by comments from two anonymous reviewers and J. Vermaat. It is SERC Contribution # XX and Contribution # XX from the Tropical Biology Program at FIU.

References

Benner, R., Peele, E.R., Hodson, R.E., 1986. Microbial utilization of dissolved organic matter from the leaves of the red mangrove, Rhizophora mangle, in the Fresh Creek Estuary, Bahamas. Estuar. Coast. Shelf Sci. 23, 607-619.

Benner, R., Hodson, R.E., 1985. Microbial degradation of the leachable and lignocellulosic components of leaves and wood from Rhizophora mangle in a tropical mangrove swamp. Mar. Ecol. Progr. Ser. 23, 221-230.

Chale, F.M., 1993. Degradation of mangrove leaf litter under aerobic conditions. Hydrobiologia 257, 177-183.

Corronado-Molina, C., 2000. Litterfall dynamics and nutrient cycling in mangrove forests of Southern Everglades, Florida and Terminos Lagoon, Mexico. Louisiana State University, Department of Oceanography and Coastal Sciences, Ph.D. Dissertation.

Cramer, G.W., Day, J.W., Conner, W.H., 1981. Productivity of four marsh sites surrounding Lake Pontchartrain, Louisiana. Am. Mid. Nat. 106, 65-72.

Cundell, A.M., Brown, M.S., Stanford, R., Mitchell, R., 1979. Microbial degradation of Rhizophora mangle leaves immersed in the sea. Estuar. Coast. Shelf Sci. 9, 281-286.

Davis, S.E., Childers, D.L., Day, J.W., Rudnick, D.T., Sklar, F.H., 2001. Carbon, nitrogen and phosphorus dynamics in a non-tidal dwarf mangrove wetland of the Southern Everglades, Florida, USA. Estuaries 42, 609-622.

Day, J.W., Day, R.H., Barreiro, M.T., Ley-Lou, F., Madden, C.J., 1982. Primary production in the Laguna de Terminos, a tropical estuary in the Southern Gulf of Mexico. Oceanol. Acta. 269-276.

Day, J.W., Corronado-Molina, C., Vera-Herrera, F.R., Twilley, R., Rivera-Monroy, V.H., Alvarez-Guillen, H., Day, R., Conner, W., 1996. A 7-year record of above-ground net primary production in a southeastern Mexican mangrove forest. Aquat. Bot. 55, 39-60.

Fell, J.W., Cefalu, R.C., Master, I.M., Tallman, A.S., 1975. Microbial activities in the mangrove (Rhizophora mangle) leaf detrital system. In: Walsh, G.E., Snedaker, S.C., Teas, H.J. (eds.), Proceedings of the International Symposium on Biology and Management of Mangroves. Institute of Food and Agriculture, University of Florida, Gainesville. 661-679

Fell, J.W., Master, I.M., Wiegert, R.G., 1981. Litter decomposition and nutrient enrichment. In: Snedaker, S.C., Snedaker, J.G. (eds.), The Mangrove Ecosystem: Research methods, 239-251. UNESCO, Bungay, U.K.

Feller, I.C., 1995. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (Rhizophora mangle). Ecol. Monogr. 65, 477-505.

France, R., Culbert, H., Freeborough, C., Peters, R., 1997. Leaching and early mass loss of boreal leaves and wood in oligotrophic water. Hydrobiologia 345, 209-214.

Harrison, P.G., Mann, K.H., 1975. Detritus formation from eelgrass (Zostera marina L.): the relative effects of fragmentation, leaching, and decay. Limnol. Oceanogr. 20, 924-934.

Johnson, L.A., Reynolds, K.A., Foote, A.L., 1993. Production and decomposition of Spartina patens in a degrading coastal marsh. In O. Magoon, W. Wilson, H. Converse, and L. Tobin, editors, 8th Symposium on Coastal and Ocean Management. American Shore and Beach Preservation Association. 349-359

Karmarkar, S.M., 1982. Senescence in mangroves. In Sen, D., Rajpurohit, K. (eds.), Tasks for Vegetation Science, 2, 173-187. Dr W. Junk Publishers, The Hague.

Koch, M.S., 1997. Rhizophora mangle L. seedling development into the sapling stage across resource and stress gradients in subtropical Florida. Biotropica 29, 427-439.

Koch, M.S., Snedaker, S.C., 1997. Factors influencing Rhizophora mangle L. seedling development in Everglades carbonate soils. Aquat. Bot. 59, 87-98.

Kruczynski, W.L., Subrahmanyam, C.B., Drake, S.H., 1978. Studies on the plant community of a north Florida salt marsh. Bull.Mar. Sci. 28, 316-334.

Lin, G., Sternberg, L., 1992. Differences in morphology, carbon isotope ratios, and photosynthesis between scrub and fringe mangroves in Florida, USA. Aquat. Bot. 42, 303-313.

