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CHANGES IN NUTRIENT CONTENT AND STABLE ISOTOPE RATIOS OF C AND N DURING DECOMPOSITION OF SEAGRASSES AND MANGROVE LEAVES ALONG A NUTRIENT AVAILABILITY GRADIENT IN FLORIDA BAY, USA

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The decomposition of the mangrove *Rhizophora mangle* and the seagrass *Thalassia testudinum* was examined using litterbags along a natural gradient in nutrient availability. Seagrass leaves had a higher fraction of their biomass in the labile pool (57%), compared to mangrove leaves (36%) and seagrass rhizomes (29%); the overall decomposition rates of the starting material reflected the fractionation into labile and refractory components. There was no relationship between the N or P content of the starting material and the decomposition rate.

Nutrient availability had no influence on decomposition rate, and mass was lost at the same rate from litterbags that were buried in the sediment and litterbags that were left on the sediment surface. The dynamics of N and P content during decomposition varied as a function of starting material and burial state. N content of decomposing mangrove leaves increased, but seagrass rhizomes decreased in N content during decomposition while there was no change in seagrass leaf N content. These same general patterns held for P content, but buried seagrass leaves increased in P content while surficial leaves decreased. $\delta^{13}C$ and $\delta^{15}N$ changed by as much as 2‰ during decomposition.

Keywords: Detritus; Decomposition; Stable carbon isotopes; Stable nitrogen isotopes; Stoichiometry

1 INTRODUCTION

Two of the most conspicuous primary producers in coastal marine environments in the Caribbean and tropical Atlantic Ocean are the seagrass *Thalassia testudinum* and the mangrove *Rhizophora mangle*. While the importance of direct grazing on these plants is receiving renewed attention (*e.g.* Valentine and Heck, 1999; Feller, 2002), it is thought that the majority of the energy flow from these plants to higher trophic levels occurs via a detrital pathway. Factors that control the decomposition of seagrass and mangrove detritus, therefore, will also control the rate at which the primary production of these vascular plants can be utilized by consumers.

Decomposition of plant biomass is dependent on the elemental composition of the biomass (Enriquez *et al.*, 1993) as well as environmental factors like temperature, water availability,

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oxygen availability, and nutrient availability. In tropical oligotrophic marine environments, low temperatures and water availability are not likely to limit decomposition, so the availability of oxygen and nutrients are likely to play important roles. Decomposition of mangrove leaves is 10–30 times faster in the presence of oxygen compared to anoxic conditions (Benner and Hodson, 1985). In very oligotrophic environments, it may be possible that decomposition rates can be limited by nutrient availability. The activity of heterotrophic bacteria, the primary decomposers of plant detritus in the ocean, can be enhanced by the addition of nutrients (López *et al.*, 1998). In fact, it has been suggested that peat formation in the oligotrophic Everglades marshes is a consequence of low rates of microbial respiration of macrophyte detritus caused by severe phosphorus limitation (Amador and Jones, 1993).

During decomposition, vascular plant detritus is metabolized by microorganisms. During this process, carbon is lost from the biomass through respiration of the microbes, but the dynamics of nitrogen and phosphorus are more complicated and may be controlled by the initial composition of the plant material. Microbial assimilation of nutrients from the environment is thought to be a necessity for the decomposition of plant material of low initial nutrient, especially nitrogen, content (Goldman *et al.*, 1987). Because of the loss of carbon during respiration and the accumulation of nutrients by the microbes associated with decomposition, the elemental ratios of the detritus may change through time. Some materials that are particularly low in nitrogen and phosphorus content when they are deposited can actually serve as a net sink of nutrients to the ecosystem for at least part of their decomposition as a consequence of microbial assimilation and inorganic accumulation of nitrogen and phosphorus. Twilley *et al.* (1986) found that leaves of *Rhizophora mangle* sequestered N from the environment during the first 6 months of decomposition, while *Avicennia germinans* leaves lost N to the environment. Decomposing mangrove leaves have also been observed to accumulate P as a consequence of sorption of phosphate onto iron oxyhydroxides (Nielsen and Andersen, 2003). Wood deposited in mangrove forests can accumulate N during the first year of decomposition (Romero *et al.*, in press).

Different primary producers can have characteristic signatures of stable isotopic composition of carbon and nitrogen. Seagrass and mangrove biomass can be readily differentiated isotopically, because seagrasses tend to be relatively enriched in ^{13}C compared to mangroves. Stable isotope ratios can be used to trace the flow of elements from different sources in ecosystems (Peterson *et al.*, 1985; Peterson and Fry, 1987), but there is some evidence that there may be changes in the carbon and nitrogen isotopic composition of seagrasses and mangroves during decomposition (Zieman *et al.*, 1984). Changes in carbon isotopic composition may result from the comparative resistance of lignin, which is depleted in ^{13}C compared to more readily metabolized compounds, to decay (Benner *et al.*, 1987). Changes in nitrogen isotopic composition are thought to arise from assimilation of DIN by the bacterial community during decomposition (Caraco *et al.*, 1998), and the magnitude and direction of the $\delta^{15}N$ changes during decomposition are dependent on the nature of the microbial community (Lehmann *et al.*, 2002) and the isotopic composition of the DIN (Caraco *et al.*, 1998). The nature of such changes in stable isotopic composition during decomposition must be understood to apply stable isotope signatures to food web analysis or paleoecological reconstructions.

In this study, we investigated the differences in decomposition rates of *Rhizophora mangle* leaves and the leaves and rhizomes of *Thalassia testudinum*. Owing to large differences in the initial elemental and biochemical composition of these plant parts, we expected that green leaves of *T. testudinum*, with relatively high N and P content, would decompose more rapidly than either seagrass rhizomes or mangrove leaves, which have a lower nutrient content. We also investigated the effect of burial on decomposition rate, and expected material in litter bags deployed on the surface of the sediment to decompose faster than buried bags because

of differences in oxygen availability. Further, we tested whether the availability of nutrients in the environment had an influence on decomposition rate by conducting decomposition experiments at five sites along a strong nutrient availability gradient. We also wanted to define whether decomposing seagrass and mangroves were sources or sinks of nutrients to their environment. Finally, we wanted to document the diagenetic changes in stable N and C composition that occurs during decomposition of freshly-deposited macrophyte detritus to help in interpreting patterns in isotope ratios in the food web and in paleoecological records in sediment cores from this ecosystem.

