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Influence of Grasshopper Herbivory on Nitrogen Cycling in Northern Gulf of Mexico Black Needlerush Salt Marshes

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Abstract Herbivory is a common process in salt marshes. However, the direct impact of marsh herbivory on nutrient cycling in this ecosystem is poorly understood. Using a ^{15}N enrichment mesocosm study, we quantified nitrogen (N) cycling in sediment and plants of black needlerush (*Juncus roemerianus*) salt marshes, facilitated by litter decomposition and litter plus grasshopper feces decomposition. We found 15 times more ^{15}N recovery in sediment with grasshopper herbivory compared to sediment with no grasshopper herbivory. In plants, even though we found three times and a half larger ^{15}N recovery with grasshopper herbivory, we did not find significant differences. Thus, herbivory can enhance N cycling in black needlerush salt marshes sediments and elevate the role of these salt marshes as nutrient sinks.

Keywords Herbivory · Nitrogen cycling · Salt marshes

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Introduction

Nutrient cycling is a key process in the transference of matter throughout ecosystems. Herbivores, decomposers, and detritivores all influence nutrient cycling, trophic transfer, and carbon and nutrient storage in ecosystems (Cebrian and Lartigue 2004). Herbivores may accelerate nutrient cycling through consumption and subsequent deposition of nutrient-rich feces on soils or sediments, where decomposers and detritivores break down the feces and accelerate nutrient cycling (Belovsky and Slade 2000; Frost and Hunter 2004; Krumins et al. 2015). Herbivores may also enhance nutrient cycling by increasing the amount of nutrients in the throughfall water due to feces and plant wounds (Nitschke et al. 2015). They can also increase carbon (C) allocation to belowground biomass and, in turn, enhance root carbon exudation. This last process may stimulate bacterial degradation of organic matter and render more nutrients available for plant uptake (Hamilton and Frank 2001).

The enhanced nutrient inputs into soils or sediments, mediated directly or indirectly by herbivores, may not necessarily translate into higher nutrient availability for plants (Christenson et al. 2002). Some of these nutrients can be exported by hydrologic flushing (Webb et al. 1995; Eshleman et al. 1998) or immobilized by microbes (Lovett and Ruesink 1995; Kagata and Ohgushi 2012). Thus, the impact of herbivores on nutrient cycling and uptake by plants depends on several factors, such as the quality and quantity of feces as well as interactions with physical forcing (e.g., tides, storms, or wind) and microbial processes.

Salt marsh herbivores, including vertebrates such as guinea pigs (Alberti et al. 2011b) and invertebrates such as snails (*Littoraria irrorata*; Sapelo Island: Silliman and Bertness 2002), grasshoppers (*Conocephalus* sp., *Orchelimum* sp., *Orphulella* sp., *Odontoxiphidium* sp.; Gulf of Mexico:

Sparks and Cebrian 2015), crabs (*Neohelice granulata*; South West Atlantic: Alberti et al. 2007, 2011a), and moths (*Haimbachia* sp.; South West Atlantic: Canepuccia et al. 2010), have been shown to play important top-down effects on macrophyte function and health in different regions of the world. For example, herbivory by the crab *N. granulata* on *Spartina densiflora* (Alberti et al. 2011a) and by the periwinkle *L. irrorata* on *S. alterniflora* (Silliman and Zieman 2001) generate important reduction in the plant aboveground biomass. However, the impact of herbivore grazing on nutrient cycling in salt marsh systems has not been assessed.

A number of processes may condition herbivore-mediated nutrient cycling and, ultimately, incorporation into plant biomass in salt marsh systems (see Adam 1990). Insect feces may be diluted and exported by currents or tides (Wotton and Malmqvist 2001; Townsend et al. 2004) at higher rates than are detrital particles because of their small size and ease for fragmentation. In addition, tides may have complex interactions with organic matter decomposition rates, accelerating or decelerating them (Pfauder and Zimmer 2005; Hemminga et al. 1988). Denitrification, an important biogeochemical process in salt marshes, may also contribute to decreased N available for plant uptake (Tobias et al. 2001, 2003). Undoubtedly, the mediation by herbivores in nutrient cycling dynamics in marsh systems is complex and merits effort for a better understanding in the face of system management in a globally changing world.