Lin, P., Wang, W., 2001. Changes in the leaf composition, leaf mass and leaf area during leaf senescence in three species of mangroves. Ecol. Engineer. 16, 415-424.

Mackey, A.P, Smail, G., 1996. The decomposition of mangrove litter in a subtropical mangrove forest. Hydrobiologia 332, 93-98.

Moran, M.A., Wicks, R.J., Hodson, R.E., 1991. Export of dissolved organic matter from a mangrove swamp ecosystem: evidence from natural fluorescence, dissolved lignin phenols, and bacterial secondary productivity. Mar. Ecol. Progr. Ser. 76, 175-184.

Nykvist, N., 1959. Leaching and decomposition of litter I. Experiments on leaf litter of Fraxinus excelsior. Oikos 10, 190-211.

O'Neill, R.V., DeAngelis, D.L., 1981. Comparative productivity and biomass relations of forest ecosystems, In: Reichle, D.E. (ed.), Dynamic properties of forest ecosystems. 411-449. Cambridge University Press, Cambridge, England.

Onuf, C.P., Teal, J.M., Valiela, I., 1977. Interactions of nutrients, plant growth and herbivory in a mangrove ecosystem. Ecology 58, 514-526.

Parsons, W., Taylor, B.R., Parkinson, D., 1990. Decomposition of aspen (Populus tremuloides) leaf litter modified by leaching. Can. J. For. Res. 20, 943-951.

Rice, D.L., Tenore, K.R., 1981. Dynamics of carbon and nitrogen during the decomposition of detritus derived from estuarine macrophytes. Estuar.Coast. Shelf Sci. 13, 681-690.

Robertson, A.I., 1986. Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (Rhizophora spp.) in northeastern Australia. J. Exp. Mar. Biol. Ecol. 102, 237-248.

Robertson, A.I., 1988. Decomposition of mangrove leaf litter in tropical Australia. J. Exp. Mar. Biol. Ecol. 116, 235-247.

Slim, F.J., Hemminga, M.A., Ochieng, C., Jannink, N.T., Cocheret de la Moriniere, E., van der Velde, G., 1997. Leaf litter removal by the snail Terebralia palustris L. and sesarmid crabs in an east African mangrove forest (Gazi Bay, Kenya). J. Exp. Mar. Biol. Ecol. 215, 35-48.

Solorzano, L., Sharp, J.H., 1980. Determination of total dissolved phosphorus and particulate phosphorus in natural waters. Limnol. Oceanogr. 25, 754-758.

Steinke, T.D., Naidoo, G., Charles, L.M., 1983. Degradation of mangrove leaf and stem tissues in situ in Mgeni Estuary, South Africa. In: Teas, H.J. (ed.), Biology and Ecology of Mangroves, 8, 141-149. Dr. W. Junk Publishers, The Hague.

Steinke, T.D., Holland, A.J., Singh, Y., 1993. Leaching losses during decomposition of mangrove leaf litter. S. Afr. J. Bot. 59, 21-25.

Sutula, M., 1999. Processes controlling nutrient transport in the southeastern Everglades wetlands, Florida, USA. Louisiana State University, Department of Oceanography and Coastal Sciences, Ph.D. Dissertation.

Tam, N., Vrijmoed, L., Wang, Y., 1990. Nutrient dynamics associated with leaf decomposition in a small subtropical mangrove community in Hong Kong. Bull. Mar. Sci. 47, 68-78.

Taylor, B.R., 1998. Air-drying depresses rates of leaf litter decomposition. Soil Biol. Biochem. 30, 403-412.

Taylor, B.R., Barlocher, F., 1996. Variable effects of air-drying on leaching losses from tree leaf litter. Hydrobiologia 325, 173-182.

Twilley, R.R., Lugo, A.E., Patterson-Zucca, C., 1986(a). Litter production and turnover in basin mangrove forests in southwest Florida. Ecology 67, 670-683.

Twilley, R.R., Ejdung, G., Romare, P., Kemp, W.M., 1986(b). A comparative study of decomposition, oxygen consumption, and nutrient release for selected aquatic plants occuring in an estuarine environment. Oikos 47, 190-198.

Untawale, A.G., Bhosle, N.B., Dhargalkar, V.K., Matondkar, S., Bukhari, S., 1977. Biochemical changes in mangrove foliage during growth and decomposition. Ind. J. Mar. Sci. 6, 104-106.

Valiela, I., Teal, J.M., Allen, S.D., Van Etten, R., Goehringer, D., Volkmann, S., 1985. Decomposition in salt marsh ecosystems: the phases and major factors affecting disappearance of above-ground organic matter. J. Exp. Mar. Biol. Ecol. 89, 29-54.

Wafar, S., Untawle, A.G., Wafar, M., 1997. Litterfall and energy flux in a mangrove ecosystem. Estuar. Coast. Shelf Sci. 44, 111-124.

White, D.A., Weiss, T.E., Trapani, J.M., Thien, L.B., 1978. Productivity and decomposition of the dominant salt marsh plants in Louisiana. Ecology 59, 751-759.