2 METHODS

2.1 Site Selection

Florida Bay is a shallow, subtropical estuary at the southern tip of the Florida peninsula (Fig. 1). The bottom of the bay is carpeted with seagrass beds, which for the most part are dominated by *Thalassia testudinum* (see Fourqurean and Robblee, 1999 for general description of the estuary). The margin of the Bay, as well as the myriad small islands within the bay, are lined with mangrove forests, which are dominated by *Rhizophora mangle*. There is a strong gradient in nutrient availability across the estuary, with relatively high N and P availability along the western mouth of the estuary compared to the strongly P-limited nature of the eastern portions of the Bay (Fourqurean *et al.*, 1992a). We conducted our decomposition experiments at 5 sites within the Bay (Fig. 1). These 5 sites are focal sites for the Florida Coastal Everglades Long Term Ecological Research program. The sites differed in salinity characteristics, as well as water colunm N and P concentrations (Tab. I). Differences in

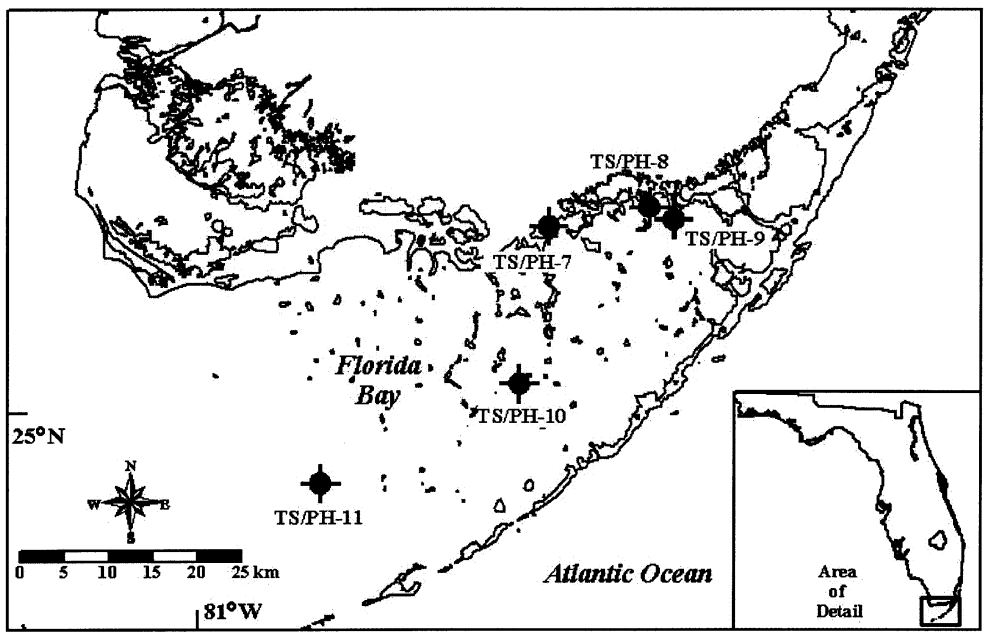

FIGURE 1 Map of study area. Symbols indicate location of litter bag decomposition experiments. Station locations: TS/PH-7, 25°11.445′N, 80°38.347′W; TS/PH-8, 25°13.963′N, 80°31.471′W;TS/PH-9, 25°10.735′N, 80°29.383′W; TS/PH-10, 25°01.484′N, 80°40.859′W; TS/PH-11, 24°54.771′N, 80°56.288′W.

TABLE I Site Characteristics.

	Site name				
	TS/PH-7	*TS/PH-8*	*TS/PH-9*	*TS/PH-10*	*TS/PH-11*
Water depth (m)	0.6–1.2	0.3–0.9	<0.2	1.2–1.5	0.9–1.5
Salinity mean (range) ‰	22.8 (8.9–37.4)	12.9 (0.4–3 8.6)	28.2 (19.7–37.9)	35.2 (26.8–43.2)	35.8 (29.5–37.05)
Mean water column TN (μM)	32.9	31.5	28.2	34.4	18.8
Mean water column TP (μM)	0.3	0.3	0.2	0.3	0.7
Dominant seagrass species	*Halodule wrightii* and *T. testudinum*	*Halodule wrightii* and *T. testudinum*	*T. testudinum*	*T. testudinum*	*Syringodium filforme* and *T. testudinum*
Local *Thalassia* nutrient content (C:N:P)	1419:66:1	891:44:1	1458:76:1	1444:84:1	634:31:1

Note: Water column salinity and nutrient characteristics of the decomposition sites for the period of the experiment (August 2001–July 2002) based on monthly determinations at each site.

nutrient availability to the benthic community at the sites was reflected in the C:N:P ratios in the dominant marine macrophytes at these sites.

2.2 Collection and Characterization of Starting Material

We used three different plant tissue types in this experiment: green leaves and living rhizomes of *Thalassia testudinum* and senescent (but still attached to the trees) yellow leaves of *Rhizophora mangle*. *Thalassia testudinum* plants were collected from two sites, Sunset Cove (25°05.4′ N, 80°27.0′ W) and Rabbit Key Basin (24°59.1′ N, 80°50.4′ W). Green leaves and living rhizomes were sorted from the plants, then thoroughly mixed to provide a homogeneous pool of each tissue type. Yellow mangrove leaves were collected from four locations [Sunset Cove, Little Blackwater Sound (25°13.1′ N, 80°25.8′ W), Peterson Keys (24°55.0′ N, 80°44.7′ W) and the mouth of the Taylor River (25°11.5′ N, 80 38.3′ W)]. All yellow leaves were placed in a large container and thoroughly mixed to produce a homogenous pool of leaves.

For initial characterization of the tissue types, 10 samples of each tissue type were collected from the homogenized pools (ca. 80 g wet weight for *Thalassia testudinum* leaves, ca. 35 g for *T. testudinum* rhizomes and *Rhizophora mangle* leaves). These samples were lyophilized and weighed to yield a wet weight/dry weight conversion factor for each tissue type, and then analyzed for elemental and isotopic content as described below.

2.3 Litter Bag Design, Deployment and Collection

Litter bags (15 cm × 15 cm) were sewn from 1 mm mesh, plastic-coated fiberglass window screen material. Aliquots of each tissue type were weighed and sealed in separate bags (nominal wet weights of ca. 80 g wet weight for *Thalassia testudinum* leaves, or 35 g for *T. testudinum* rhizomes and *Rhizophora mangle* leaves). In addition to the plant material, each bag contained a stamped plastic label that served as a permanent identification marker. By applying the appropriate wet weight to dry weight conversion, the initial dry weight for each aliquot was determined.

At each of the five sites, 21 litter bags of each tissue type were deployed both underwater at the sediment surface and buried ca. 20 cm deep in the sediment on August 6, 2001. Litter bags were collected on 10 August, 24 August, 6 October, 17 November 2001, 25 February and 20 July 2002. Our target was to collect 3 bags of each tissue type from buried and surface locations at all 5 sites at each collection period, but we occasionally lost bags. In all instances, there were at least duplicate collections. The litter bags were transported on ice back to the laboratory for cleaning.

2.4 Sample Collection, Cleaning and Sorting

The outsides of the litterbags were thoroughly rinsed, and the contents of the bags were collected over a 1 mm mesh. Sediment adhering to the decomposing plant tissues was gently rinsed away, but it was not possible to remove all of this carbonate material. Any macroinvertebrates in the bags were removed from the sample. Cleaned detritus from each litter bag was lyophilized. Dried leaves were weighed and then ground to a fine powder using a Wiley Mill and stored in sealed glass vials at $-4\,^{\circ}$C until elemental and isotopic analyses. In order to remove inorganic carbonates from the detritus samples, they were treated with fuming HCl before δ^{13}C analysis.

2.5 Elemental and Isotopic Analyses

Powdered samples were analyzed in duplicate for carbon and nitrogen content using a CHN analyzer (Fisons NA1500). Phosphorus content was determined by a dry-oxidation, acid hydrolysis extraction followed by a colorimetric analysis of phosphate concentration of the extract (Fourqurean *et al.*, 1992b). Elemental content was calculated on a dry weight basis (*i.e.* mass of element/dry weight of sample $\times$ 100%); elemental ratios were calculated on a mole:mole basis.

