

Coastal wetland stability maintained through counterbalancing accretionary responses to chronic nutrient enrichment

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Abstract. The link between anthropogenically modified nutrient loading and coastal wetland stability is not well understood due to limited data from long-term experiments and inconsistent findings from investigations thus far. In this study, we present results from a 13-year oligohaline marsh fertilization experiment aimed at determining whether eutrophic conditions compromise ecosystem stability, defined here as the capacity to keep pace with sea level rise and resist the erosive forces of high-energy meteorologic events. To accomplish this objective, we measured soil surface elevation change and soil shear strength, along with a suite of regulatory processes that included belowground standing crop, belowground decomposition, organic and mineral matter accumulation, soil accretion, and shallow subsidence. Our results identified an apparent compensatory effect of nutrient enrichment on accretionary processes whereby shallow subsidence, attributed to reduced live root standing crop, was balanced by enhanced accretion resulting from greater organic matter accumulation at the soil surface. Consequently, the rate of marsh elevation change measured over a five-year period was unaffected after more than a decade of experimental nutrient enrichment. Furthermore, the structural integrity of the soil matrix did not deteriorate under elevated nutrient conditions; decomposition rates were similar to control plots, and although live root standing crop was reduced, the root system was evidently stronger, as soil strength tended to increase rather than decrease after nutrients were provided for 13 years. Our data suggest that enhanced nutrient loading is an unlikely destabilizing mechanism in this coastal marsh and possibly others. However, additional long-term research will be required in a diverse range of habitats and environmental settings before broad-based, general conclusions concerning the effects of nutrient enrichment on coastal wetland stability can be made with a high degree of certainty.

Key words: *belowground standing crop; elevation change; Louisiana; mineral sediment accumulation; nutrient enrichment; oligohaline marsh; organic matter accumulation; organic matter decomposition; shallow subsidence; soil accretion; soil shear strength; wetland stability.*

INTRODUCTION

Anthropogenic alterations to global nutrient budgets are coupled to an array of ecological impacts currently affecting estuarine and near-shore marine environments around the world (Diaz and Rosenberg 2008). Consequently, a growing number of valuable ecosystem services are at risk of being compromised by nutrient-induced degradation of coastal habitats (MEA 2005, Barbier et al. 2011). Coastal wetlands occupy a critical interface between upland nutrient sources and estuarine receiving basins, serving as nutrient sinks that buffer adjacent ecosystems (Fisher and Acreman 1999, Valiela and Cole 2002, Sousa et al. 2008). Numerous fertilization experiments have demonstrated the nutrient assimilation and transformation capacity of these ecologically

important ecosystems via enhanced plant growth and nutrient uptake (Sullivan and Daiber 1974, Mendelsohn 1979, Cargill and Jefferies 1984, Boyer et al. 2001, Drake et al. 2009, Frost et al. 2009, Graham and Mendelsohn 2010) and microbially mediated processes such as denitrification (Davis et al. 2004, Gardner and White 2010, Koop-Jakobsen and Giblin 2010, VanZomeren et al. 2012). Soil sorption, burial, and organic matter accumulation have also been identified as important long-term nutrient sinks in coastal wetlands (DeLaune et al. 1981, White and Howes 1994, Sundarshwar and Morris 1999, Drake et al. 2009, Loomis and Craft 2010).

Although coastal wetlands are important regulators of near-shore water quality, they are also vulnerable to eutrophication. Nutrient over-enrichment can influence an array of functional and structural characteristics, including primary production, community metabolism, consumer activity, carbon sequestration, competitive hierarchies, and species composition, to name a few (Morris and Bradley 1999, Pennings et al. 2002, Crain

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2007, Bertness et al. 2008, Slocum and Mendelsohn 2008, Frost et al. 2009, Graham and Mendelsohn 2010, Ramirez et al. 2012). Eutrophic conditions can further influence ecosystem structure and function by creating an environment that is prone to species invasions and loss of biodiversity (Chambers et al. 1999, Silliman and Bertness 2004, Tyler et al. 2007). Indeed, these implications underscore the importance of understanding how excess nutrient availability affects complex feedbacks that regulate ecosystem stability, as global climate change threatens coastal wetlands around the world with inundation due to a higher sea level and more intense storms (Knutson et al. 2010, IPCC 2013). Yet the links between nutrient enrichment, altered structure and function, and ecosystem stability are currently not well established.

