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Stephen E. Davis
Department of Wildlife and Fisheries Sciences, Texas A&M University

Dan Childers
Department of Biological Sciences and Southeast Environmental Research Center, Florida International University, childers@fiu.edu

Gregory B. Noe
U.S. Geological Survey

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The Contribution of Leaching to the Rapid Release of Nutrients and Carbon in the Early Decay of Wetland Vegetation

Stephen E. Davis, III[1a], Daniel L. Childers[2], and Gregory B. Noe[3]

[1]*Department of Wildlife & Fisheries Sciences, MS 2258, Texas A&M University, College Station, TX 77843; 979-458-3475 (voice), 979-845-4096 (fax), sedavis@tamu.edu*

[2]*Department of Biological Sciences & SE Environmental Research Center, Florida International University, Miami, FL 33199; 305-348-3101 (voice), 305-348-4096 (fax), childers@fiu.edu*

[3]*U.S. Geological Survey, 430 National Center, Reston, VA 20192; 703-648-5826 (voice), 703-648-5484 (fax), gnoe@usgs.gov*

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[a] Corresponding author

Abstract

Our goal was to quantify the coupled process of litter turnover and leaching as a source of nutrients and fixed carbon in oligotrophic, nutrient-limited wetlands. We conducted poisoned and non-poisoned incubations of leaf material from four different perennial wetland plants (*Eleocharis* spp., *Cladium jamaicense*, *Rhizophora mangle*, and *Spartina alterniflora*) collected from different oligotrophic freshwater and estuarine wetland settings. Total phosphorus (TP) release from the P-limited Everglades plant species (*Eleocharis* spp., *C. jamaicense*, and *R. mangle*) was much lower than TP release by the salt marsh plant *S. alterniflora* from N-limited North Inlet (SC). For most species and sampling times, total organic carbon (TOC) and TP leaching losses were much greater in poisoned than non-poisoned treatments, likely as a result of epiphytic microbial activity. Therefore, a substantial portion of the C and P leached from these wetland plant species was bio-available to microbial communities. Even the microbes associated with *S. alterniflora* from N-limited North Inlet showed indications of P-limitation early in the leaching process, as P was removed from the water column. Leaves of *R. mangle* released much more TOC per gram of litter than the other species, likely contributing to the greater waterborne [DOC] observed by others in the mangrove ecotone of Everglades National Park. Between the two freshwater Everglades plants, *C. jamaicense* leached nearly twice as much P than *Eleocharis* spp. In scaling this to the landscape level, our observed leaching losses combined with higher litter production of *C. jamaicense* compared to *Eleocharis* spp. resulted in a substantially greater P leaching from plant litter to the water column and epiphytic microbes. In conclusion, leaching of fresh plant litter can be an important autochthonous source of nutrients in freshwater and estuarine wetland ecosystems.

Introduction

Litter produced by deciduous and evergreen trees is the primary mechanism by which nutrients are returned to the soil (Swift et al., 1979). Herbaceous plants also shed leaves and other aboveground parts, contributing to the recycling of nutrients and organic matter (Teal, 1962; Moran & Hodson, 1989). This pool of litter represents a relatively large, labile reservoir of organic matter to soil decomposer communities (Gosselink & Kirby, 1985; Benner et al., 1986). Although resorption prior to leaf abscission can be an effective means of conserving vital elements in many plant species, there is still a substantial outflow of organic and inorganic nutrients from trees and macrophytes via leaf senescence and decomposition (Tukey, 1970; Gosz et al., 1973; Aerts, 1996; Killingbeck, 1996; Maie et al., 2006).

The initial leaching phase of wood and leaf litter decomposition typically lasts from a few days to a few weeks, yet it is responsible for substantial loss of mass and release of materials such as carbon, nitrogen, and phosphorus to the environment (Ibrahima et al., 1995; Taylor & Bärlocher, 1996; Davis et al., 2003; Romero et al., 2005). Given that standing water or saturated soil conditions expedite this abiotic process (Tukey, 1970), the coupled process of litter production and leaching may be an especially important autochthonous source of nutrients and fixed carbon in oligotrophic, nutrient-limited wetland systems.

In order to address this, we conducted leaching studies on leaf material from four different perennial wetland plants (*Eleocharis* spp., *Cladium jamaicense*, *Rhizophora mangle*, and *Spartina alterniflora*) collected from different oligotrophic freshwater and estuarine wetland settings. Our objectives were: 1) to quantify the time-dependent release of C, N, and P from each of these species when immersed in water, 2) to evaluate the role of biological processes in governing these physically-driven losses of C, N, and P from each species, and 3) using

published values on litter production in each of these wetland systems, we wanted to develop C, N, and P budgets for each species associated with early (i.e. < 3 weeks) decay. A common goal underlying these objectives was to identify links between oligotrophic status in wetland ecosystems and leaching as a mechanism for the internal recycling of both limiting and non-limiting elements.

Based on previous work by Davis et al. (2003), we hypothesized that leaching alone would be responsible for greater loss of materials than biotic processes (i.e. microbial degradation) during the first three weeks of decomposition. However, we expected the biological contributions to litter decay to increase over this period of time, as microbial colonization increased and leachable materials were exhausted. Lastly, given that these plants were all collected from oligotrophic, nutrient-limited systems, we anticipated that high resorption efficiency would result in would result in relatively low leachable fractions of limiting elements (Feller et al., 1999; Richardson et al., 1999). In other words, we expected that the quantity of phosphorus (normalized to dry mass of plant tissue) leached from phosphorus-limited plant tissue would be considerably less than phosphorus leached from a nitrogen-limited plant, and vice versa.