All isotopic analyses were measured at the SERC Stable Isotope Laboratory using standard elemental analyzer isotope ratio mass spectrometer (EA-IRMS) procedures. The EA was used to combust the organic material and to reduce the formed gases into N_2 and CO_2, which were measured on a Finnigan MAT Delta C IRMS in a continuous flow mode. The samples' isotopic ratios (R) are reported in the standard delta notation (‰): $\delta(‰) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$. These results are presented with respect to the international standards of atmospheric nitrogen (AIR, N_2) and Vienna Pee Dee belemnite (V-PDB) for carbon. Analytical reproducibility of the reported δ values, based on sample replicates, was better than $\pm$0.2‰ for δ^{15}N and $\pm$0.08‰ for δ^{13}C.

2.6 Data Analysis

Decomposition rates were calculated by fitting a single-component exponential decay model to the time series data:

$$\frac{W_t}{W_0} = e^{-kt} \tag{1}$$

where W_0 = initial dry mass, W_t = mass remaining at time t, and k = the exponential decay constant. A two-component exponential decay model allowed us to better describe loss of mass through time. The two-component model is a summation of two of single component models. Relatively easily degraded compounds (labile substrate) such as sugars, starches, and proteins will be rapidly utilized by decomposers, while materials such as cellulose, fats,

waxes, tannins, and lignins are more recalcitrant and will be lost at relatively slower rates. This can be represented as:

$$\frac{W_t}{W_0} = \alpha e^{-k_1} + (1 - \alpha)e^{-k_2} \tag{2}$$

where W_0 = initial dry mass, W_t = mass remaining at time t, α = the labile portion of initial material (fast decay component), $1 - \alpha$ = the refractory portion of initial material (slow decay component), k_1 = decay constant for the labile component, and k_2 = decay constants for the refractory component.

To characterize the overall pattern of net mineralization or accumulation of C, N and P, we calculated the amount of each element remaining compared to the initial mass of that element at the beginning of the incubation:

$$X \text{ remaining}_t = \frac{W_t X_t}{W_0 X_0} \tag{3}$$

where X remaining$_t$ (%) = the fraction of element X remaining at time t compared to initial conditions, W_t = the dry weight of the sample at time t, X_t = the nutrient concentration in the sample at time t, W_0 = initial dry weight of the sample, and X_0 = the initial concentration of nutrient in the sample.

2.7 Statistical Analysis

Differences in decomposition rates among tissues types, burial status and sites were analyzed using a split-plot ANCOVA design, with SITE as a random effect and TISSUE type, and BURIAL status as fixed effects. TIME was the covariate and was calculated as the number of days since the beginning of the experiment. We were interested in testing whether the slopes through time were significantly influenced by SITE, TISSUE and BURIAL; hence the critical effects were the interaction terms in the ANCOVA that included TIME. We used the SITE as a proxy for nutrient availability, since the sites were located along a documented gradient of phosphorus availability in the Bay (Fourqurean *et al.*, 1992a; 1993).

3 RESULTS

There were large differences in the characteristics of the tissue types at the initiation of the experiments (Tab. II). Mangrove leaves had a lower water content and higher C content than the seagrass tissues. Seagrass leaves had the highest initial nutrient content, followed by seagrass rhizomes and mangrove leaves; however, the N:P ratio of the three tissue types were similar. The seagrass tissues had stable carbon isotope ratios more enriched than mangrove leaves, and it is interesting to note that the seagrass leaves were 2‰ more depleted in ^{13}C than seagrass rhizomes even though they came from the same plants.

3.1 Decomposition Rates

There were large differences in the decay rates of tissue types (ANCOVA, TIME × TISSUE effect, $F = 16.9$, d.f. = 2.8, $p = 0.001$), but there were no consistent differences in the decay rates among sites (TIME × TISSUE × SITE effect, $Z = 0.97$, $p = 0.17$) or burial condition (TIME × BURIAL effect, $F = 0.39$, d.f. = 1.4, $p = 0.57$). Leaves of *Thalassia testudinum*

TABLE II Characteristics of Starting Plant Material.

	Tissue type		
	Thalassia leaves	*Thalassia rhizomes*	*Rhizophora leaves*
Dry wt:wet wt	0.118 ± 0.003	0.144 ± 0.001	0.342 ± 0.035
C content (%of dry wt)	33.4 ± 0.4	32.0 ± 0.3	44.6 ± 0.5
N content (%of dry wt)	2.30 ± 0.03	1.39 ± 0.09	0.51 ± 0.07
P content (%of dry wt)	0.098 ± 0.003	0.055 ± 0.007	0.018 ± 0.001
C:N:P	883:52:1	1503:56:1	6209:61:1
δ^{13}C (‰)	-10.7 ± 0.2	-8.6 ± 0.1	-28.7 ± 1.4
δ^{15}N (‰)	6.0 ± 0.3	4.8 ± 0.2	5.5 ± 0.5

Note: Values are means $\pm$ 1 SE, $n = 10$. C:N:P is expressed as mol:mol:mol.

decomposed at a faster rate ($k = 0.017\ d^{-1}$) than either *T. testudinum* rhizomes ($k = 0.003\ d^{-1}$) or *Rhizophora mangle* leaves ($k = 0.006\ d^{-1}$, Fig. 2). After 348 days of decomposition, $5\% \pm 2\%$ ($\pm$1 SE) of the original mass of *T. testudinum* leaves remained in the litter bags, compared to $49\% \pm 6\%$ of rhizomes and $22\% \pm 2\%$ of *R. mangle* leaves.

The pattern in the residuals (Fig. 2) suggested that the single-component exponential decay model (Eq. 1) was not adequate to describe the initial rapid mass loss of these three tissue types, so we fit the two-component model (Eq. 2) to the data pooled by species across sites and burial conditions (Tab. III). The two-component decay model yielded a more accurate representation of the mass remaining (Fig. 2). *Thalassia testudinum* leaves had a higher proportion of initial mass in the labile pool ($57\% \pm 7\%$) than seagrass rhizomes ($29\% \pm 6\%$) or *Rhizophora mangle* leaves ($36\% \pm 3\%$). The decay rates of the labile pool (k_1) of seagrass and mangrove leaves were similar and higher than the rate for the labile fraction of seagrass rhizomes (Tab. III), while the refractory component of seagrass leaves decomposed faster than either seagrass rhizomes or mangrove leaves.

3.2 Changes in Nutrient Concentrations During Decomposition

The carbon, nitrogen and phosphorus concentrations in the decomposing plant material changed through time, and the patterns of change were dependent on both the starting tissue type and the burial condition (Fig. 3). Initial C content of *Rhizophora mangle* leaves (44.6% of dry weight) was higher than either leaves (33.4%) or rhizomes (32.0%) of *Thalassia testudinum* (Tab. II). The dynamics of C content during decomposition were different among tissue types (ANCOVA, TIME $\times$ TISSUE effect, $F = 8.9$, d.f. $= 2.8$, $p = 0.009$) as well as between burial condition (TIME $\times$ BURIAL effect, $F = 23.68$, d.f. $= 1.4$, $p = 0.008$). Furthermore, the relationship between the time course of C content between buried and surface conditions varied among tissue type (TIME $\times$ TISSUE $\times$ BURIAL effect, $F = 6.36$, d.f. $= 2.8$, $p = 0.022$). However, there was no effect of site on the changes in C content (TIME $\times$ TISSUE $\times$ SITE effect, $Z = 0.80$, $p = 0.21$). Carbon content of *T. testudinum* leaves initially increased in both buried and surface incubations, but after the first few weeks, C content decreased, with a faster decrease in the surficial incubations. In contrast, there was little change in C content of *T. testudinum* rhizomes in either surface of buried bags. There was a marked divergence of C content of *R. mangle* leaves between surface and buried incubations. Buried mangrove leaves continued to increase in C content throughout the incubation, but the C content in surficial incubations began to decline after the first 2 months of incubation.