To remain stable, coastal wetlands must (1) maintain an intertidal elevation by accreting soil vertically at a rate that paces relative sea level rise, and (2) resist the erosive forces of storm-generated waves and surge. Both vertical accretion and erosion resistance are mediated in large part by plant biomass contributions to soil organic matter (Nyman et al. 2006, McKee et al. 2007, Howes et al. 2010, Kirwan and Mudd 2012). However, recent research provides conflicting evidence as to the fate of coastal wetlands enduring chronically eutrophic conditions. For example, some have concluded that excess nutrient availability causes coastal wetland deterioration, and consequently, increased vulnerability to tidal inundation and erosion (Turner et al. 2009, Kearney et al. 2011, Deegan et al. 2012). Others have observed no net deleterious effect of enhanced nutrient supply on ecosystem function or the ability of coastal wetlands to keep pace with sea level rise (Langley et al. 2009, Anisfeld and Hill 2012, Day et al. 2013), and in a few cases, have even shown that nutrient enrichment stimulates accretionary processes (Morris et al. 2002, Fox et al. 2012). Furthermore, direct evidence supporting the proposition that nutrient enrichment creates a soil environment that is more susceptible to erosion is limited in scope (Turner et al. 2009, Turner 2011). Thus, accurately predicting the consequences of coastal wetland eutrophication and mitigating against any potential losses of important ecological and economic services caused by coastal wetland degradation requires a better understanding of the effects of nutrient enrichment on ecosystem stability.

In this paper, we present results from a 13-year oligohaline marsh fertilization experiment that investigated the effects of nutrient enrichment on soil surface elevation change, soil shear strength, and the belowground processes that regulate them, including belowground standing crop, belowground decomposition, organic and mineral matter accumulation, soil accretion, and shallow subsidence, to determine whether excess nutrient loading compromises the capacity to maintain an intertidal elevation and resist erosion. We predicted that eutrophic conditions enhance organic and mineral

matter deposition at the soil surface (a result of increased aboveground biomass and stem density), reduce living root and/or rhizome standing crop, but have no effect on the rate of belowground organic matter decomposition. Thus, we expected that nutrient enrichment does not compromise elevational stability due to the combined effects on individual processes, but the structural integrity of the soil matrix deteriorates as a consequence of reduced belowground standing crop.

MATERIALS AND METHODS

Site description and experimental design

We established a fertilization experiment in a *Sagittaria lancifolia* L. dominated oligohaline (i.e., intermediate-brackish) marsh located along the Tchefuncte River ~1 km north of its point of drainage into Lake Pontchartrain, Louisiana, USA (30°23'21" N, 90°09'37" W), a brackish estuary with hydrologic connection to the Gulf of Mexico. This study site is a relatively fertile, river-fed coastal wetland with a diverse plant community (Slocum and Mendelsohn 2008) and Histosol soil (Kenner Series [Trahan et al. 1990]). Marsh flooding results from a combination of microtidal influence (10-cm tide range [Swenson and Chuang 1983]), wind shifts during frontal passages that affect water levels in Lake Pontchartrain and the Tchefuncte River, and rainfall-driven fluctuations in Tchefuncte River discharge. Hydrologic characteristics of a nearby site ~300 m from the present study area within the same relatively uniform contiguous marsh platform indicate that soil surface inundation occurs on average (1999–2006) approximately every other day to a depth of 15 cm with surface water that has the following average water quality characteristics: salinity = 1.6 g/L, inorganic nitrogen (N) = 0.26 mg/L, total N = 0.79 mg/L, and total phosphorus (P) = 0.11 mg/L (Graham and Mendelsohn 2010).

In July 1999, we established three 2 × 2 m plots at each of five randomly selected locations (i.e., statistical blocks) along a 200-m transect paralleling a small bayou that drains into the Tchefuncte River ($n = 15$ plots total). Randomly selected plots at each location initially received three N–P–potassium (K) fertilization treatments ($n = 5$ per treatment): an unfertilized control, a “medium” fertilization treatment consisting of 200 kg N·ha⁻¹·yr⁻¹, 51 kg P·ha⁻¹·yr⁻¹, and 99 kg K·ha⁻¹·yr⁻¹, or a “high” fertilization treatment consisting of 1200 kg N·ha⁻¹·yr⁻¹, 306 kg P·ha⁻¹·yr⁻¹, and 594 kg K·ha⁻¹·yr⁻¹. Nutrient enrichment treatment levels were maintained for 13 years using a blended fertilizer mixture containing 3.6% ammoniacal-N, 12.2% urea-N, 9.2% P₂O₅-P, and 7.8% K₂O-K, which was applied twice during the growing season by surface broadcast in April and July of 1999 through 2011. Our medium fertilization treatment level approximated nutrient loading rates measured in wetlands near the Caernarvon diversion of the Mississippi River (234 kg N and 20 kg P·ha⁻¹·yr⁻¹ [Lane et al. 1999]), whereas our high