Materials and Methods

Between August 2000 to July 2002, we conducted leaching experiments on leaf material from four different wetland species. In 2000, we leached senesced, yellow leaves collected from an estuarine dwarf red mangrove (*Rhizophora mangle*) wetland along Taylor River, Everglades National Park, Florida USA (Table 1). In 2001, we leached senesced tissue from two freshwater macrophytes (*Cladium jamaicense* leaves and *Eleocharis* spp. culms) collected in southeast

Everglades National Park, just south of the C-111 canal (Table 1). Both Everglades wetlands and associated plant communities are highly oligotrophic and limited by phosphorus availability (Davis, 1989; Koch & Snedaker, 1997; Noe et al., 2001). Finally, in 2002, we leached senesced leaf blades of *Spartina alterniflora* that were collected from North Inlet, South Carolina USA (Table 1). Studies of this pristine salt marsh ecosystem indicate that macrophyte productivity is strongly limited by the availability of nitrogen, although soil microbial processes are phosphorus limited (Sundareshwar et al., 2003).

For all four species, only leaf material above the mean high water mark was collected, which we assumed had not been significantly leached already. Leaves were air-dried from the time of collection to the initiation of the experiment—approximately 48 hours later. Leaves were weighed and incubated in 250 ml, clear, square, glass bottles containing 240 ml of water from each site. For all four species, we used approximately 1–4 g air-dried leaf material in each incubation bottle. Incubations lasted no longer than 21 days, as this is the timeframe needed to fully capture the shift from abiotic to biotic contributions to decomposition (Davis et al., 2003). We assumed that ambient surface water from each wetland would provide the most realistic, wetland-specific environment for the early decay of each species. However, prior to each set of incubations, we filtered (GF/F) the water to reduce variability in large particles (> 0.7 μm) between different water sources. The source water for each set of incubations was fresh (i.e., 0 ‰), except for the *S. alterniflora* incubation, which was mesohaline (15 ‰; Table 2).

To help distinguish the contribution of leaching from microbial processes in the early phase (< 3 weeks) of leaf decomposition, we added a poison (2 ml of a 1% solution of NaN_3) to half the bottles. The other half of the bottles received 2 ml of de-ionized water. All the bottles from each study were incubated next to one another (spaced 2–5 cm apart from one another) in

an outdoor setting in shallow (< 0.5 m) water under ambient temperature and sunlight conditions. All treatment combinations were conducted in triplicate for each set of incubations. In order to understand how leaching losses changed over time, we sacrificed three "poisoned" and three "non-poisoned" bottles after 1, 2, 5, 10 and 21 days of incubation. Studies have shown that much of the leachable fraction is exhausted after 24 hours (Webster & Benfield, 1986). However, for some components, leaching can be detected for several days (Ibrahima et al., 1995).

During each sampling, leaves were removed from the bottles and water samples were collected. Water samples were stored in 125 ml, HDPE bottles at 4°C until analyzed for C, N, and P content. All water nutrient analyses were conducted at the Southeast Environmental Research Center's laboratory at Florida International University. Samples were analyzed for total phosphorus (TP) according to a modification of the dry ashing, acid-hydrolysis technique (Solorzano & Sharp, 1980), for total nitrogen (TN) using an Antec 7000N total nitrogen analyzer, and for total organic carbon (TOC) using a hot platinum catalyst, direct injection analyzer (Shimadzu model TOC-5000).

To ensure that changes in water nutrients were solely due to the leaves, control bottles containing only water or water + poison were incubated for the entire 21-day length of each experiment. Nutrient concentrations from the control bottles were compared with initial concentrations to determine changes in C, N, and P fractions associated with water column or photochemical processes. Paired t-tests were used to determine significant differences between initial and final concentrations ($P < 0.05$). Since NaN_3 was selected as the poison in this experiment, TN concentrations were more than an order of magnitude higher in the bottles

containing NaN_3. Therefore, we are unable to report on the fluxes of TN in bottles containing the poison.

Because we used air-dried leaf material, an accurate means of estimating initial oven-dried mass was needed in order to normalize calculated releases of C, N, and P. To accomplish this, we converted oven-dried mass to air-dried mass for each species (Table 1). These conversions were generated from 25–30 individual leaves of each species that were weighed after being air-dried during the same period of time as the experimental leaves (≤ 48 hours), then oven-dried to a constant mass at 70 ºC. The conversion for each species involved multiplying by the initial, air-dried mass in order to estimate initial dry mass for each experimental leaf.

The changes in nutrients in bottles containing leaf material and poison were assumed to be the result of leaching. For those without poison, we assumed that both leaching and biological processes were at work in governing C, N, and P dynamics. We calculated total releases from each incubation bottle as the change in the molar quantities of TOC, TN, and TP from initial source water, normalized to the predicted initial dry mass of leaf material in each bottle per time of incubation (in moles X gdw leaf material^{-1} time^{-1}). We do not present data on rates of C, N, and P release, but these values can be easily estimated by dividing the total release by the number of days incubated (i.e., 1 or 21).