Table 1: Water concentrations and fluxes (± standard deviation) of TOC, TN, and TP in mangrove leaf leaching bottles over time. Fluxes of C, N, and P were calculated as change in water concentration over time normalized to grams dry weight (gdw) of each leaf. There was a net release of all constituents from the leaf to the water column. Different letters represent significant differences over time ($p<0.05$) using single factor ANOVAs and Tukey post-hoc comparisons.

Constituent (treatment level)	Day	Concentration (µmol)	Letter	Flux (µmol gdw^{-1} d^{-1})
TOC	0	168 ± 1	A	
(no azide)	1	781 ± 286	A	1259 ± 574
	2	919 ± 219	AB	340 ± 127
	5	1513 ± 225	AB	543 ± 174
	10	2364 ± 207	B	442 ± 109
	21	3061 ± 873	B	284 ± 131
TN	0	11.7 ± 0.1	A	
(no azide)	1	14.6 ± 0.8	A	13.9 ± 2.7
	2	15.1 ± 0.5	AB	3.2 ± 0.2
	5	19.9 ±1.3	B	5.3 ± 1.9
	10	23 ± 1.5	B	3.5 ± 1.2
	21	29.1 ± 1.7	C	1.9 ± 0.3
TP	0	0.03 ± 0.01	A	
(no azide)	1	0.13 ± 0.03	A	0.2 ± 0.07
	2	0.19 ± 0.04	A	0.1 ± 0.02
	5	0.61 ± 0.19	B	0.2 ± 0.03
	10	0.4 ± 0.02	AB	0.08 ± 0.02
	21	0.52 ± 0.06	B	0.04 ± 0.00
TOC	0	173 ± 0	A	
(azide)	1	207 ± 7	AB	215 ± 54
	2	997 ± 465	AB	827 ± 342
	5	1186 ± 403	ABC	468 ± 196
	10	1483 ± 1032	BC	169 ± 92
	21	2964 ± 448	C	219 ± 47
TP	0	0.04 ± 0.01	A	
(azide)	1	0.11 ±0.01	AB	0.16 ± 0.05
	2	0.43 ± 0.18	B	0.33 ± 0.19
	5	0.36 ± 0.12	B	0.15 ± 0.08
	10	0.38 ± 0.17	B	0.07 ± 0.03
	21	0.56 ± 0.02	B	0.04 ± 0.00

Table 2: Percent changes in relative C, N, and P content from initial values during the decomposition of a number of estuarine macrophytes. Studies were categorized as "litterbag", if leaf material was contained within a mesh bag of some sort, or "leaching", if leaf material was incubated directly in water without a litterbag. All changes are reported as percentages of initial relative values. Positive values indicate an increase while negative values indicate a decrease in litter content. Some values were calculated from tabular data, but most were estimated from plotted data.

Study type	Species	Tissue treatment	Time (days)	% chg. in rel. C	% chg. in rel. N	% chg. in rel. P	Reference
leaching	*Avicennia marina*	oven-dried material, submerged	2		3	-17	Chale 1993
litterbag	*Rhizophora mangle*	fresh material, submerged	7	<1	30		Cundell et al. 1979
litterbag	*Aegiceras corniculatum*	air-dried material, tidally inundated	13	19	2	22	Tam et al. 1990[a]
litterbag	*Avicennia marina*	air-dried material, tidally inundated	13	10	-18	-52	Tam et al. 1990[a]
litterbag	*Kandelia kandel*	air-dried material, tidally inundated	13	9	-39	50	Tam et al. 1990[a]
leaching	*Avicennia marina*	fresh material, poisoned	14		8	-72	Steinke et al. 1993
leaching	*Avicennia marina*	air-dried material, poisoned	14		1	-84	Steinke et al. 1993
litterbag	*Spartina alterniflora*	air-dried material, tidally inundated	14	6	7		Valiela et al. 1985[b]
litterbag	*Spartina patens*	air-dried material, tidally inundated	14	-2	<1		Valiela et al. 1985[b]
litterbag	*Rhizophora mangle*	fresh material, submerged	15	9	50		Fell et al. 1975
leaching	*Spartina alterniflora*	fresh material, submerged	15	-1	3	13	Twilley et al. 1986b
litterbag	*Avicennia marina*	fresh material, submerged	21	1	38	-42	Steinke et al. 1983
litterbag	*Brugueira gymnorrhiza*	fresh material, submerged	21	-1	36	-50	Steinke et al. 1983
leaching	*Rhizophora mangle*	fresh material, submerged	21	3	-2	-34	this study[c]