At the beginning of the incubations, both *Thalassia testudinum* tissues had much higher N content than *Rhizophora mangle* leaves (Tab. II). Nitrogen content changes during decomposition were different among tissue types and burial conditions (ANCOVA, TIME $\times$ TISSUE $\times$ BURIAL effect, $F = 6.3$, d.f. $= 2.8$, $p = 0.023$). There was no influence of the site of incubation

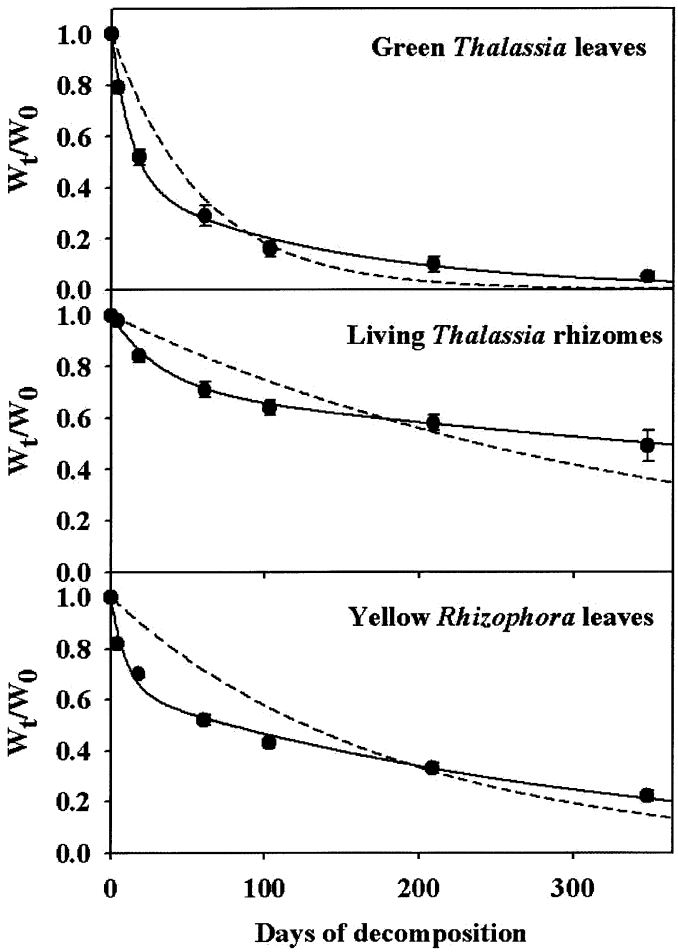

FIGURE 2 Mass loss as a function of tissue type. Symbols represent the mean ± 1 SE ($n = 20$) of all bags collected from all sites, both on the surface of the sediment and buried. Dashed line is the best fit of the single-component decay model (Eq. (1)); solid line is the best fit of the two-component decay model (Eq. (2)). Values of the model parameters and goodness-of-fit statistics are in Table III.

on N dynamics. There was an initial drop in N content of *T. testudinum* leaves, followed by a slow increase in N content in buried bags but no further change in surficial bags (Fig. 3). Buried and surficial seagrass rhizomes behaved similarly, with a rapid initial loss of N content followed by no net change after the first month of incubation. In contrast, leaves of *R. mangle* slowly accumulated N in both buried and surficial incubations.

TABLE III Values of Decomposition Model Parameters, See Text for Description of Models and Details of the Methods Used to Obtain the Estimates.

	Single-component model		*Two-component model*			
	k (d^{-1}, ±1SE)	R^2	α	k_1 (d^{-1}, ±1SE)	k_2 (d^{-1}, ±1SE)	R^2
Thalassia leaves	0.017 ± 0.001	0.51	0.57 ± 0.07	0.082 ± 0.017	0.007 ± 0.002	0.81
Thalassia rhizomes	0.0032 ± 0.0002	0.31	0.29 ± 0.06	0.033 ± 0.014	0.0012 ± 0.0004	0.59
Rhizophora leaves	0.0064 ± 0.0002	0.53	0.36 ± 0.03	0.104 ± 0.019	0.0031 ± 0.0002	0.84