We used analysis of variance (ANOVA) to determine the effect of time on early decay of leaf material, comparing the yield of C, N, and P leached from all species after 1 day of incubation to total fluxes after 21 days of incubation. We also used ANOVA to determine the effect that the poison had on releases of C, N, and P in each species to discern the time-dependence of biological contributions to these releases. Lastly, we used ANOVA to determine species effects on releases of each of these constituents over a three-week period of time. For

each of these analyses, Tukey-Kramer post-hoc tests were used to determine differences between treatment means of significant ANOVAs ($P < 0.05$). By doing these analyses and focusing on initial, 1-day releases and 21-day yield, we hoped to generate a better understanding the role of microbes in governing the fate of leached C, N, and P for each species.

Results

All species released a significant amount of TOC, TN, and TP after just 1 day (Figures 1–3), compared to control bottles (i.e., those without leaves) that showed no significant change in these constituents over each of the 3-week experiments (see Table 2 for initial concentrations of TOC, TN, and TP in each water source). We also collected C, N, and P data from each set of incubations after 2, 5, and 10 days of incubation, but these data only followed the trends we observed after 1 and 21 days. Therefore, we chose to omit these days from our discussion and focus on the time end-members of these experiments.

For all species and poison treatment combinations, 21-day total releases of TOC and TP were always significantly greater than 1-day total releases, indicating that a substantial pool of leachable materials still existed within the leaves after one day (ANOVA; $p < 0.0001$). However, the rate of release was highest in the first day for all species (ANOVA; $p < 0.0001$).

When comparing within species, *R. mangle* leaves released an order of magnitude more TOC than the other three species regardless of the addition of poison (ANOVA; $p < 0.0001$). From Day 1 to Day 21, the amount of TOC released by *R. mangle* jumped by more than ten-fold (Figure 1). The other species did not exhibit this same magnitude of trend for TOC release, as the increases from Day 1 to Day 21 shown by *C. jamaicense*, *Eleocharis spp.*, and *S. alterniflora* were each less than three-fold (Figure 1). For these same three species, the difference between

poisoned and non-poisoned incubations was significant (poisoned > non-poisoned) during both days of sampling (Table 3), indicating a sustained biological effect on the early release of TOC. *Rhizophora mangle* leaves revealed a similar biological effect after 1 day of immersion. However, we could not statistically differentiate poisoned releases of TOC from non-poisoned releases by Day 21 in the mangrove leaf incubations (Table 3, Figure 1).

The amount of TP leached from these four species was considerably less than the amount of TOC released, ranging from sub-μmole levels of TP (e.g., all Everglades species after 1 day of incubation) to as much as 13.5 μmoles TP gdw^{-1} from *S. alterniflora* blades after 21 days. Overall, *Spartina alterniflora* blades released significantly more (by about an order of magnitude) TP than leaf material from the three Everglades species (ANOVA; $p < 0.0001$), which were limited by P availability in their respective natural settings. Total phosphorus leached from poisoned and non-poisoned incubations containing *R. mangle* leaves were not different after 1 day, but poisoned releases were more than twice those of non-poisoned incubations after 21 days. All other species showed significantly higher releases of TP after 1 day in the presence of poison (Table 3, Figure 2).

From Day 1 to Day 21, total release of TP by *S. alterniflora* blades increased, but the increases were most noticeable in the non-poisoned incubations, which more than doubled (Figure 2). In fact, after 21 days, poisoned and non-poisoned releases of TP by *S. alterniflora* were not significantly different (Table 3). After 21 days of incubation, all three Everglades species showed a significantly greater release of TP with poison (Table 3; Figure 2).

Release of TN could only be discerned in the non-poisoned incubations, as the NaN_3 poison interfered with our ability to detect significant TN change. Non-poisoned releases of TN from *Eleocharis spp*. culms were significantly greater than those by *R. mangle* and *C.*

jamaicense, but neither group could be distinguished from TN releases by *S. alterniflora*, the species we assumed to be limited by N in its natural environment (ANOVA; $p < 0.005$; Figure 3). Incubations containing *S. alterniflora* leaf material showed little net change in TN levels from Day 1 to Day 21, while the three Everglades species yielded more TN after 21 Days and showed similar trends in disparity between Day 1 and Day 21(Figure 3)

Discussion

As expected, we saw much lower release of phosphorus from leaves of species collected in P-limited wetlands (Everglades National Park) compared to a N-limited wetland (North Inlet, SC). In fact, we estimate that the flux of P from leaching litter to a 1-m^2 patch of N-limited *S. alterniflora* ecosystem was up to two orders of magnitude greater than for the P-limited Everglades species (Table 4). Further, these releases were substantially lower in the presence of biological processes that appeared to prevent the release of that P to the water column.

Although we did not measure the P content of the leaf tissue (or the biofilm layer that developed on it), we assumed that the difference between TP release in poisoned and non-poisoned incubations was the result of microbes on the surface of the leaf mobilizing leached P. Our measurements of water column TOC, TN, and TP reflected the initial concentrations of these constituents plus the contribution of leached material and microbes suspended in the water column. Since we considered 'total' fractions in our analyses, declines in water column [TOC], [TN], and [TP] or differences between poisoned and non-poisoned incubations at a given time interval were assumed to be the result of respiration losses (C and N) or incorporation into microbial biomass on the leaf surface (C, N, and P).