Table 2: continued

Study type	Vegetation	Tissue treatment	Time (days)	% chg. in rel. C	% chg. in rel. N	% chg. in rel. P	Reference
litterbag	*Rhizophora mangle*	fresh material, submerged	70	-22	75		Cundell et al. 1979
litterbag	*Aegiceras corniculatum*	air-dried material, tidally inundated	81	-5	59	-30	Tam et al. 1990[a]
litterbag	*Kandelia kandel*	air-dried material, tidally inundated	81	-9	-15	200	Tam et al. 1990[a]
leaching	*Spartina alterniflora*	fresh material	93	2	90	93	Twilley et al. 1986b
leaching	*Avicennia marina*	oven-dried material	98		105	-32	Chale 1993
litterbag	*Avicennia marina*	air-dried material, tidally inundated	109	6	26	50	Tam et al. 1990[a]
litterbag	*Rhizophora mangle*	fresh material, submerged	115	21	148		Fell et al. 1975
litterbag	*Avicennia marina*	fresh material, submerged	175	-10	91	-54	Steinke et al. 1983
litterbag	*Rhizophora mangle*	air-dried material, tidally-inundated	180		209	200	Day et al. 1982[d]
litterbag	*Brugueira gymnorrhiza*	fresh material, submerged	189	11	164	-55	Steinke et al. 1983
litterbag	*Rhizophora mangle*	fresh material	361	6	181	207	this study
litterbag	*Spartina alterniflora*	air-dried material, tidally inundated	700	-19	157		Valiela et al. 1985[b]
litterbag	*Spartina patens*	air-dried material, tidally inundated	700	-2	250		Valiela et al. 1985[b]

[a] Freshly-picked green leaves were used in this study.

[b] Data taken from un-enriched low marsh and high marsh sites.

[c] Data from non-poisoned bottles only.

[d] Data collected from Estero Pargo, MX site.

List of Figures

Fig. 1. Map of the Southern region of Everglades National Park with Taylor Slough borders and indication (*) of litter collection and decomposition sites (A & B) adjacent to Taylor River. Units for lat/long are in degrees with decimal minutes.

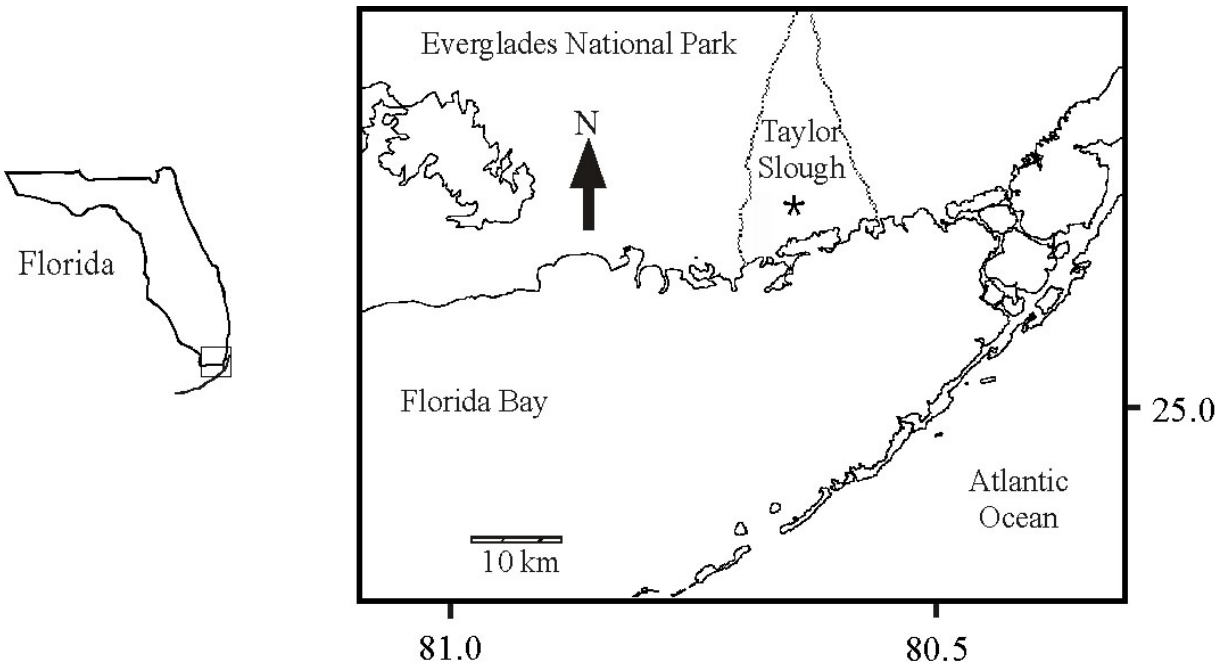
Fig. 2. Cell plots of: a) % dry mass remaining, b) relative C, N, and P and c) absolute C, N, and P in red mangrove leaves over the course of the 21-day leaching experiment. Bars indicate standard deviation of three replicates.

Fig. 3. Molar ratios of C:N (top) and N:P (bottom) in red mangrove leaves over the course of the 21-day leaching experiment. Bars indicate standard deviations of three replicates.