fertilization treatment level was originally based on the level of N enrichment needed to achieve maximum aboveground biomass in stands of *Spartina alterniflora* L. (Mendelssohn 1979), but also represents conditions of more extreme nutrient enrichment, such as in Narragansett Bay marshes where calculated N loading rates exceeded $10\,000\text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (Wigand et al. 2003).

In August 2001, each $2 \times 2\text{ m}$ plot was split into two $1 \times 2\text{ m}$ plots to identify the possible effects of herbivory. Exclusion fencing (2.5 cm mesh, plastic-coated wire) was installed around one of the two split-plots chosen at random to exclude medium- to large-sized ground-dwelling herbivores (e.g., nutria). Fertilization continued as before, regardless of fencing, thus creating a nutrient enrichment by herbivory factorial treatment arrangement, with six treatment combinations replicated at five locations. However, this paper focuses only on the effects of nutrient enrichment, as described in *Statistical analysis*.

Surface elevation change, soil accretion, and shallow subsidence

We measured soil surface elevation change over a five-year period from 2005 to 2010 (7–12 years after initiating fertilization) using rod surface-elevation tables (rSETs [Cahoon et al. 2002]). A total of 15 rSETs (one per plot) were established in July 2004 along the centerline separating the exclosed split-plots from the non-exclosed split-plots. Benchmark rods were driven in to the soil until refusal, $\sim 6\text{--}10\text{ m}$, and allowed one year to equilibrate. On 27 June 2005, initial baseline rSET measurements were made along six directional headings within each plot (three directions per split-plot, each separated by 45°) following standard operating procedures (Cahoon et al. 2002). Subsequent measurements were repeated every 6–12 months thereafter for a total of eight readings over an 1823-day (5-year) time period ending on 24 June 2010. Cumulative elevation change over time was then calculated for each arm-direction as the pin-averaged difference between the baseline readings and each successive measurement.

We determined soil accretion as the vertical accumulation of mineral sediment and organic matter above two $0.25 \times 0.25\text{ m}$ feldspar marker horizons laid down in each plot (one per split-plot) at the time of the baseline rSET readings on 27 June 2005. All subsequent accretion measurements coincided with each successive elevation change measurement. For each accretion measurement, soil cores that penetrated the feldspar layer were extracted using a cryogenic coring apparatus (Cahoon et al. 1996), which prevented compaction and preserved an intact (i.e., frozen) feldspar layer. Upon extraction, the height of material above the feldspar layer was measured to the nearest millimeter at three to four locations around each core, and averaged.

Simultaneous measurements of surface elevation change and soil accretion were utilized to determine shallow subsidence. Prior to calculation, elevation

change measurements by arm-direction were averaged to obtain a single value for each split-plot (two per plot) for each time period. Shallow subsidence was then calculated by difference (i.e., accretion – elevation change = subsidence). This method accounts for subsidence that occurs between the bottom of the benchmark rod and the feldspar marker horizon initially located at the soil surface, but not at depths below the benchmark rods. However, deep subsidence was assumed to be uniform across the 200-m study area during the five-year measurement timeframe and considered negligible compared to shallow subsidence (Törnqvist et al. 2006).

Mineral sediment and organic matter accumulation

In conjunction with each accretion measurement, except those in April 2007, mineral sediment and organic matter accumulation were measured by collecting a separate core to the same depth as the feldspar horizon using a 7.62 cm diameter aluminum core tube. The contents of each core were dried and weighed to determine soil bulk density (Blake and Hartge 1986), and then ground and combusted at 550°C to determine organic/mineral matter content (Christenson and Malmros 1982). The product of vertical accretion, soil bulk density, and soil organic/mineral matter content was then utilized to calculate mineral sediment and organic matter accumulation over time.