The disparity between poisoned and non-poisoned treatments in our study was greatest in the two freshwater Everglades macrophytes (*C. jamaiscense* and *Eleocharis spp.*) and in *S. alterniflora*. Less TP leached to the water with live microbial communities, suggesting that a significant portion of P leached from the plants in this study was labile and available to microbes. It is likely that the leached P boosted microbial activity in these treatments, as P not only limits primary production, but also microbial processes in this wetland (Davis, 1989, Amador & Jones, 1993).

The same may be true for *S. alterniflora*. Although N limits primary productivity in North Inlet (SC) salt marshes, Sundareshwar et al. (2003) showed that P limits soil microbial respiration. This appeared to be the case early in our incubations when epiphytic microbial communities on dead leaf material reduced P leaching into the water column by half (Figure 2). However, as time progressed, molar ratios of TN:TP in *S. alterniflora* incubations suggested a precipitous decline in N availability relative to P—with TN:TP averaging 11 in source water and less than 2 after 21 days in poisoned incubations (Figure 4). This trend was supported by TP and TN releases by *S. alterniflora* after 21 days.

That there was no difference between poisoned and non-poisoned release of TP after 21 days suggests that there was little demand for leached TP by epiphytic microbes at that time. Further, no difference in the total amount of TN released by *S. alterniflora* in non-poisoned incubations after 1 day versus after 21 days suggests that TN releases were diminished by epiphytic microbes sometime between Day 1 and 21. Based on the change in molar TN:TP over the duration of these incubations, it is likely that N became limiting to the microbial community shortly after the first day of this set of incubations—when TN:TP averaged approximately 3 (Figure 4; Figure 6). All Everglades species showed a trend in water column TN:TP similar to *S.*

alterniflora, but 21-day ratios were still over an order of magnitude higher, indicating P-limitation throughout the duration of the leaf incubations (Figure 4).

Dwarfed *Rhizophora mangle* in the southern Everglades is widely thought to be limited by P availability (Koch & Snedaker, 1997; Feller et al., 1999). However, it may be that the lack of a biological effect on TP release after 1 day was the result of water column microbes in this wetland being limited by the availability of labile organic carbon. We observed a two-fold reduction in TOC released from *R. mangle* leaves after one day when biological activity was present (Figure 1). This corresponded with the lack of a 1-day difference in TP leaching between poisoned and non-poisoned incubations. After the large, 1-day pulse of TOC from these leaves, biological activity likely shifted back to P-limitation, as evidenced by the significant difference between poisoned and non-poisoned releases of TP after 21 days and the lack of a significant difference between poisoned and non-poisoned releases of TOC after this same period of time had elapsed (Figures 1 and 2).

Dead *R. mangle* leaves represent a potentially large source of leachable OC to the surrounding ecosystem (Table 4), supporting the observation that mangroves are a significant source of DOM to Everglades estuarine ecosystems (Jaffé et al., 2004). Everglades mangrove ecosystems have higher surface water DOC concentrations, and more of this DOM is potentially labile compared to upstream oligotrophic freshwater wetlands (Maie et al., 2005). However, freshwater oligotrophic wetlands of the Everglades can also be a net source of potentially labile carbohydrates and proteinaceous material (Lu et al., 2003).

The different Everglades species exhibited a range of abiotic P leaching losses. The maximum amount of TP leached from *Eleocharis* spp. in the first day in the poisoned bottles whereas *S. alterniflora*, *C. jamaicense*, and *R. mangle* leached TP at progressively slower rates

through Day 21. The two freshwater Everglades species showed interesting contrasts in abiotic P leaching. Although both *C. jamaicense* and *Eleocharis* spp. leached similar amounts of TP after 1 day in the poisoned bottles, after 21 days *C. jamaicense* leached twice as much TP compared to *Eleocharis* spp., but this was a statistically insignificant difference. The greater inherent leachability of the P remaining in *C. jamaicense* litter after re-adsorption compared to *Eleocharis* spp. is surprising given the lower concentration of P in dead *C. jamaicense* leaves than *Eleocharis* spp. culms (Rubio & Childers, in review). In the end, the microbially mediated release of TP from non-poisoned *C. jamaicense* was nearly identical to non-poisoned *Eleocharis* spp. culms and *R. mangle* leaves.

Leaching of nutrients from *C. jamaicense* litter results in larger ecosystem fluxes despite similar mass-specific leaching rates from litter as *Eleocharis* spp. The annual net primary productivity of *C. jamaicense* is much greater than *Eleocharis* spp. in the Everglades, translating into a difference in litter production between these two herbaceous species (Daoust & Childers, 2004; Childers et al., in review; Table 4). This results in a larger flux of P from soil to plant litter in the water column via translocation in *C. jamaicense* marsh (7.49 mmol P m^{-2} yr^{-1}) compared to *Eleocharis* spp. sloughs (1.10 mmol P m^{-2} yr^{-1}; Noe & Childers, in review). The higher litter production of *C. jamaicense* compared to *Eleocharis* spp. also results in much larger fluxes of P, N, and C from this litter to the water column via leaching (Table 4). Using the non-poisoned leaching data from this study, we estimate the annual P flux from litter to the water column by leaching to be 0.69 and 0.10 mmol P m^{-2} yr^{-1} for *C. jamaicense* and *Eleocharis* spp., respectively. Thus, 9% of total litter P flux is leached into the water column for both species.