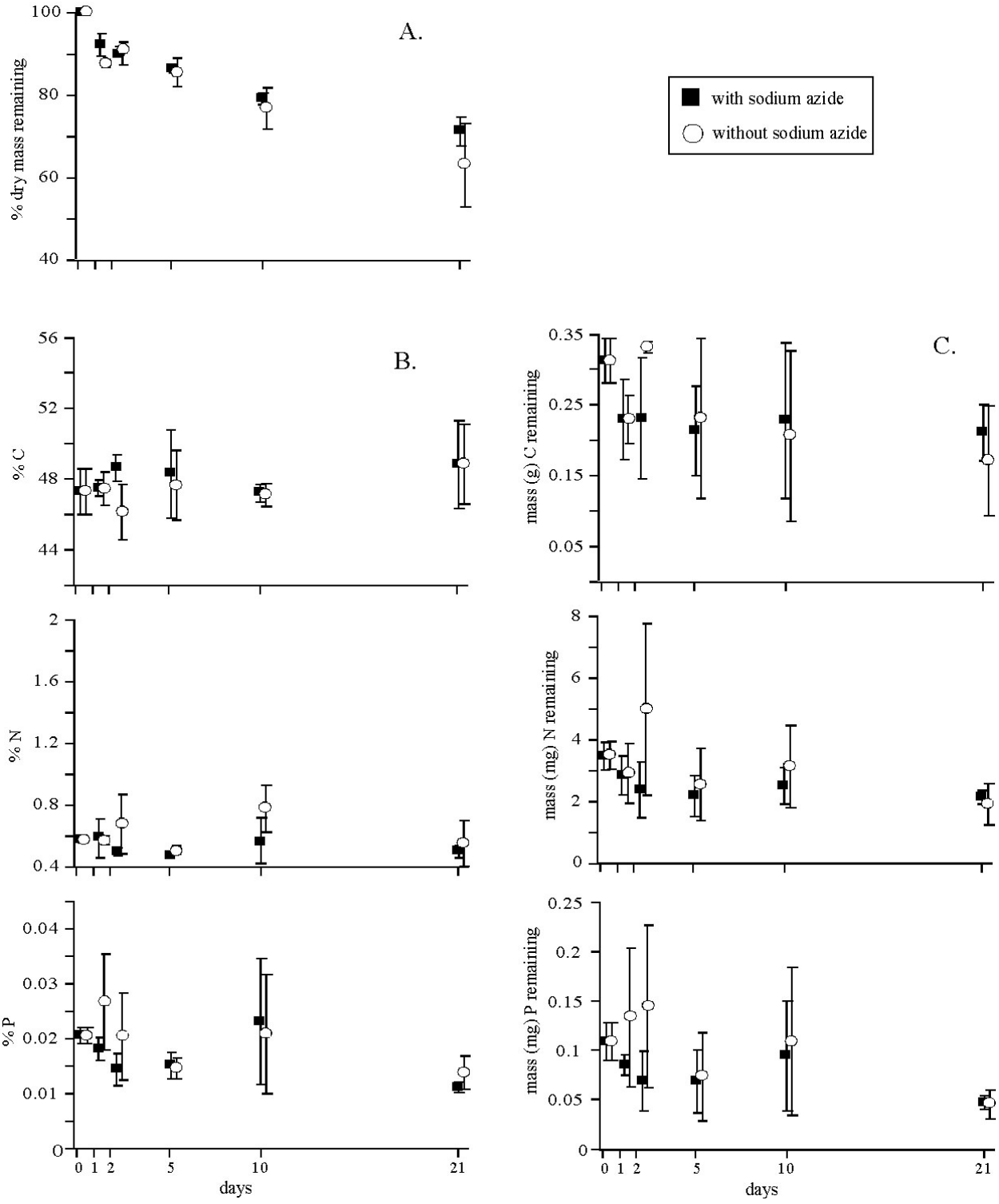
Fig. 4. Cell plots of: a) % dry mass remaining, b) relative C, N, and P and c) absolute C, N, and P in red mangrove leaves over the course of the 361-day litterbag experiment. Bars indicate standard deviation of three replicates.

Fig. 5. Molar ratios of C:N (top) and N:P (bottom) in red mangrove leaves over the course of the 361-day litterbag experiment. Bars indicate standard deviations of three replicates.