To improve our understanding, we examined the role of grasshopper grazing on nutrient cycling and N uptake in black needlerush (*Juncus roemerianus*) marshes, which are ubiquitous in the Northern Gulf of Mexico (Dardeau et al. 1992; Eleuterius 1976). Plant productivity and standing aboveground and belowground biomass in these marshes have been well characterized (Gabriel and de la Cruz 1974; de la Cruz and Hackney 1977; Hopkinson et al. 1980; Hunter et al. 2015). Leaf litter decomposition occurs slowly due to high lignin and low nutrient content in the plants (de la Cruz and Gabriel 1974; Stout and de la Cruz 1981; Christian et al. 1990; Hunter et al. 2015). Grasshoppers are prominent herbivores in these marshes, and their leaf consumption levels may vary widely in space and time, although modest levels of herbivory are often encountered (Parson and de la Cruz 1980; Wason and Pennings 2008; Hunter et al. 2015; Sparks and Cebrian 2015). Thus, grasshopper grazing, through the production of nutrient rich feces, could have a significant impact on nutrient cycling and plant uptake rates in black needlerush marshes. Using a mesocosm study with grasshopper feces and litter addition, we investigated this topic.

Materials and Methods

In northern Gulf of Mexico, marshes grazed by grasshoppers follows a marked seasonal cycle, starting in early spring and ending in late summer or early fall (Smalley 1960; Davis and Gray 1966; Carrier 2013). We conducted our experiment during mid-summer, a period where both peaks of grasshopper grazing and needlerush leaf biomass typically occur (Hackney et al. 1978; Stout 1984; Hunter et al. 2015).

Production of Labeled Material

To obtain the enriched plants, we added 100 mg of potassium nitrate (99 ^{15}N atom%, Cambridge Isotope Lab) at every low tide during June 2013 in a 2 m × 3 m area of a black needlerush salt marsh situated 0.4 km (30° 15′ 06.2″ N 88° 04′ 58.4″ W) from the Dauphin Island Sea Lab (DISL). One week before starting the experiment, we clipped leaves at the surface level from the ^{15}N-enriched area in the marsh to obtain ^{15}N-enriched litter. Clipped leaves (hereafter litter) were then dried in an oven at 60 °C.

Mesocosms

Unlabeled (no ^{15}N enrichment) and labeled (^{15}N enriched) plants were taken out from the sediment and transported to an outdoor flow-through facility at the DISL where the experiment was run. Unlabeled plants were taken out from the same marsh as labeled plants but 200 m away to avoid isotopic contamination. The sediment attached to the roots and rhizomes of unlabeled and labeled plants was profusely rinsed off, and the plants planted in plastic containers (45 cm × 30 cm × 35 cm) filled with unlabeled sediment collected at the study marsh.

Each plastic container represented an experimental replicate and had 67% of ^{15}N-labeled plants and 33% of unlabeled plants. They were encased in a 1.5-m tall PVC frame covered in tulle cloth to exclude or include grasshoppers depending on the treatment. The containers were distributed in groups of three in six bathtubs (Fig. 1). Bathtubs were 1 m in height, 0.5 m in width, and 1 m in length. The natural diurnal tidal cycle (mean amplitude of 40 cm) was mimicked in the bathtubs using an array of bilge pumps and timers (Fig. 1). With this setup, tidal oscillations and subsequent nutrient flushing were similar to the natural salt marsh.

To assess the transfer of ^{15}N from labeled litter and plants to unlabeled plants through the decomposition of grasshopper feces and leaf litter, we divided the containers in three treatments: (1) ^{15}N-labeled leaf litter and plants with grasshoppers, which generated ^{15}N-enriched feces, hereafter named "Herbivory" treatment, (2) ^{15}N-labeled leaf litter and plants with no grasshoppers, hereafter named "No herbivory" treatment, and (3) ^{15}N-labeled plants with no labeled leaf litter nor grasshoppers, hereafter named "Control."