Phosphorus uptake from fresh litter by epiphytic microbes can be estimated by the difference in leaching fluxes between poisoned and non-poisoned treatments, equal to 1.55 and

0.07 mmol P m^{-2} yr^{-1} for *C. jamaicense* and *Eleocharis* spp., respectively, or 21% and 6% of total litter P flux, respectively. This much larger flux of P to epiphytic microbes on *C. jamaicense* compared to *Eleocharis* spp. could have large feedbacks on ecosystem P cycling and transport. Phosphorus in microbial biomass is more labile and likely has faster turnover rates than the refractory P remaining in plant litter, and could be more easily transported downstream through long-term nutrient spiraling processes. The larger sum of P leaching fluxes from litter to both the water column and epiphytic microbes in *C. jamaicense* marsh (2.23 mmol P m^{-2} yr^{-1}) compared to *Eleocharis* spp. sloughs (0.16 mmol P m^{-2} yr^{-1}) represents a greater recycling of P from *C. jamaicense* plants to other ecosystem components in the soil and water column of this oligotrophic, P-limited ecosystem. Finally, the increase in the P content of decomposing litter in the Everglades (Davis, 1991; Qualls & Richardson, 2000) could be explained, in part, by microbial mobilization of P leaching from litter and not solely uptake of water column P.

Conclusions

Abiotic leaching accounted for the greatest loss of C, N, and P from leaves of the four species we considered. As expected, TP release from P-limited Everglades plant species was much lower than TP release by an N-limited North Inlet (SC) salt marsh plant. The presence of microbial activity diminished the observed leaching yield, as normalized releases of C and P in non-poisoned incubations were usually significantly lower than in the poisoned incubations. This suggests that that biological degradation of leaves in wetland settings may in fact be stimulated by the physical process of leaching that results in a rapid, labile energy source or limiting elements such as phosphorus or nitrogen for microbial decomposers. Leaching of

nutrients from plant litter to the water column can represent a large flux of nutrients in oligotrophic ecosystems.

Long-term Ecological Research in the Florida Coastal Everglades seeks to understand the role of wetland hydrology in driving materials exchange (carbon, nitrogen, phosphorus, suspended material, etc.) and productivity patterns at the land-sea interface. Our results suggest that early leaf litter decay (i.e., leaching and microbial colonization) can contribute to local regulation of surface water quality. However, analogous studies should be conducted in the field to ascertain the actual contribution of early macrophyte decay to spatial and temporal patterns in wetland ecosystem function. Further, studies such as these should also consider gradients of ecosystem fertility and trophic status to fully understand the interactions between biological and physical processes in the early decay of wetland plant tissue.

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Table 1: Physical location, description of collection sites, the ratio of oven-dried mass to air-dried mass (± stdev) for each species, and the date (month/year) of each collection and experiment. Site identifiers in parentheses refer to exact locations of FCE-LTER and North Inlet NERR sampling stations.

Site	Lat/Long (decimal degrees)	Wetland type	Fertility / Nutrient status	Species collected	Oven:Air mass (stdev)	Collection Date
SE Everglades, FL (TS/Ph 4)	25.315 N / -80.522 W	FW slough	oligotrophic, P-limited	*Cladium jamaicense*	0.879 (± 0.007)	Mar. 2001
SE Everglades, FL (TS/Ph 5)	25.295 N / -80.520 W	FW marsh	oligotrophic, P-limited	*Eleocharis spp.*	0.795 (± 0.006)	Apr. 2001
Taylor River, FL (TS/Ph 7b)	25.197 N / -80.642 W	mangrove	oligotrophic, P-limited	*Rhizophora mangle*	0.354 (± 0.019)	Aug. 2000
Clambank Creek, SC (North Inlet, CB)	33.334 N / -79.193 W	salt marsh	oligotrophic, N-limited	*Spartina alterniflora*	0.842 (± 0.004)	Jul. 2002

Table 2: Initial concentrations of salinity, TOC, TN, and TP in water sources used for each leaching experiment.

Experiment (species)	**Salinity (‰)**	**TOC (mM)**	**TN (µM)**	**TP (µM)**
C. jamaicense	0	1.16	66.95	0.33
Eleocharis spp.	0	2.02	134.49	0.17
R. mangle	0	1.01	36.38	0.12
S. alterniflora	15	0.22	17.24	1.59