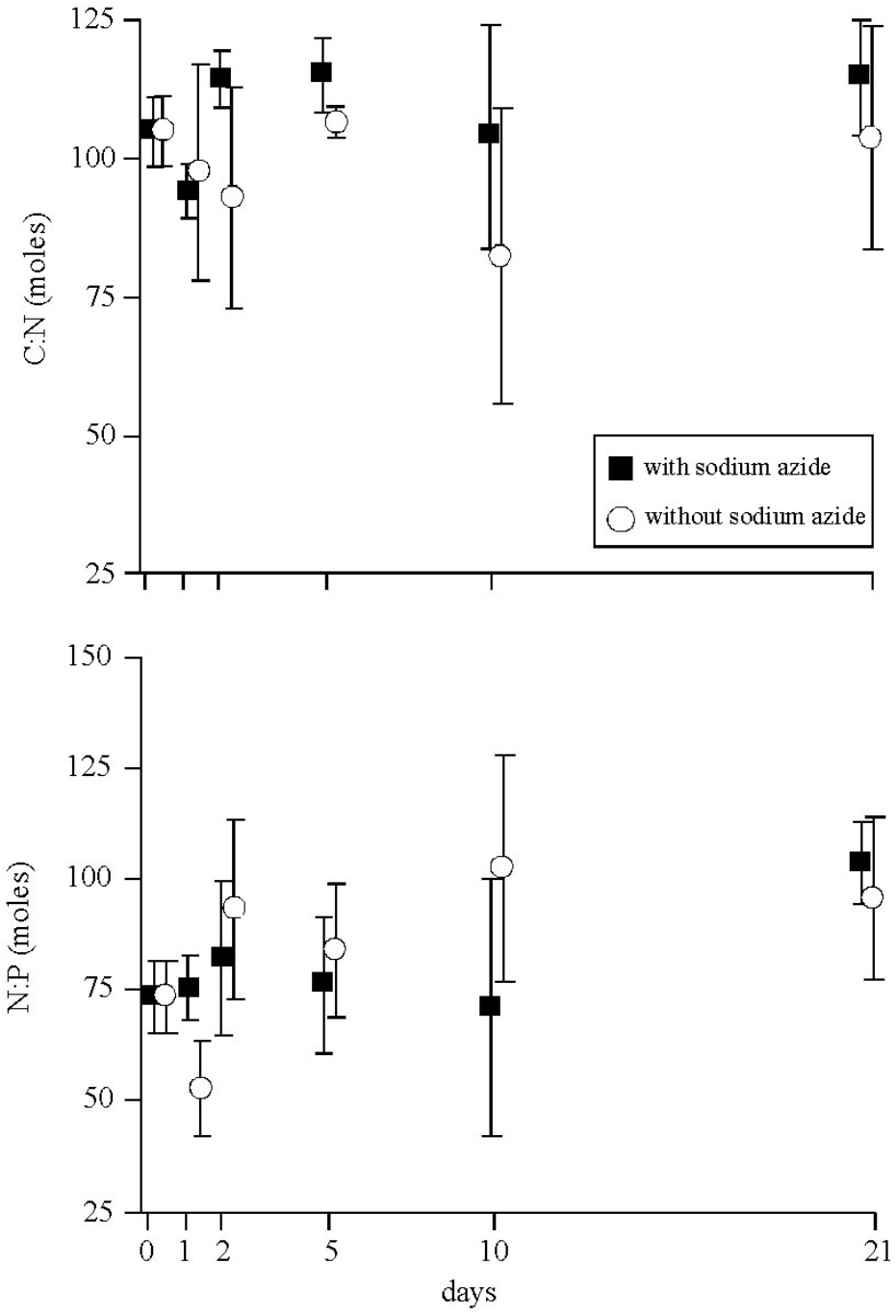
Fig. 6. Regression of % change in litter N content versus time for a number of decomposing estuarine macrophytes (5 species of mangrove and 2 species of cordgrass). Tabular data and reference for each decomposition study are provided in Table 2. Data from this study indicated with open circles.


Everglades National Park
N
Taylor
Slough
Florida
Florida Bay
Atlantic
Ocean
10 km
25.0
81.0
80.5