In the "Herbivory" treatment, three grasshoppers were enclosed in each container. Grasshoppers (*Conocephalus* sp. and *Orchelimum* sp.) were caught in the same marsh as plants

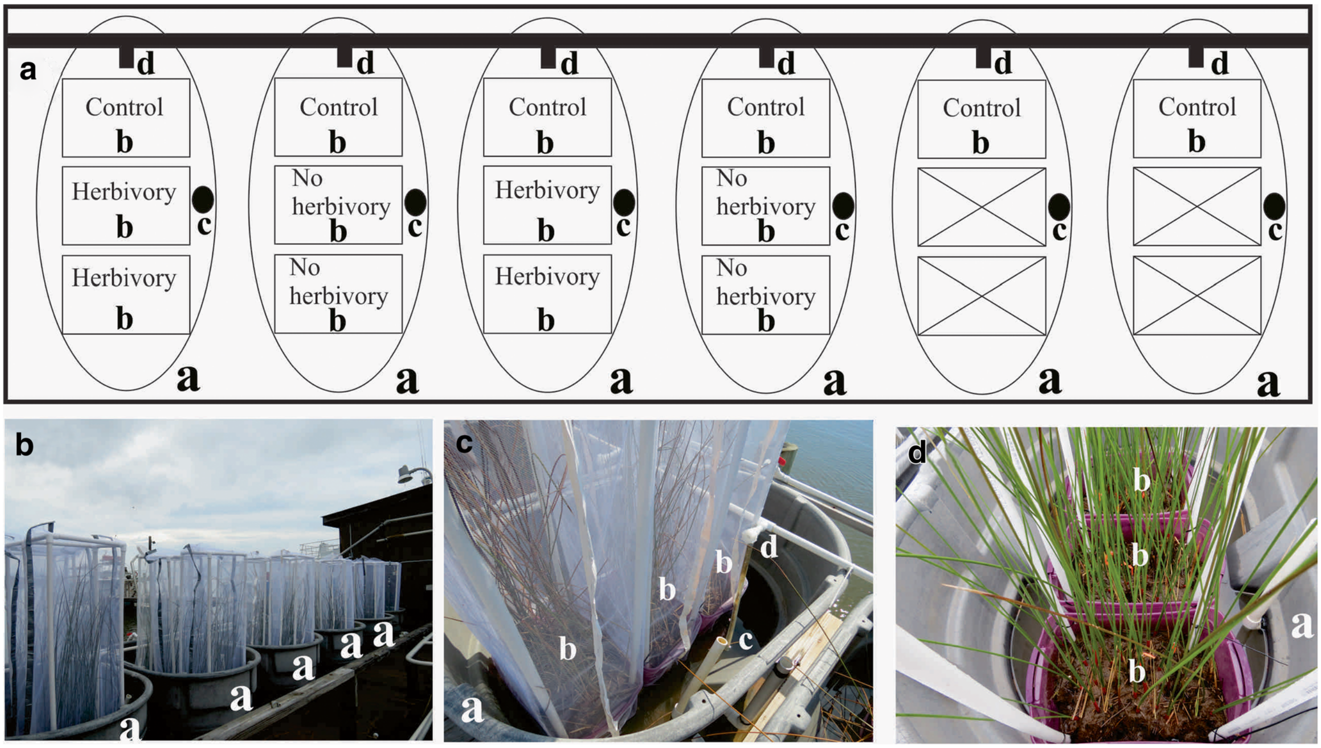

Fig. 1 **a** Diagram of the experimental design. Containers with a cross are lost replicates. Hereafter, lowercase letters mean a = bathtubs, b = containers, c = drain pipe, d = bobbin for tidal flushing. **b** Photograph of the bathtubs with the containers inside of them with tulle cloth. **c** Close-up of one bathtub with the three containers and the artificial tidal pipe system. **d** Close-up of the plants and litter in the three containers without the tulle cloth

were taken from using a sweep net (Wason and Pennings 2008). In the "Herbivory" and "No herbivory" treatment, 4 g DW (0.02 ± 0.001 g of N and 0.001 ± 0.00007 g of ^{15}N) of labeled leaf litter was put on the surface of the sediment. Density of plants, leaf litter, and grasshoppers in the experimental containers mimicked values obtained through field sampling of the study marsh at the time of the experiment (July 2013).