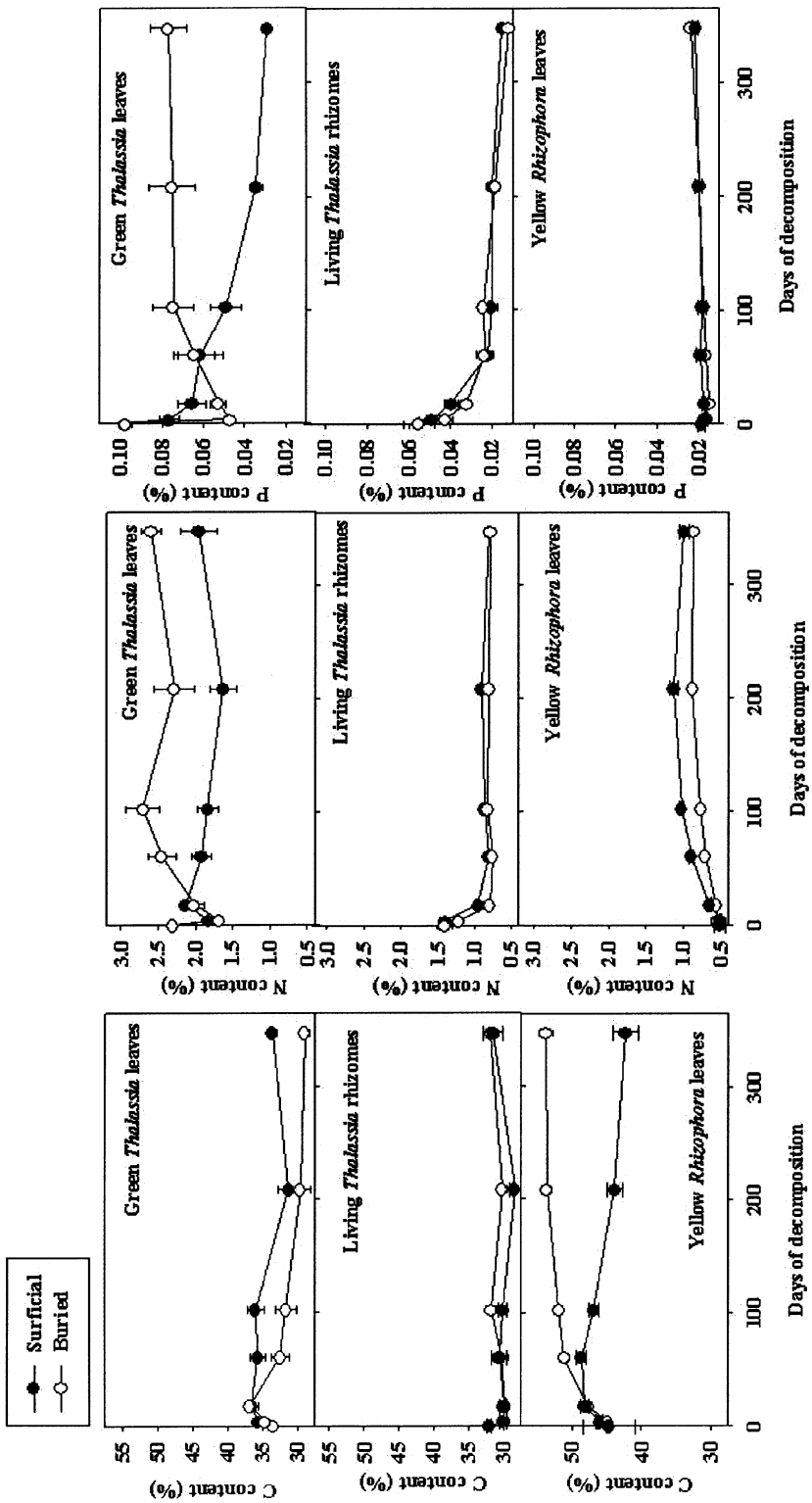

FIGURE 3 Change in carbon, nitrogen and phosphorus content of detritus as a function of initial composition and burial status. Symbols are the means of all samples from all sites at a time period, error bars are ±1 SE. Elemental contents are expressed as % of the dry weight of a sample.

Phosphorus dynamics during decomposition were similar to the patterns observed for nitrogen (Fig. 3). There were no effects of the site on P dynamics, but there were different patterns of P content during decomposition among tissue types (ANCOVA, TIME × TISSUE effect, $F = 32.5$, d.f. $= 2.8$, $p < 0.001$) and between burial condition (TIME × BURIAL effect, $F = 23.0$, d.f. $= 1.4$, $p = 0.009$). In buried *Thalassia testudinum* leaves, there was an initial loss of over 50% of the P content in the first week of the incubation, but subsequently P content increased until it reached about 75% of the initial content. In contrast, P content continued to decrease in the surficial incubations throughout the incubation. Buried and surficial incubations of *T. testudinum* rhizomes followed a similar pattern on exponential decay of P content through the incubation. There was little change in P content of either surficial or buried *Rhizophora mangle* leaves.

Differential loss rates of elements led to some marked changes in the ratios of elements through decomposition (Fig. 4). There was an initial rapid increase in the C:N of seagrass leaves, likely as a result of cell death and lysing of the green leaves. The C:N of buried seagrass leaves rapidly declined to roughly the value of the starting material, while the detritus in the surficial incubation had consistently higher C:N than the buried leaves. In contrast, the C:N of seagrass rhizome material increased during the first month of incubation, with little change after the first month. C:N of the mangrove leaves decreased steadily towards an asymptote of ca. 75 in buried incubations, compared to ca. 55 in surficial incubations. The C:P dynamics of detritus was different than the C:N dynamics. C:P of surficial seagrass leaf detritus increased through the study period, but there was little net change in buried seagrass leaves. C:P of seagrass rhizomes increased linearly through the incubations. Mangrove leaf detritus showed an initial rapid loss of P compared to C, followed by a slow decrease of C:P for the remainder of the incubation. The markedly different pattern in C:N and C:P during the incubation of seagrass leaf detritus led to a divergence in N:P of seagrass detritus depending on whether the detritus was buried or not. N:P of surficial samples continued to increase through the experiment. N:P of seagrass rhizome detritus also increased through the experiment. In contrast, initial increases in N:P of mangrove leaf detritus stopped after about 100 days of incubation.

3.3 Nutrient Accumulation/Loss During Decomposition

None of the tissue types accumulated C, N or P during decomposition (Fig. 5), despite the fact that in some instances the nutrient content of the remaining detritus increased during the incubation (Fig. 3). The rate of loss of C, N and P was influenced by tissue type and by burial status, but not by location (ANCOVA). *Thalassia testudinum* leaves lost C, N and P faster in the buried incubations compared to sediment surface incubations, while there was no difference between the elemental loss rates of buried and surficial *T. testudinum* rhizomes. After 1 year of incubation, there was about 3× as much remaining C in decomposing rhizomes compared to the leaves of *T. testudinum*. Mangrove leaves were intermediate between the two seagrass tissues in the amount of C remaining. Nitrogen loss generally followed C loss for seagrass tissues, but mangrove leaf detritus lost N at a slower rate than it lost carbon (Fig. 5) because of the marked increase in N content of the remaining detritus over the course of the incubation (Fig. 3). Phosphorus loss was similar to C loss for both seagrass leaves, but *T. testudinum* rhizomes lost P faster than C (Fig. 5) owing to the rapid decrease in the P content of the remaining material (Fig. 3).

3.4 Changes in Isotope Ratios During Decomposition

Throughout the experiments, small changes in the C stable isotope content of the decomposing plant materials did not obscure the initial differences in $\delta^{13}C$ of the starting materials (Fig. 6).