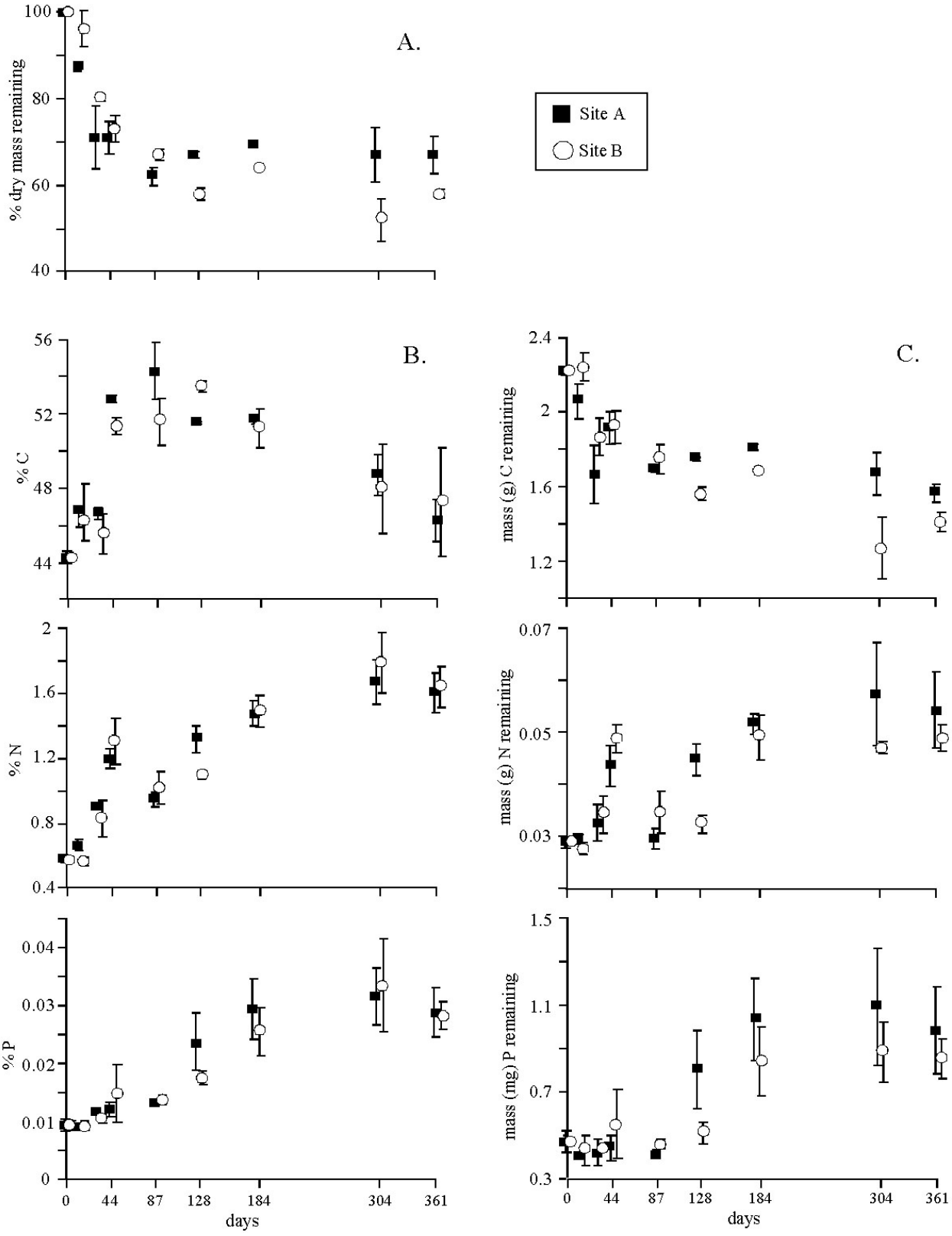
1


A.
B.
C.
% dry mass remaining
% C
% N
% P
mass (g) C remaining
mass (mg) N remaining
mass (mg) P remaining
with sodium azide
without sodium azide
days
days