In each bathtub, there were two containers with the same treatment, either "Herbivory" or "No herbivory," and a third container with the "Control" treatment (see Fig. 1). This experimental setup is a nested design for the "Herbivory" and "No herbivory" treatments, while the "Control" treatment distribution was spread across the entire mesocosm study area to correct the values of the other two treatments. This experimental setup allowed for a correction of potential contamination of the ^{15}N signature in unlabeled plants (e.g., due to rhizome and root exudation and/or remaining sediment attached to the rhizomes and roots in transplanted labeled plants) and to subtract natural abundances of ^{15}N for the calculations of atom% excess (see "Isotope Analysis and Calculations" section). Each treatment had four containers.

Three weeks after starting the experiment, leaf herbivory in the "Herbivory" treatment containers had become intense (approximately 20% more than what was observed in the natural salt marsh) so grasshoppers were removed from the containers at that time. Plants were left in the containers for an additional 45 days to ensure sufficient time for isotope incorporation from grasshopper feces and leaf litter. At the end of this period, we collected sediment samples (2 cm deep) and harvested all of the originally unlabeled plants in each container. To estimate the amount of ^{15}N atom % excess we added to the containers, we harvested unlabeled plants and collected litter in the natural salt marsh together with labeled plants and litter prior to the experiment. All samples were rinsed and oven dried at 60 °C. These samples were then ground, packaged, and analyzed at the Utah State University Isotope Laboratory (USU), where they were analyzed by continuous-flow direct combustion and mass spectrometry using a Europa Scientific SL-2020 system with an accuracy of 0.5 per mil.

Isotope Analysis and Calculations

To estimate ^{15}N % recovery of sediment and unlabeled plants in each container, we used the following equation:

$$^{15}\mathrm{N}_{\mathrm{recovery}}(\%) = \frac{^{15}\mathrm{N}_{\mathrm{sample}} \times \mathrm{Total}\ \ \mathrm{N}_{\mathrm{sample}}}{^{15}\mathrm{N}_{\mathrm{added}} \times \mathrm{Total}\ \ \mathrm{N}_{\mathrm{added}}} \times 100$$

where $^{15}\mathrm{N}_{\mathrm{sample}}$ was estimated by subtracting the average atom % of sediment or unlabeled plants in control containers from the atom % of sediment or unlabeled plants in treatment containers (i.e., atom % excess), Total N_{sample} is the total mass of N in sediment or unlabeled plants of treatment containers, $^{15}N_{added}$ is estimated by subtracting the atom % of natural unlabeled plants and litter to labeled plants and labeled litter, respectively (i.e., atom % excess) and then by summing atom % excess of labeled litter and plants in each container, and Total N_{added} was estimated by summing total mass of N in labeled plants and litter in each container.

Statistical Analysis

To evaluate differences between leaf grazing degree in the natural salt marsh and our experiment, we performed a mixed-effect model with location as a fixed factor (experiment vs natural salt marsh, two levels) and Plot/Container as a random factor (four levels). To evaluate if leaf growth was affected by experimental manipulation, we performed a one-way ANOVA comparing the five treatments separately for small and large leaves. To evaluate if leaf growth was affected by ^{15}N labeling, we performed a mixed-effect model with the fixed factor Labeling Manipulation and the random factor Container.

To evaluate if herbivory affected ^{15}N recovery % in sediment and plants, we performed a mixed-effect model with Presence of herbivory as a fixed factor and Bathtub as a random factor. Mixed-effect models were fitted using the "nlme" package for R (Pinheiro et al. 2016). The best model was chosen by using the likelihood ratio test. We checked by visual inspection of the residual plot that the statistical assumptions of homoscedasticity and normality were not violated. To achieve these assumptions, both sediment and plants were transformed to its square root.