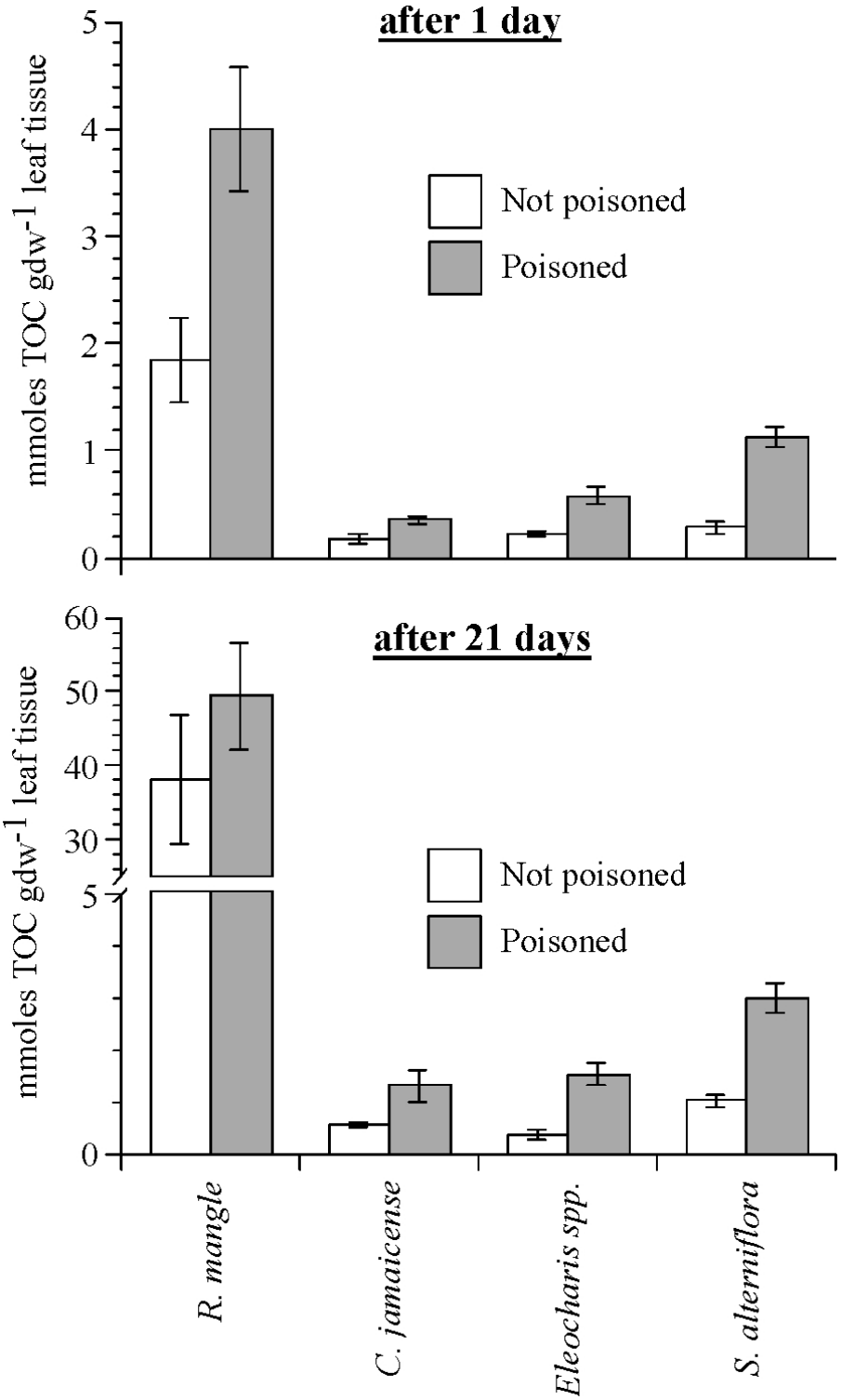
Table 3: *P*-values from one-factor ANOVAs testing the effect of poison on the release of TOC and TP from each species after 1 day and after 21 days of incubation. In all significant tests ($P < 0.05$), releases from leaves in poisoned bottles were greater than releases in non-poisoned bottles. 'N.S.' indicates no significant difference in the release of a given constituent between poisoned and non-poisoned bottles.

Species	**1 Day (TOC)**	**21 Days (TOC)**	**Day 1 (TP)**	**21 Days (TP)**
R. mangle	0.0060	N.S.	N.S.	0.0375
C. jamaicense	0.0052	0.0110	0.0129	0.0483
Eleocharis spp.	0.0028	0.0014	0.0117	0.0086
S. alterniflora	0.0002	0.0003	0.0010	N.S.