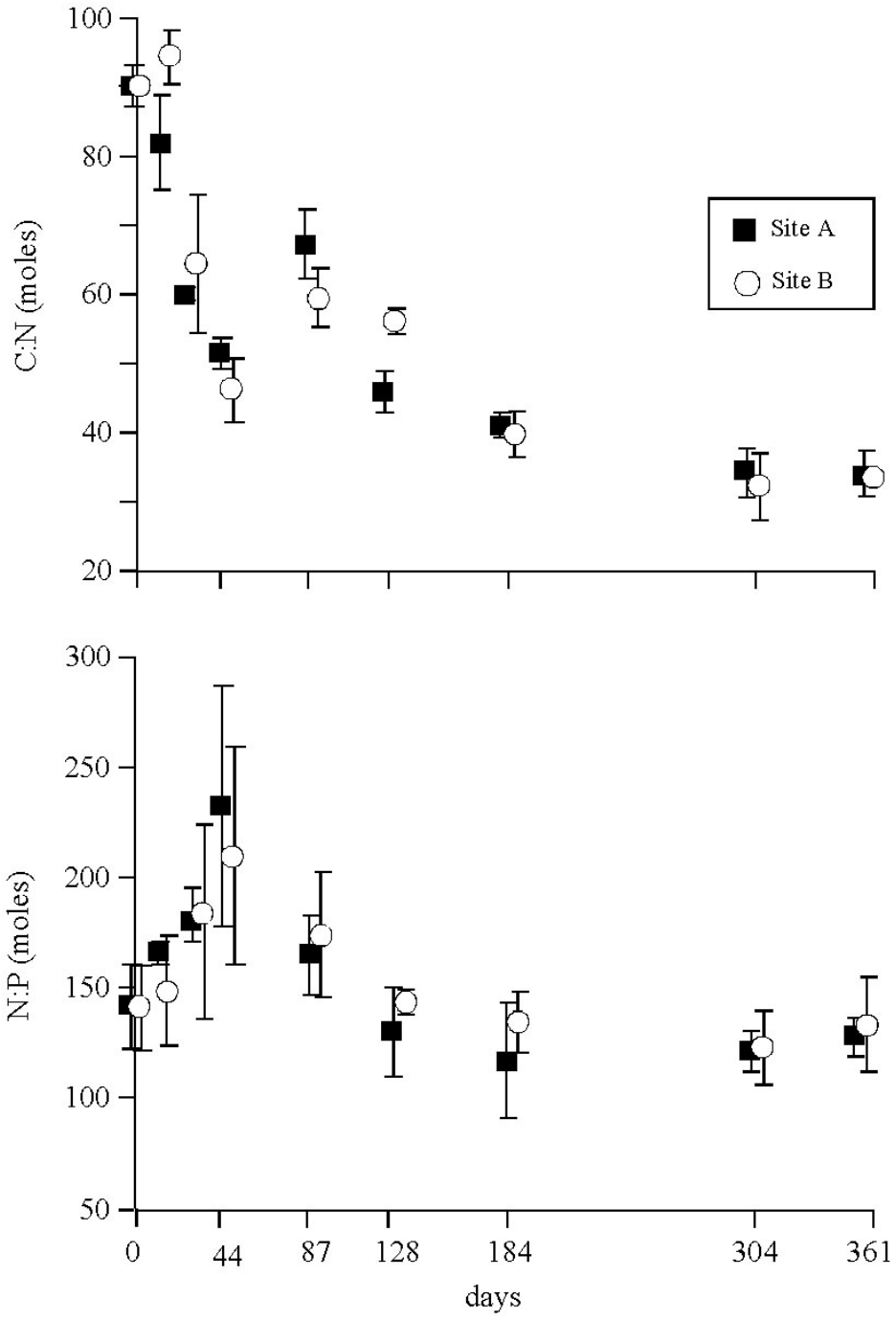
1


C:N (moles)
125
100
75
50
25
with sodium azide
without sodium azide
N:P (moles)
150
125
100
75
50
25
0
1
2
5
10
21
days

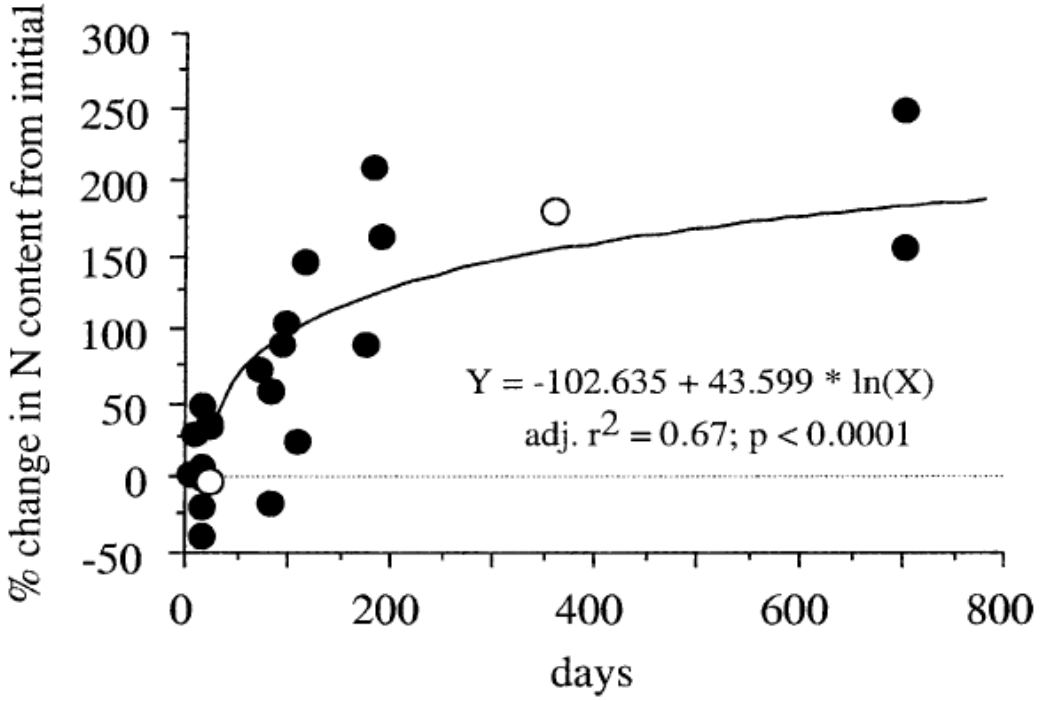
1


A.
B.
C.
Site A
Site B
% dry mass remaining
% C
% N
% P
mass (g) C remaining
mass (g) N remaining
mass (mg) P remaining
days
0
44
87
128
184
304
361

1


C:N (moles)
100
80
60
40
20
Site A
Site B
N:P (moles)
300
250
200
150
100
50
0
44
87
128
184
304
361
days

1


% change in N content from initial
300
250
200
150
100
50
0
-50
0
200
400
600
800
days
Y = -102.635 + 43.599 * ln(X)
adj. r2 = 0.67; p < 0.0001

1