Results

Before starting the experiment, marsh-labeled plants and litter had 0.4321 ± 0.014 atom % ^{15}N while marsh-unlabeled plants had 0.3707 ± 0.0006 atom % ^{15}N and experiment-unlabeled plants had 0.3690 ± 0.0007 atom % ^{15}N. In the mesocosm experiment, we found 15 times more ^{15}N recovery % for sediment ($\chi^2 = 6.39$, df = 1, $p < 0.05$, Figs. 2 and 3) in the "Herbivory" than in the "No herbivory" treatment indicating that herbivory enhances the movement of nitrogen towards the sediment. We did not find statistical differences for ^{15}N recovery % in unlabeled plants ($\chi^2 = 2.97$, df = 1, $p > 0.05$; Figs. 2 and 3) even though the mean for the "Herbivory" treatment is three times and a half larger than the "No herbivory" treatment.

Discussion

Our study shows that grasshoppers can enhance sediment N cycling in black needlerush-dominated salt marshes, as well as a tendency that it can enhance also in plants. Similar results have been found in other habitats (Table 1). Lovett and Ruesink (1995) also reported feces enrichment for gypsy moths fed with enriched black oak. In a ^{15}N enrichment experiment with gypsy moth feces and black oak leaf litter, soil and red oak seedlings showed higher enrichment with enriched feces than with enriched litter after 2 years (Christenson et al. 2002). Higher enrichment occurred in soils of Scot pine forests with enriched European sawfly feces than with enriched pine litter (Fogal and Slansky 1985). The values found in our study are similar to the ones reported in these terrestrial ecosystems (see Table 1). These results can be surprising taking into account that our study lasted only 3 months, while the studies for terrestrial ecosystem lasted between 1 and 3 years, and that our system is under tidal influence, which could export feces out of the system. Moreover, grasshopper herbivory on black needlerush marshes in the northern Gulf of Mexico is frequently modest, although variable in time and space (Parson and de la Cruz 1980; Wason and Pennings 2008; Hunter et al. 2015; Sparks and Cebrian 2015). In our experiment, grazing levels averaged 1.35 (SD = 1.37) on a

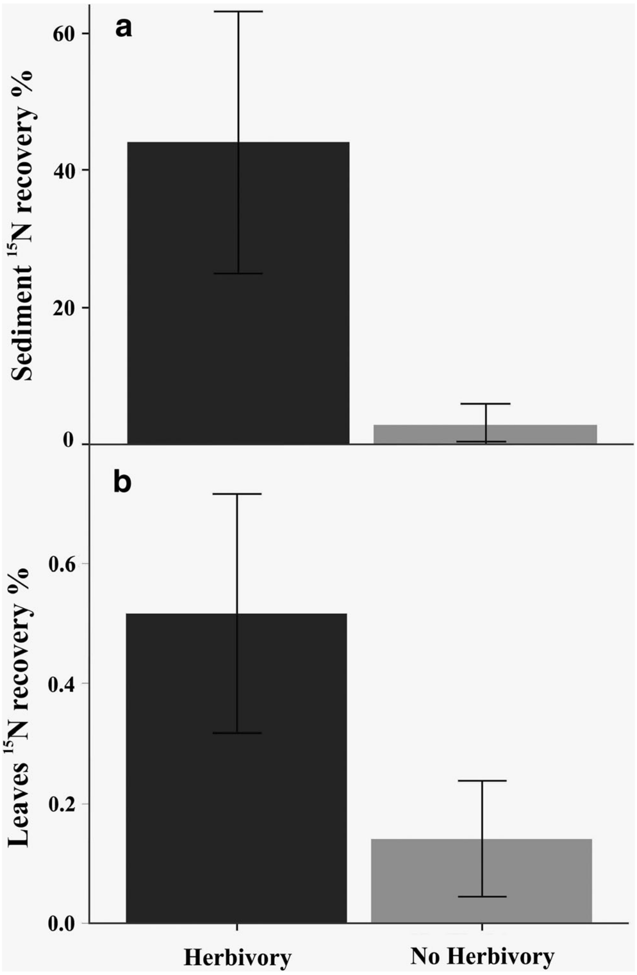

Fig. 2 ^{15}N recovery % (mean + SD) for sediment (**a**) and plants (**b**) with and without herbivory in the mesocosm experiment