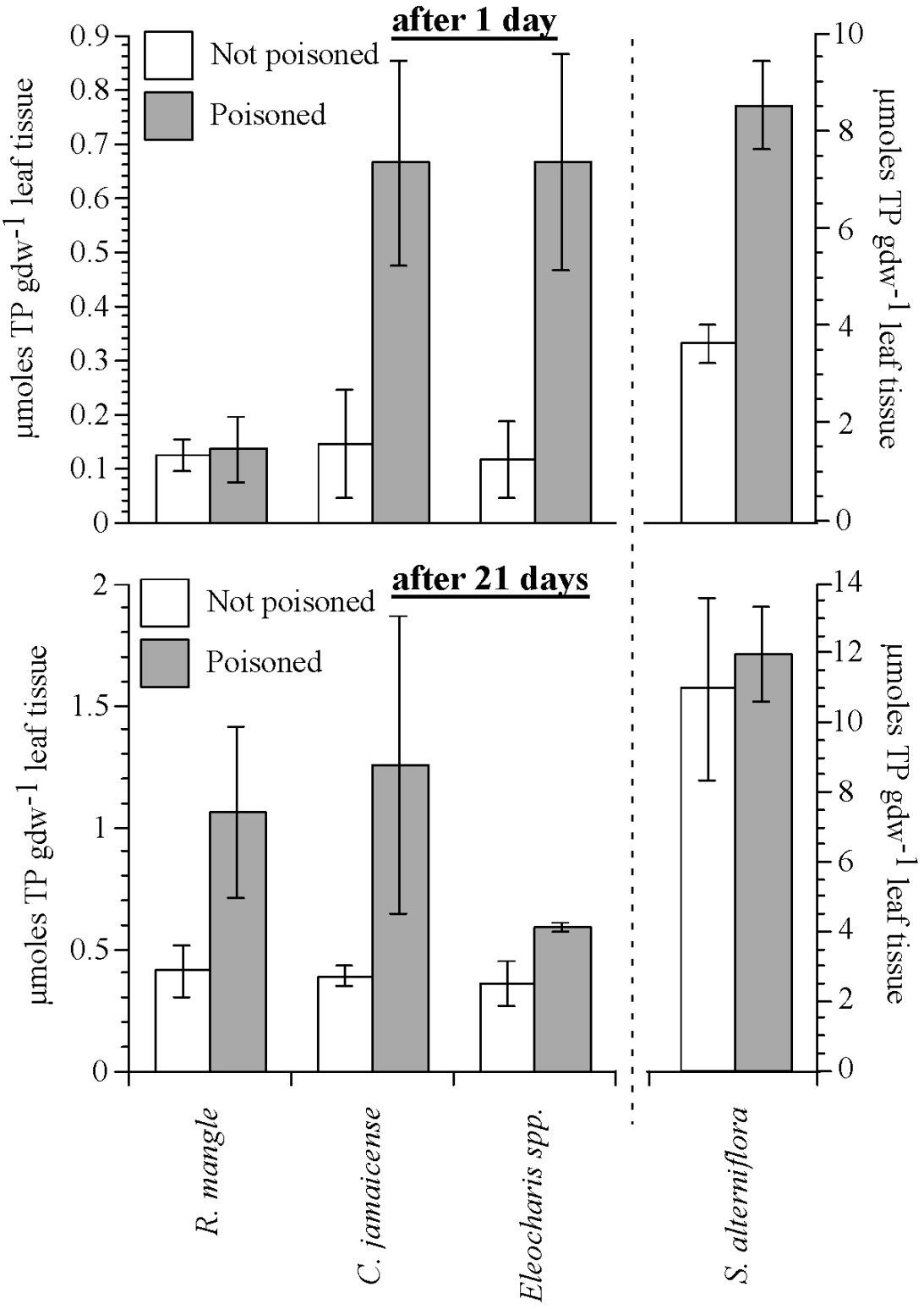
Table 4: Fluxes of nutrients in a representative 1-m^2 patch of wetland (mol m^{-2} yr^{-1}) associated with the leaching of fresh detritus from different plant species, estimated from the product of mean leaching fluxes (mol g dw^{-1}) in this study and litterfall production values (g m^{-2} yr^{-1}) from the literature. Leaching fluxes to water column are derived from the non-poisoned treatments, leaching fluxes to epiphytic microbes are derived as the difference between poisoned and non-poisoned treatments. Nitrogen fluxes were not measured in poisoned treatments. [a] Noe and Childers (in review); [b] Rivera-Monroy et al. (in preparation); [c] Morris and Haskin (1990).

Flux	*C. jamaicense*	*Eleocharis* spp.	*R. mangle*	*S. alterniflora*
Litterfall production (g dw m^{-2} yr^{-1})	1,789 [a]	281 [a]	120 [b]	635 [c]
Leaching flux to water column (mmol m^{-2} yr^{-1})				
TOC	870	90	4,500	610
P	0.69	0.10	0.05	6.93
N	25	4.8	1.4	7.0
Leaching flux to epiphytic microbes (mmol m^{-2} yr^{-1})				
TOC	1,400	330	1,300	1,300
P	1.55	0.07	0.08	0.62

List of Figures


after 1 day
mmoles TOC gdw-1 leaf tissue
5
4
3
2
1
0
Not poisoned
Poisoned
after 21 days
mmoles TOC gdw-1 leaf tissue
60
50
40
30
5
0
Not poisoned
Poisoned
R. mangle
C. jamaicense
Eleocharis spp.
S. alterniflora