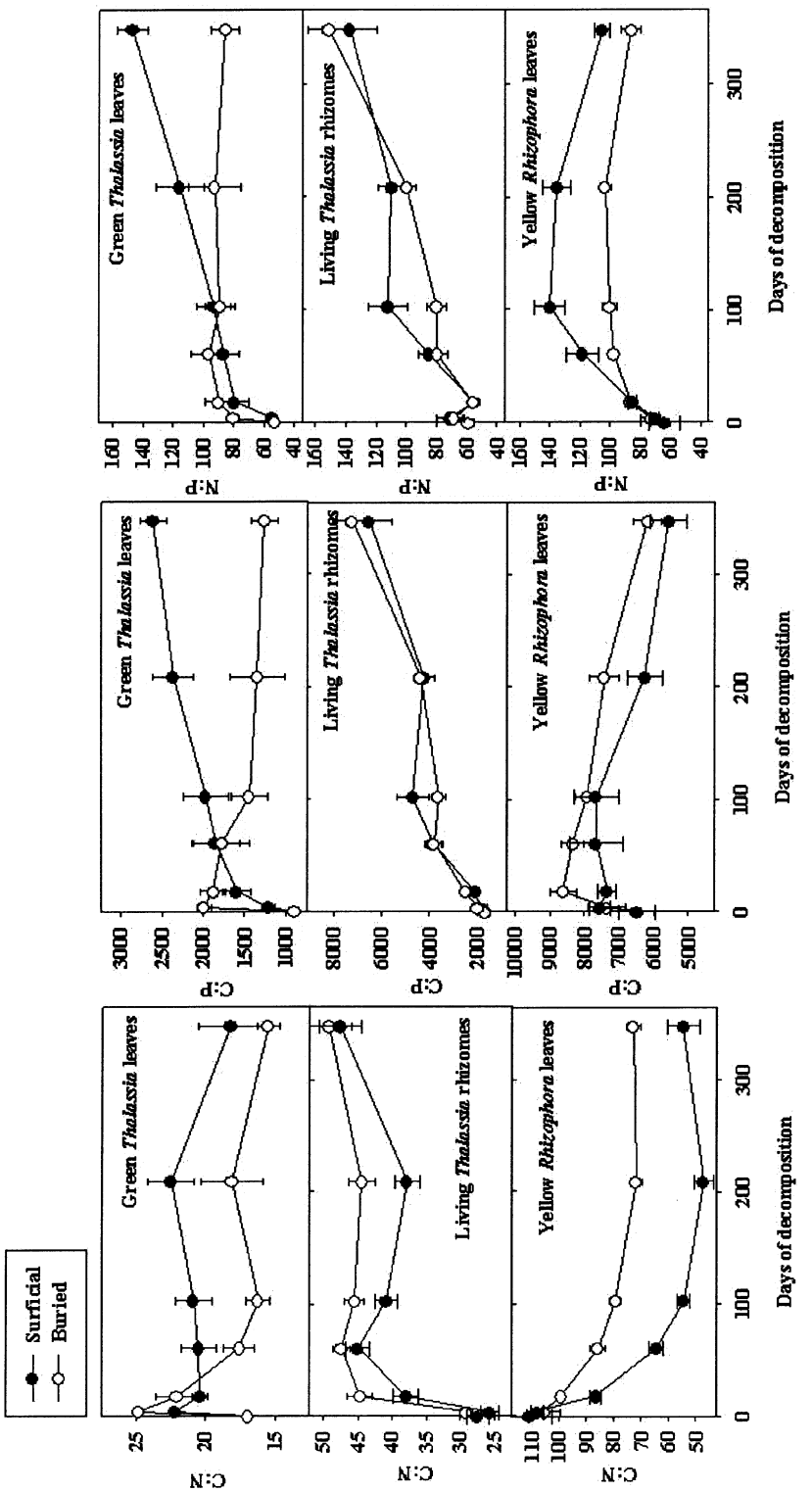

FIGURE 4 Change in elemental ratios (mol:mol) of Carbon, Nitrogen and Phosphorus of detritus as a function of initial composition and burial status. Symbols are the means of all samples from all sites at a time period, error bars are ± 1 SE.

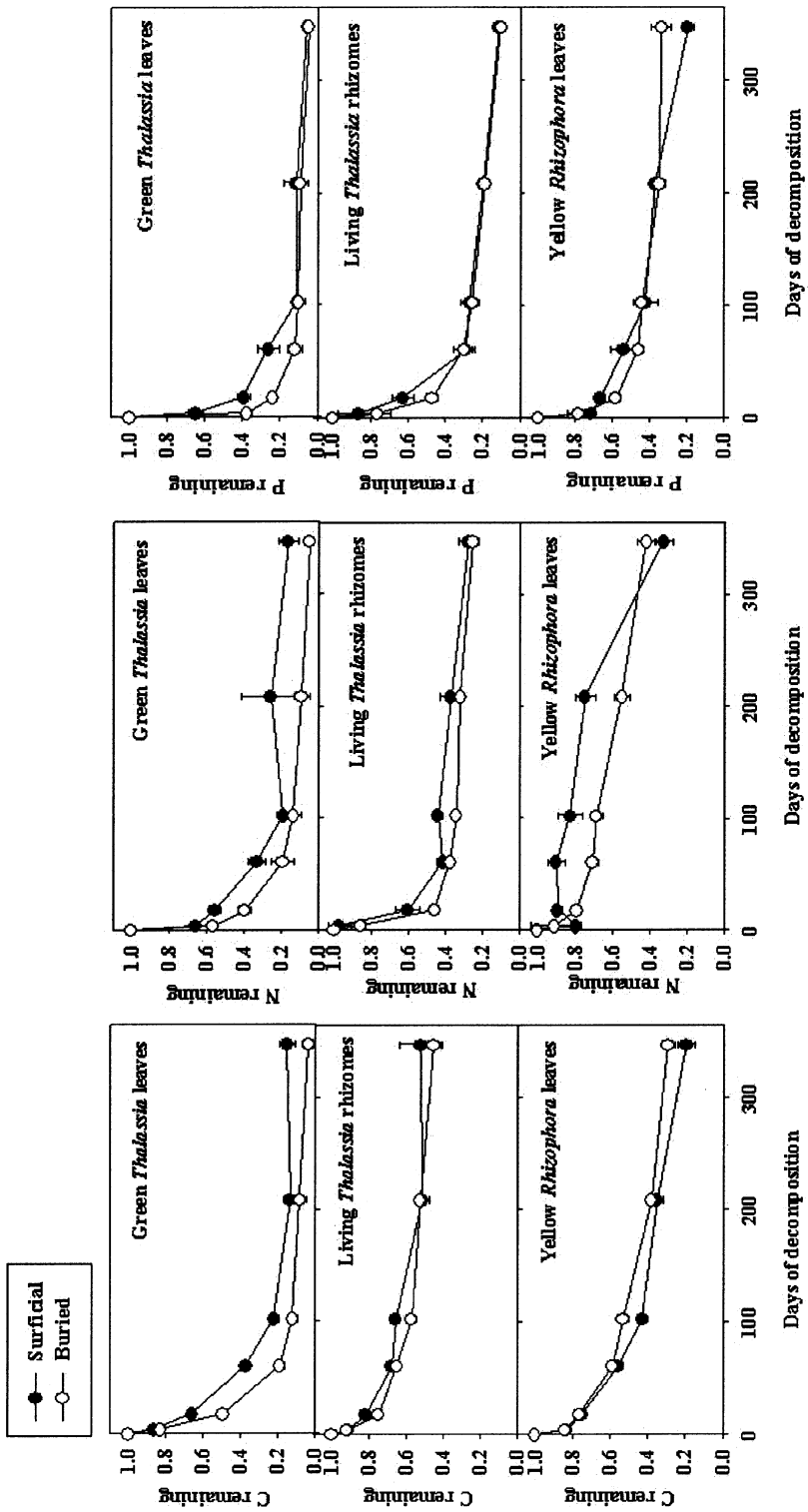

FIGURE 5 Change in the fraction remaining of carbon, nitrogen and phosphorus of detritus (see Eq. (3)) as a function of initial composition and burial status. Symbols are the means of all samples from all sites at a time period, error bars are ±1 SE.

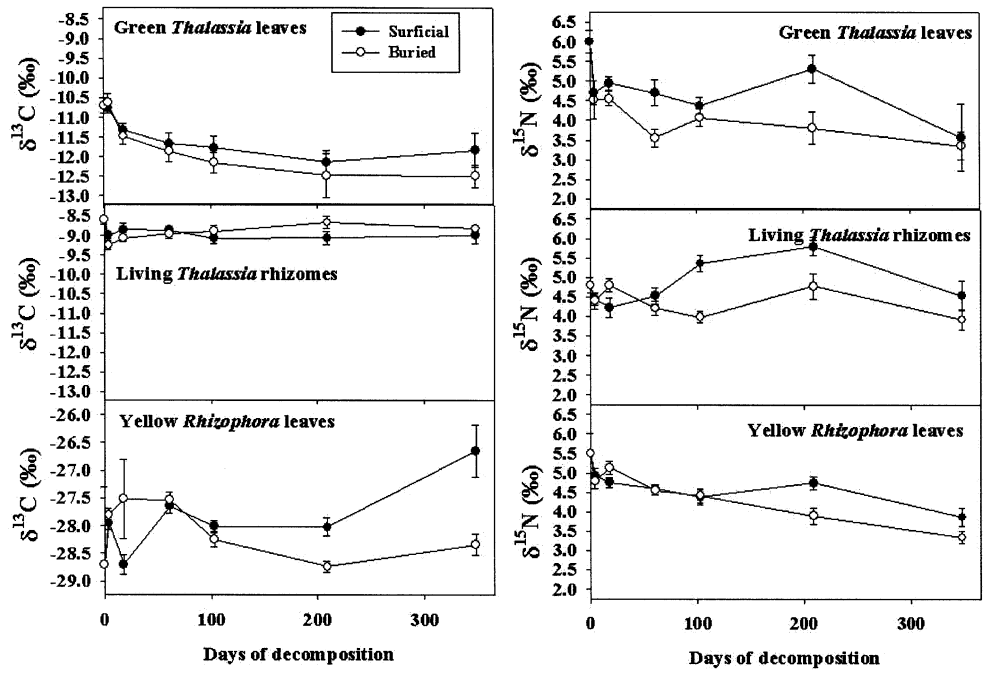

FIGURE 6 Change in stable isotopic ratios of carbon and nitrogen of detritus as a function of initial composition and burial status. Symbols are the means of all samples from all sites at a time period, error bars are ±1 SE.