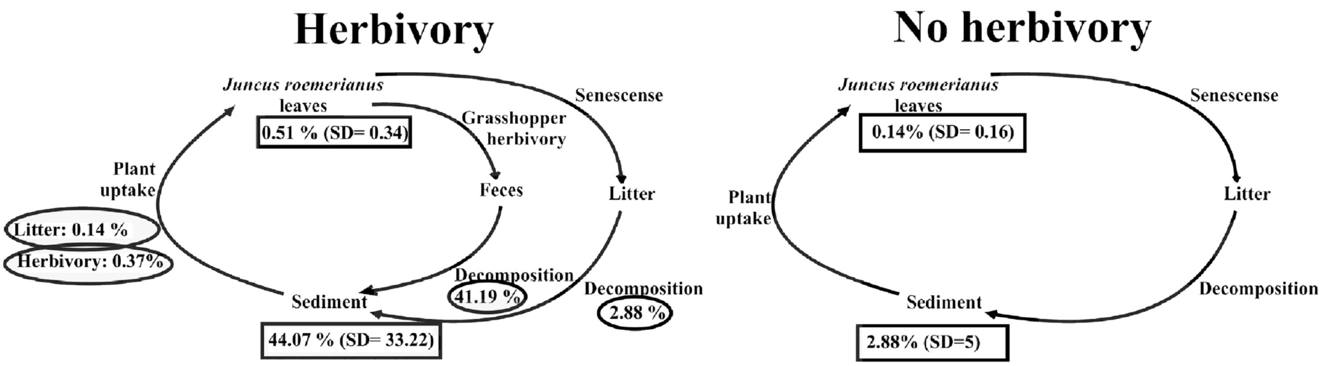

Fig. 3 Diagram of ^{15}N recovery % (percentage from the initial ^{15}N in labeled plants and litter) for sediment and plants. The percentages inside circles indicate the ^{15}N recovery through herbivory or litter pathways (estimated by subtracting the values obtain for sediment and plants in the "No herbivory" treatment to the values obtained for sediment and plants in the "Herbivory" treatment), while the percentages inside squares indicate the total ^{15}N recovery for that compartment

range of 0 to 5 (see Sparks and Cebrian 2015). Thus, despite relatively modest levels of herbivory, short time period, and tidal flushing, our results suggest that grasshoppers can have an important role in nutrient cycling in black needlerush marshes sediment, similar to what was found for terrestrial systems.

Such enhancement in nutrient cycling likely occurs through the production of feces. Tree and marsh plant detritus decomposes slowly, and nutrients may remain immobilized in the detritus for a relatively long time (Enríquez et al. 1993). For example, 78% of the initial ^{15}N remained as undecomposed black oak detritus after 2 years (Christenson et al. 2002) and 35.6% in beech detritus after 3 years (Zeller et al. 2000). Black needlerush leaves decompose at a rate of approximately 40% per year (de la Cruz and Gabriel 1974; Christian et al. 1990), and significant detritus nutrient immobilization may also occur in these marshes (Hunter et al. 2015). N in herbivore feces is mobilized more quickly than the N of plant tissues (Christenson et al. 2002) and can have higher nutrient contents (Le Mellec et al. 2009). In addition, lignin and other fibrous compounds may be partially digested in feces. Thus, herbivore feces functionally transform less available-nutrient, hardy leaf detritus into richer detritus that are more easily degradable by microbes, which eventually results in higher nutrient cycling rates.