Belowground organic matter decomposition

We measured belowground decomposition using litterbags (6 cm wide \times 30 cm long, 1-mm nylon mesh) filled with a manually homogenized, 1-g (air-dried) sample of the naturally occurring soil macro-organic matter mixture collected from a representative location within the study marsh. To determine the initial oven-dried mass of the litterbag fill material, 10 1-g air-dried samples were dried to a constant mass at 60°C and weighed ($0.89 \pm 0.005\text{ g}$; mean \pm SE). In August 2005 (year 7 of fertilization), 16 litterbags were inserted into the soil of each plot (eight bags per split-plot) using a hand trowel so that the material inside each bag was positioned between 10 and 15 cm below the soil surface. One randomly selected bag was subsequently retrieved from each split-plot after approximately 1 week, 3 weeks, 6 weeks, 3 months, 6 months, 1 year, 1.5 years, and 2 years. Upon retrieval, the material remaining inside each bag was carefully rinsed over a 1-mm mesh screen to insure complete removal of sediment, and any obvious ingrown roots and rhizomes were discarded. The remaining material was then dried to constant mass at 60°C and weighed.

Soil shear strength

We determined soil shear strength in both the dormant and active growing seasons (February and September 2011; 12 and 13 years after initiating fertilization, respectively) using a 5 cm long shear vane

attached to a direct-reading torque gauge (Geotechnics Limited, Auckland, New Zealand). During each season, soil shear strength was measured at four sampling locations in each plot (two per split-plot) from the soil surface to a depth of 50 cm in 5-cm intervals. The procedure consisted of inserting the shear vane into the soil, twisting the vane until soil failure, pushing the vane in to the soil an additional 5 cm, and repeating.

Belowground standing crop

We determined belowground standing crop biomass by extracting two 7.62 cm diameter by 50 cm long soil cores from each plot (one per split-plot) in September 2011, after 13 years of fertilization. Upon removal, cores were sectioned into 5-cm increments and subsequently sieved over a 2-mm mesh screen to remove mineral sediment and fine particulate organic matter. The material from each increment was then categorized as live roots, live rhizomes, and dead roots + rhizomes using a combination of characteristics that included color, turgidity, and evidence of decomposition (e.g., epidermal lesions and resistance to breakage). When necessary, a dissecting microscope (3 \times magnification) was used to examine the belowground material in more detail. After sieving and sorting, all material was dried to a constant mass at 60°C and weighed. The belowground material was then assessed in three different ways: by depth as collected, summed over the top 30 cm of soil (i.e., the active rooting zone), and in the top 5 cm of soil only (i.e., the most likely region of observable treatment effects). The maximum depth increment to which living roots and rhizomes extended (i.e., rooting depth) was also determined.

Statistical analysis

We performed all data analyses using SAS (2011). Prior to statistical analysis, temporal measurements of mineral sediment and organic matter accumulation, soil accretion, shallow subsidence, and elevation change by arm-direction were converted to rates using linear regressions forced through the origin. Decomposition rates (i.e., exponential decay [k] constants) were obtained in the same manner after data were natural log-transformed to fit an exponential decay curve. Subsequent statistical tests were performed on regression-based rates only. For elevation change, rates by rSET arm-direction were used to increase statistical power, but specified as nested sampling units (i.e., subsamples) to avoid pseudo replication.

As previously stated, this paper focuses only on the effects of nutrient enrichment, although an herbivory treatment was included in the experimental design. To justify doing so, we used multivariate analysis of variance (MANOVA) to test the overall effects of nutrient enrichment, herbivory, and their interaction on all dependent variables as a group. Prior to performing the MANOVA, estimates of belowground standing crop were summed by depth, and soil shear

strength was averaged by depth and season. Overall, the MANOVA test statistic (Wilks' lambda) indicated that the effect of nutrient enrichment ($P = 0.06$) and herbivory ($P = 0.07$) warranted further independent investigation, but the nutrient \times herbivory interaction was insignificant ($P = 0.68$). Nonetheless, our statistical model included the complete split-plot experiment within a randomized block design, which tested the effects of nutrient enrichment (whole-plot), herbivory (split-plot), season (soil shear strength only), the repeated effect of soil depth (soil shear strength and belowground standing crop only), and their interactions using a mixed model analysis of variance (ANOVA). Differences among treatment means were tested post-ANOVA using the Tukey-Kramer multiple comparison test. In addition, we used Pearson correlation analysis to identify a bivariate relationship between soil shear strength and rooting depth.