Seagrass rhizome detritus changed little over the year, and there were no differences observed as a result of burial status. In contrast, there was a significant and steady decline in $\delta^{13}C$ of seagrasses during decomposition, so that over the course of the 1 year incubation the detritus became depleted in ^{13}C by ca. 2‰. Changes in the $\delta^{13}C$ of mangrove leaves were pronounced, and there was a difference in surficial and buried treatments. Surficial mangrove leaves became more enriched in the ^{13}C over the 1 year, with a change of ca. 2‰. Initial increases during the first week of incubation of the $\delta^{13}C$ of buried mangrove leaves were offset by a slow decrease for the remainder of the experiment. The patterns in stable N isotope ratios through time were more complicated than for stable C isotopes (Fig. 6). In general, detritus became depleted of ^{15}N during decomposition. *Thalassia testudinum* leaves showed an initial loss of ^{15}N, with a decrease in $\delta^{15}N$ of over 2‰ in the first week of decomposition followed by a slower decline thereafter. There was comparatively little change in the $\delta^{15}N$ of seagrass rhizomes compared to the leaves. Mangrove leaves exhibited a steady decline in $\delta^{15}N$ over the experiment, with 1 yr old detritus ca. 2‰ lighter than the initial material.

4 DISCUSSION

The rates of mass loss and the dynamics of the elemental and stable isotopic composition of decomposing macrophyte biomass composition were all dependent on the characteristics of the materials at the beginning of the decomposition as well as their burial state, but there were no differences attributable to the location of the decomposition sites along the nutrient availability gradient in Florida Bay. Differences in decay rate among the different plant tissues could only partly be explained by the quality of the material as measured by the nutrient

content of the tissues, indicating that other physical or biochemical properties of the materials are important in determining their decay rates. Decomposing seagrass leaves and rhizomes and mangrove leaves lost C faster than they lost N or P, but they were a net source of N and P to the ecosystem for the first year of their decomposition.

Mass loss rates of seagrass and mangrove leaves determined in this study were in the ranges reported in the literature. Seagrass leaf decomposition rates (Tab. III) were within the range of 0.001–0.110 d^{-1} reported in the literature (Enriquez *et al*., 1993; Harrison, 1989). Data on decomposition rates of seagrass rhizomes are few, but it is clear that rhizomes decompose more slowly than leaves. In fact, Holmer *et al.* (2002) did not find any measurable weight loss of rhizomes of the seagrass *Enhalus acoroides* in a 6 week decomposition experiment. Rhizomes of the temperate species *Zostera marina* have reported decay rates of 0.004–0.008 d^{-1}; while rhizomes of *Thalassia testudinum* have been measured to decay at a rate of 0.0007–0.001 d^{-1} in Florida Bay (Kenworthy and Thayer, 1984). We found that rhizomes decayed substantially faster than this previous report (Tab. III); however the decay rate of the more refractory components of the rhizomes (k_2) were similar to the previous report. Mangrove leaf decomposition rates were within the reported range of 0.001–0.063 d^{-1} (Robertson *et al.*, 1992). There was no significant simple correlation between the initial nutrient content of these three tissue types (Tab. II) and the decomposition rates.

The two component exponential decay model fit the mass loss data much better than the single component decay model, indicating that there were two distinct modes of mass loss from the detritus samples: an initial rapid loss followed by a slower decomposition rate. The initial rapid decomposition could be due to initial abiotic leaching of freshly dead material (Davis *et al.*, 2003) or to the rapid metabolism of labile compounds such as proteins and simple sugars by bacteria. Whatever the mechanisms, about 57% of the initial dry mass of seagrass leaves had a half-life of only 8.5 days, 36% of mangrove leaves had a half life of 6.7 days, and 29% of seagrass rhizomes had a half life of 21.0 days (Tab. III). Our estimation of the amount of mangrove leaf material in the labile pool made by fitting the two component decomposition model to our weight loss data is quite close to the 33% loss in weight via abiotic leaching alone measured by Davis *et al.* (2003). The remaining more refractory material of all three tissue types had much longer half-lives (99–693 days). It is interesting that neither the amount of material in the labile fraction (α) or the decay rate of the labile fraction (k_1) were significantly correlated with the initial N or P content of the detritus. Seagrass rhizomes had a higher nutrient content than the mangrove leaves, but a slower decay rate and a smaller labile fraction.

Beneath the rhizosphere in Florida Bay sediment deposits, the sediments contain ca. 2–4% organic matter and the stable carbon isotopic signature of this residual organic matter suggests a seagrass origin for much of the organic matter (Orem *et al.*, 1999). However, care must be taken when interpreting small variations in the isotopic signature of organic matter in such sediments. Differential decay rates of seagrass tissues suggest that more of the seagrass rhizome material that is deposited is preserved in sediments than leaf material. Differences in production of these tissues obscure this simple relationship, because seagrass leaf production is ca. 5 times the rhizome production (Bittaker and Iverson, 1976; Kenworthy and Thayer, 1984). Further, the 2‰ difference in the $\delta^{13}C$ of seagrass leaves and rhizomes measured in this study implies that small differences in the relative deposition rate of seagrass leaves and rhizomes could lead to variability on the isotopic content of the organic matter in the sediment. Given that there was no diagenetic change in $\delta^{13}C$ of seagrass rhizome detritus in our experiments and a decrease of ca. 2‰ in $\delta^{13}C$ of seagrass leaves during decomposition (Fig. 6), organic matter in sediments below seagrass beds should be expected to be up to 2‰ more enriched in ^{13}C than the seagrass leaves in the area if most of the residual organic matter in the sediments had a seagrass rhizome origin rather than an origin as more rapidly

decomposing seagrass leaves, or up to 2‰ more depleted in ^{13}C if more rapidly produced seagrass leaves contributed the most to the residual organic matter. In Florida Bay, Orem *et al.* (1999) found that the fine sediment fraction of the organic matter in sediments below living seagrass beds was ca. 5‰ lighter than the $\delta^{13}C$ of living seagrasses at the top of the core, perhaps partially as a result of the isotopic depletion we observed during seagrass leaf decomposition (Fig. 6).

There were no significant effects of burial status on mass loss rate, despite the facts that the sediments in Florida Bay are largely anoxic and decay rates of macrophytes are generally an order of magnitude slower in anoxic conditions (*e.g.* Benner and Hodson, 1985). This may be a result of the warm conditions in the area, higher sediment biological oxygen demand, and constant re-suspension of fine sediments in the Bay causing surficial litterbags to also go anoxic. We did not collect oxygen availability data within the litterbags, but our surficial bags tended to get buried under a thin layer of fine sediment. We have noticed that even single mangrove leaves sitting on the sediment surface in Florida Bay can be anoxic on the bottom and apparently oxidized on the top, as evidenced by the presence of black metal sulfides on the bottom surfaces of leaves.