Our experiment ran for 9 weeks. This time period was long enough to allow for isotope incorporation into the sediment and plants, but at the same time short enough to avoid experimental spurious effects and/or artificial conditions. However, while this duration may have allowed for most feces decomposition and cycling, it does not allow for long-term leaf litter decomposition. Thus, it is possible that N recovery in sediment and plants from leaf litter decomposition in black needlerush marshes is higher than quantified in our experiment. Nevertheless, even accounting for long-term leaf litter decomposition (40% of leaf litter is decomposed per year), our results suggest that grasshopper herbivory has a significant role in marsh nutrient cycling. In fact, the values obtained in our study are probably underestimated because grasshoppers consumed both labeled and unlabeled plants and we are quantifying the ^{15}N recovery % coming only from the labeled plants. Taking into consideration this dilution error and the

Table 1 Comparison of ^{15}N recovery (percentage from the initial) for different species with ^{15}N enrichment methodology

Studied species	Type of study	^{15}N source	Compartment	% of ^{15}N recovery	Duration	Reference
Quercus velutina litter to *Quercus rubra* seedlings	Field experiment	Feces	Soil (0–3 cm)	17	2 years	Christenson et al. 2002
			Leaves	0.12		
		Litter	Soil (0–3 cm)	1.9		
			Leaves	0.093		
Quercus rubra	Mesocosm	Feces	Soil (0–5 cm)	32.07	1 year	Frost and Hunter 2007
			Leaves	10.88		
Fagus sylvatica	Field experiment	Litter	Soil (0–2 cm)	37.9	3 years	Zeller et al. 2000
			Leaves	2		
Juncus roemerianus	Mesocosm	Feces + litter	Sediment (0–2 cm)	44.07	3 months	Our study
			Leaves	0.51		
		Litter	Sediment (0–2 cm)	2.88		
			Leaves	0.14		

large difference in the means of the two treatments, the not significant differences in plants could become significant ones.

In addition, grasshoppers can enhance nutrient cycling through means other than direct consumption and feces production. Grasshoppers feed on the thin nutrient-rich outermost layer along the upper half of black needle leaves (Parson and de la Cruz 1980). The deep indentations and shredding left with this feeding behavior promotes breakage of leaf upper sections, which may still have substantial green, photosynthetically active areas (Sparks and Cebrian 2015). Detrital green leaves produced as a result of herbivory normally have higher nutrient contents than senesced, brown leaves that shed naturally (Risley and Crossley 1993), and as a result, they also decompose faster than their senesced, brown counterparts (Menendez and Sanmartí 2007). In fact, in Appalachian forested watersheds green litter produced by herbivory is an important source of N to the soil (Risley and Crossley 1988, 1993). This could also be the case in black needlerush marshes in the Northern Gulf of Mexico, given the magnitude of apparent leaf breakage due to grasshopper herbivory (Hunter et al. 2015; Sparks and Cebrian 2015). The role of grasshoppers in nutrient cycling, both through direct consumption and feces production and through increased breakage of green leaf sections, could be heightened in marshes subject to high levels of anthropogenic nutrient enrichment, where higher leaf nutrient contents may lead to more intense herbivory levels (Sparks and Cebrian 2015).

Salt marshes are known for being a sink of anthropogenic derived nutrients by incorporating the excess nutrients in their biomass (Valiela et al. 2000). In this sense, *J. roemerianus* salt marshes can be important sinks of N because they effectively remove N from pore water (Sparks et al. 2015), but, conversely, *J. roemerianus* salt marshes have low herbivory rates and decomposition rates, which results in large amounts of biomass left for storage or export outside the ecosystem (Hunter et al. 2015). In this sense, our study gives new insight of how low to moderate herbivory rates can enhance nutrient cycling within the ecosystem. Enhanced nutrient cycling intensifies the role of these salt marshes as nutrient sinks through the incorporation of N in the sediment and potentially in their biomass. This enhancement could also affect sediment metabolism (Vivanco et al. 2015) and lead to higher plant nutritional quality, which can accelerate decomposition rates (Enríquez et al. 1993) and herbivory levels (Sparks and Cebrian 2015).

Conclusion

Our study indicates that herbivory enhances sediment N cycling in black needlerush salt marshes, even with low/moderate herbivory rates and under tidal influence, which in turn can enhance the role of salt marshes as N sinks. Thus, any changes in the grasshopper population, for example, due to human disturbance, could have an effect in the nutrient cycling of salt marshes, and therefore in their ecosystem function.

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