For all statistical tests, we verified assumptions of normality and homoscedasticity by examining normal probability and residual plots, respectively. To meet these assumptions, live (root + rhizome) standing crop in the top 5 cm of soil and soil shear strength data required cube root transformation, while the remaining belowground standing crop data, excluding dead biomass in the top 5 cm of soil, required natural log transformation. For presentation of results, untransformed arithmetic means and standard errors (SE) were used.

RESULTS

Belowground standing crop

Dead (root + rhizome) standing crop was relatively uniform throughout the 50-cm soil profile, but the standing crops of live roots and rhizomes decreased significantly ($P \leq 0.05$) with increasing depth (Fig. 1a). Living root standing crop was similar in the 0–5 cm and 5–10 cm depth increments, significantly lower in the 10–15 cm depth increment, negligible from 15 to 35 cm in depth (i.e., ≤ 3 g/m² per 5 cm depth increment), and absent at deeper depths to 50 cm. Live rhizome standing crop followed a similar depth distribution as roots, but biomass was uniform to a slightly deeper depth of 15 cm. Below 15 cm, rhizome standing crop decreased rapidly, becoming absent at depths deeper than 20 cm.

Rooting depth (i.e., the depth extent of living roots and rhizomes) showed an increasing trend with increasing nutrient enrichment, but differences among treatment means were not significant ($P = 0.11$; Fig. 1b). In contrast, the standing crop of live roots decreased significantly with increasing nutrient enrichment in the top 5 cm, and showed a similar nonsignificant decreasing trend in the top 30 cm of soil (Table 1). As a result of significantly lower live root standing crop in the top 5 cm of soil, nutrient enrichment also tended to influence live (root + rhizome) standing crop within the 0–5 cm depth increment ($P = 0.08$), although treatment means were not statistically different from each other ($P = 0.15$, Tukey-Kramer multiple comparison test). Nutrient

enrichment did not significantly affect live rhizome, dead (roots + rhizomes), or total (live + dead) standing crop in either the top 5 cm or top 30 cm of soil, or live (roots + rhizomes) standing crop in the top 30 cm of soil.

Belowground organic matter decomposition

Belowground organic matter decomposition in litterbags was generally slow, but followed a typical exponential decay curve (Fig. 2a). An initial loss in mass of ~10% occurred for all treatments in the first week, but this was followed by additional losses of <15% over the next two years. As a result, >75% of the material remained at the end of the deployment period, regardless of treatment. Decay (k) constants were similar among fertilized and control plots, though the rate of decomposition was significantly higher in moderately enriched plots compared to those receiving the high nutrient enrichment treatment (Fig. 2b).

Soil shear strength

The depth profile of soil shear strength ranged from 10.0 ± 0.4 kPa to 6.6 ± 0.3 kPa (Fig. 3a). Soil strength was uniform from 0 to 15 cm, decreased significantly from 15 to 30 cm, and remained relatively constant from that level to a depth of 50 cm. The strength of the soil profile (0–50 cm) was significantly greater in the dormant season compared to the active growing season (main effect of season, $P = 0.0001$; 8.7 ± 0.2 kPa vs. 7.4 ± 0.2 kPa, respectively). The strength of the soil profile also tended to increase with increasing nutrient enrichment ($P = 0.10$, Tukey-Kramer multiple comparison test; Fig. 3b). Corresponding with the effect of nutrient enrichment, there was a highly significant, positive correlation between soil strength and rooting depth ($r = 0.63$, $P = 0.0002$; Appendix: Fig. A1).

Mineral sediment and organic matter accumulation

Mineral sediment and organic matter accumulation on the soil surface (i.e., above the feldspar marker horizon) were approximately equal in mass, but each followed a distinctly different pattern over time. Mineral sediment accumulation followed a pattern consistent with sediment deposition accompanying the landfall of Hurricanes Katrina and Gustav on 29 August 2005 and 1 September 2008, respectively (Fig. 4a). In all plots, soil surface mineral matter content was elevated initially following both hurricanes but not sustained over time. High nutrient enrichment plots tended to have higher rates of mineral matter accumulation compared to moderately enriched plots ($P = 0.06$, Tukey-Kramer multiple comparison test), but neither treatment was different from the control (Fig. 4b). In contrast, organic matter accumulated relatively steadily over time, though to a lesser extent hurricane impacts also appeared to positively influence organic matter accumulation, particularly in plots receiving high nutrient enrichment after Hurricane Gustav (Fig. 4c). However, the consistent response to fertilization throughout the measurement