Despite the fact that there were no differences in decay rate comparing buried and surficial samples, there were differences in the patterns in nutrient concentration during decomposition between buried and surficial litter bags. Buried mangrove leaves increased in C content, asymptoting at over 50% carbon, while surficial leaves had roughly the same C content at the end of the year's incubation (≈43%, Fig. 3) as at the beginning of the experiments (Tab. II). Despite these differences in the carbon content as a fraction of the dry weight, there was no consistent difference in the C remaining during the experiments for buried and surficial mangrove leaves (Fig. 5). In contrast, surficial mangrove leaf detritus had a higher N content through the course of the experiments than buried samples. Seagrass leaves behaved differently than mangrove leaves; buried seagrass leaves had higher N and P content through the experiment than surficial leaves (Fig. 3). There were no consistent differences in elemental content between surficial and buried seagrass rhizomes. One potential reason for the higher nutrient content in buried versus surficial treatments is that concentrations of N and P in sediment porewater in Florida Bay (Fourqurean *et al.*, 1992b) are 2–3 orders of magnitude higher than surface water (Fourqurean *et al.*, 1993) – but the higher concentrations of N in surficial mangrove leaf detritus can not be explained with the same argument. Perhaps more rapid microbial colonization of N-poor surficial mangrove leaf detritus was responsible for the greater N content of the surficial samples.

We observed little change in the P content of mangrove leaves during decomposition (Fig. 3) and consequently P was lost from the mangrove leaf detritus throughout the incubation (Fig. 5) in contrast to the accumulation of P that Nielsen and Andersen (2003) observed for decomposing *Rhizophora* leaves from a SE Asian mangrove forest. This difference may be a consequence of the relative availability of iron in the two mangrove forests. Fe concentrations were quite high in the soils studied by Nielsen and Andersen (2003), and Fe-bound P was the largest component of the total P. In contrast, Fe concentrations in the biogenic carbonate sediments of Florida Bay are very low and Fe-bound P is a small fraction of the P pool (Chambers *et al.*, 2001). Experimental addition of Fe in Florida Bay can cause an increase in P concentrations and P availability at the sediment surface (Chambers *et al.*, 2001), so it is reasonable to assume that our detritus samples could have accumulated P if Fe were more available in the environment.

Time courses of elemental ratios (Fig. 4) indicated that quite different processes were involved in decomposition of the different tissue types. C:N declined during the course of mangrove decomposition. This decline has been documented in many other studies (*e.g.* Newell *et al.*, 1984; Twilley *et al.*, 1986; Robertson, 1988; Holmer and Olsen, 2002), and

has been attributed to the respiratory loss of CO_2 and the uptake of N from the environment by the microbial decomposers. In contrast, there was no net change in C:N in the more N-rich seagrass leaves during decomposition. Holmer and Olsen (2002) report a similar relative behavior of C:N of seagrass and mangrove leaves during decomposition, and many others have noted a modest change in C:N of seagrass leaves during decomposition (*e.g.* Newell *et al.*, 1984; Zieman *et al.*, 1984; Walker and McComb, 1985). Differences in the C:N trajectories of seagrass and mangrove leaves have been explained by the C:N differences of the starting material: low C:N materials have sufficient food quality to decompose rapidly, but microbes must accumulate N in order to metabolize high C:N material. This explanation does not help explain the behavior of the C:N of seagrass rhizomes, however. The C:N of rhizomes was intermediate between mangrove leaves and seagrasses at the beginning of the experiment (Tab. II), but C:N rapidly increased during the incubations, suggesting that the food quality of rhizome detritus decreased during decomposition. Studies of P content dynamics during decomposition are relatively rare, but owing to the P-limited nature of Florida Bay we paid close attention to this factor. The patterns in P content through time roughly mirrored the change in N content (Fig. 3), but increasing N:P through time for all three tissue types suggested that N was retained or accumulated more efficiently that P in the decomposing detritus.

Seagrass leaves became depleted in ^{13}C during decomposition, seagrass rhizomes did not change $\delta^{13}C$, and mangrove leaves in surficial incubations became enriched in ^{13}C. The depletion observed in seagrass leaves was expected, because more refractory lignocelluloses are isotopically depleted compared to the bulk $\delta^{13}C$ of plants (Benner *et al.*, 1987). However, the increase in $\delta^{13}C$ by $\approx$2‰ during decomposition of surficial mangrove leaves was opposite our expectations. Perhaps the observed increase was the result of accumulation of microbial C that had an origin from a seagrass-C influenced pool of available C. Alternatively, both the depletion of seagrass leaves and the enrichment of mangrove leaves could be explained by the colonization of the detritus of both tissue types by microphytobenthos with a $\delta^{13}C$ signature of ca. 22–24‰. We did see relatively consistent decreases of ca. 2‰ in the $\delta^{15}N$ of all three tissue types during decomposition, potentially in response to the immobilization of environmental N sources by microbes during decomposition.

Our original hypotheses about the dependence of decomposition rate on nutrient availability were not supported by our data, but there were weaknesses in our experimental design that influence our ability to make firm conclusions about the importance of nutrient availability. There were no site differences in decomposition rate, despite the strong P availability gradient that has been documented across the Bay (Fourqurean *et al.*, 1992a; 1993). It should be noted that neither water column nutrient concentrations nor seagrass C:N:P (Tab. I) indicated a smooth gradient across sites; rather only one site on the seaward edge of the estuary (TS/PH 11) had substantially higher P availability than the 4 other sites on the interior of the Bay by these indicators. However, decomposition at this high-P site was not different than at the interior sites. Also, decomposition rates measured in this study were similar to rates measured at other, more nutrient-rich, locations. Apparently, P availability was sufficient for the decomposer community despite the P-limited nature of primary production across the Bay. This may be because our litter bags were deployed in the sediment or on the sediment surface. Heterotrophic processes in the sediment release P as organic matter is oxidized, and the increase in hydrogen ion production as a consequence of aerobic and anaerobic respiration can cause the dissolution of the carbonate muds to which P is bound, making P more available (Jensen *et al.*, 1998; Ku *et al.*, 1999; Burdige and Zimmerman, 2002). It may also be that decomposition in general is not nutrient limited in the sea. Tam *et al.* (1998) found no differences in the decay rates of mangrove leaves in areas receiving municipal wastewater compared to control areas.

5 CONCLUSIONS

Our data suggest that it is difficult to make generalizations about the processes and rates of decomposition of macrophyte biomass in the sea. Decomposition was relatively insensitive to the nutrient availability in the environment, and the initial nutrient content of the plant tissues proved to be a poor predictor of either decay rate or the processes involved in decomposition. Tissue-specific differences in physical structure and biochemical composition may override differences in litter quality as indicated by C:N. We did find that carbon stable isotope ratios changed during the first year of decomposition, suggesting that stable C content of residual organic matter in sediment deposits can only be used as an indicator of source if the processes leading to changes in isotopic content are understood. We also found a difference in the isotopic signature of different parts of the same plant that were large enough to be of concern to interpreters of paleoecological records. Substantial decreases in the stable N isotope ratio during decomposition suggest that δ^{15}N of sedimentary organic N should not be used as an indicator of the isotopic content of the source organic matter without careful studies of organic matter diagenesis.

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