2


after 1 day
Not poisoned
Poisoned
µmoles TP gdw-1 leaf tissue
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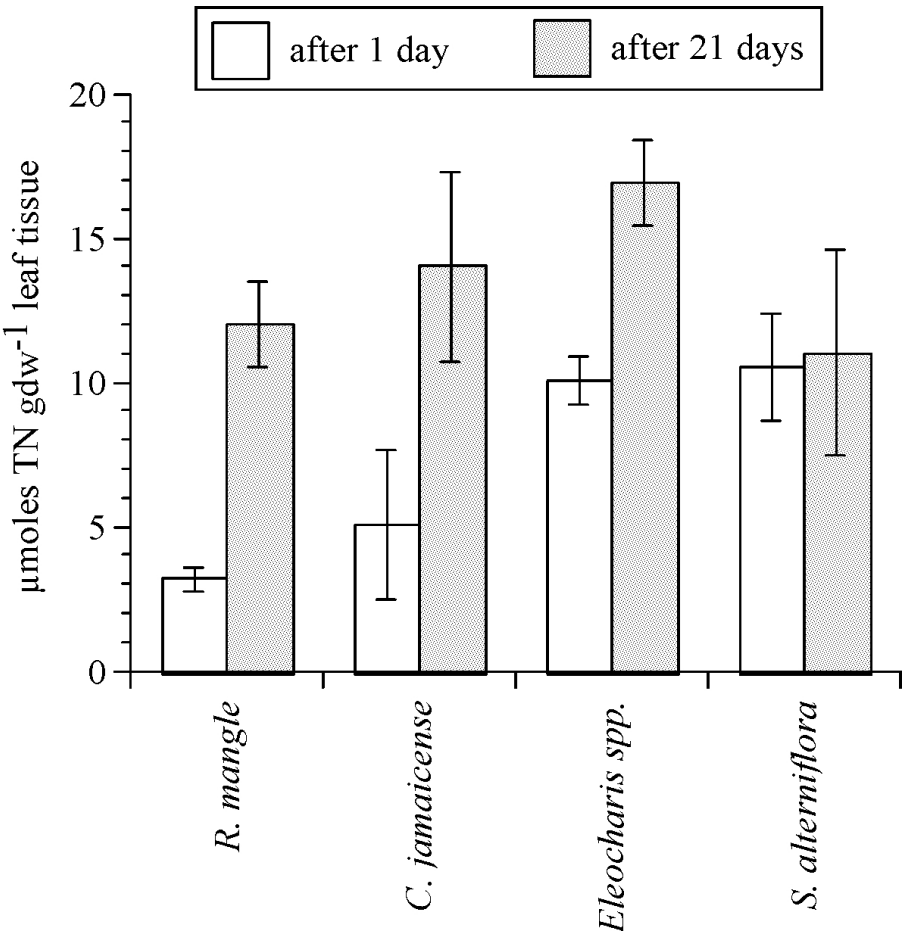
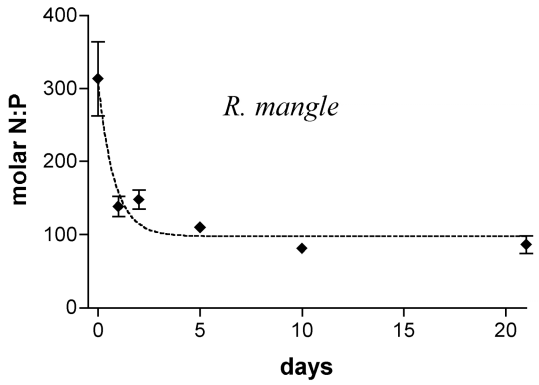
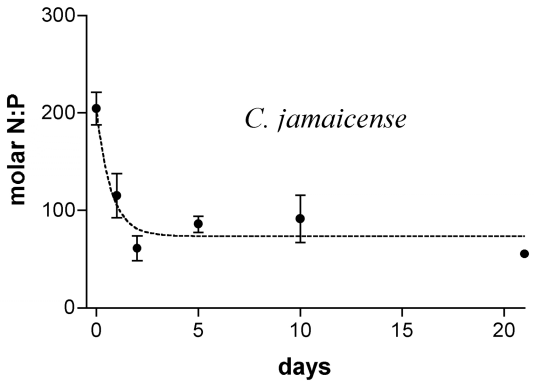
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
0
2
4
6
8
10
after 21 days
Not poisoned
Poisoned
µmoles TP gdw-1 leaf tissue
0
0.5
1
1.5
2
0
2
4
6
8
10
12
14
R. mangle
C. jamaicense
Eleocharis spp.
S. alterniflora

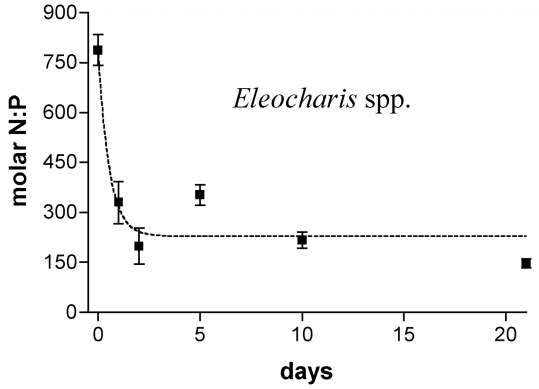
2

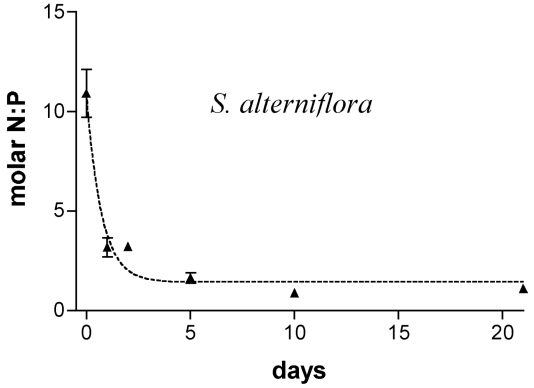

after 1 day
after 21 days
µmoles TN gdw-1 leaf tissue
20
15
10
5
0
R. mangle
C. jamaicense
Eleocharis spp.
S. alterniflora

2


R. mangle
molar N:P
days
0
100
200
300
400
0
5
10
15
20


C. jamaicense
molar N:P
days
0
100
200
300
0
5
10
15
20


Eleocharis spp.
molar N:P
days
0
150
300
450
600
750
900
0
5
10
15
20


S. alterniflora
molar N:P
days
0
5
10
15
0
5
10
15
20