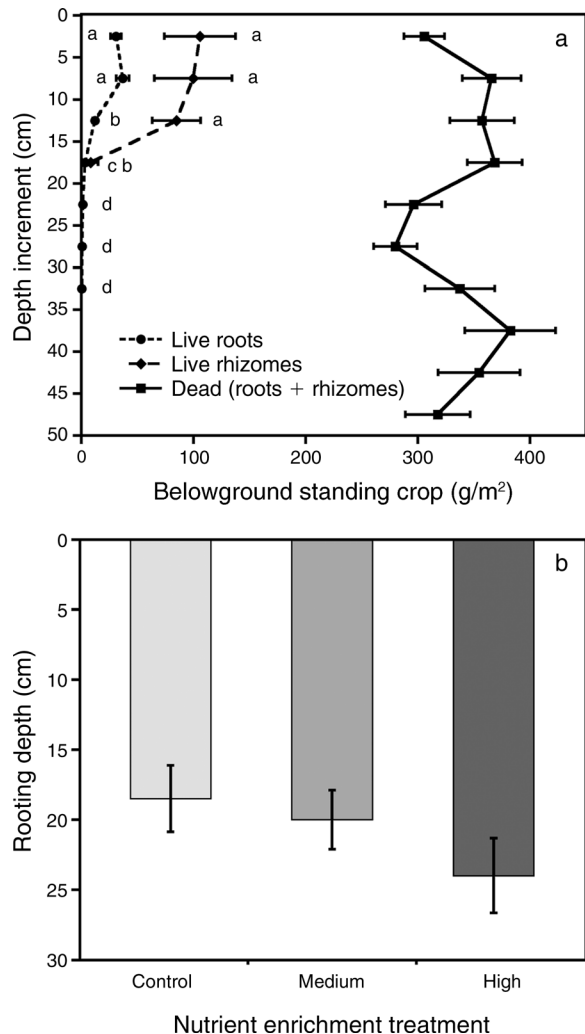


FIG. 1. (a) Live root, live rhizome, and dead standing crop (mean \pm SE) with respect to depth (5 cm increments, 0–50 cm; averaged over split-plot herbivory and whole-plot nutrient enrichment treatments). Different letters identify differences among means ($P \leq 0.05$; Tukey-Kramer multiple comparison test). Where two letters appear at the 15–20 cm depth increment, the letter on the left indicates live roots and the letter on the right live rhizomes. At depths below 20 cm, live rhizomes were not present, and letters indicate living roots. Below 35 cm, living roots were absent. (b) Rooting depth (mean \pm SE) with respect to whole-plot nutrient enrichment treatments (averaged over split-plot herbivory treatments).

time frame (except in June 2008) resulted in overall rates of organic matter accumulation that increased significantly with increasing nutrient enrichment (Fig. 4d).

Accretion, elevation change, and shallow subsidence

Patterns of soil accretion, elevation change, and shallow subsidence (i.e., accretion minus elevation change) were consistent throughout the study (Fig. 5). Surface accretion increased uniformly in all plots over time, though at rates that were significantly greater with increasing nutrient enrichment (Fig. 5a, b). However,

TABLE 1. Belowground standing crop (g/m^2) in the top 5 cm and top 30 cm of soil.

| Depth and standing crop | Control | Medium | High |
|-------------------------|----------------------|----------------------|---------------------|
| 0–5 cm | | | |
| Live roots | 45 ^a ± 11 | 33 ^{ab} ± 6 | 14 ^b ± 3 |
| Live rhizomes | 97 ± 32 | 182 ± 86 | 39 ± 15 |
| Live (roots + rhizomes) | 142 ± 37 | 215 ± 89 | 53 ± 15 |
| Dead (roots + rhizomes) | 307 ± 34 | 315 ± 28 | 294 ± 35 |
| Total (live + dead) | 450 ± 59 | 530 ± 102 | 347 ± 43 |
| 0–30 cm | | | |
| Live roots | 112 ± 25 | 90 ± 18 | 55 ± 9 |
| Live rhizomes | 253 ± 76 | 367 ± 146 | 277 ± 126 |
| Live (roots + rhizomes) | 365 ± 85 | 457 ± 158 | 332 ± 130 |
| Dead (roots + rhizomes) | 2097 ± 150 | 1928 ± 146 | 1897 ± 104 |
| Total (live + dead) | 2462 ± 188 | 2385 ± 223 | 2229 ± 110 |

Notes: Significantly different effects of nutrient enrichment treatments (mean ± SE) are shown by different superscript letters ($P \leq 0.05$, Tukey-Kramer multiple comparison test).

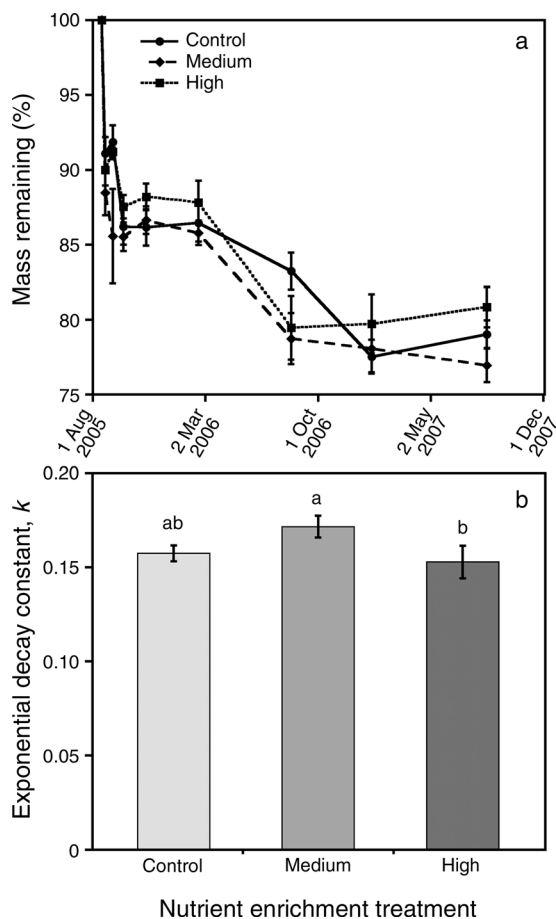


FIG. 2. (a) Percentage mass remaining over time and (b) exponential decay rates of belowground organic matter in litterbags (mean ± SE) with respect to whole-plot nutrient enrichment treatments (averaged over split-plot herbivory treatments). In panel (b), different letters identify differences among means ($P \leq 0.05$; Tukey-Kramer multiple comparison test).

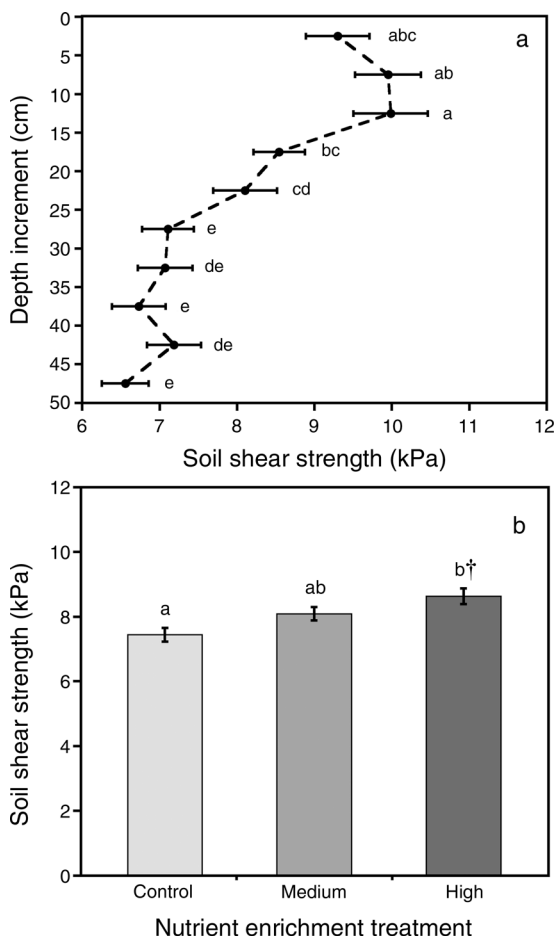


FIG. 3. Soil shear strength (mean ± SE) with respect to (a) depth (5-cm increments, 0–50 cm; averaged over split-plot herbivory and whole-plot nutrient enrichment treatments) and (b) whole-plot nutrient enrichment treatments (averaged over split-plot herbivory treatments, season, and depth). Different letters identify differences among means ($P \leq 0.05$, † $0.05 < P \leq 0.10$; Tukey-Kramer multiple comparison test).

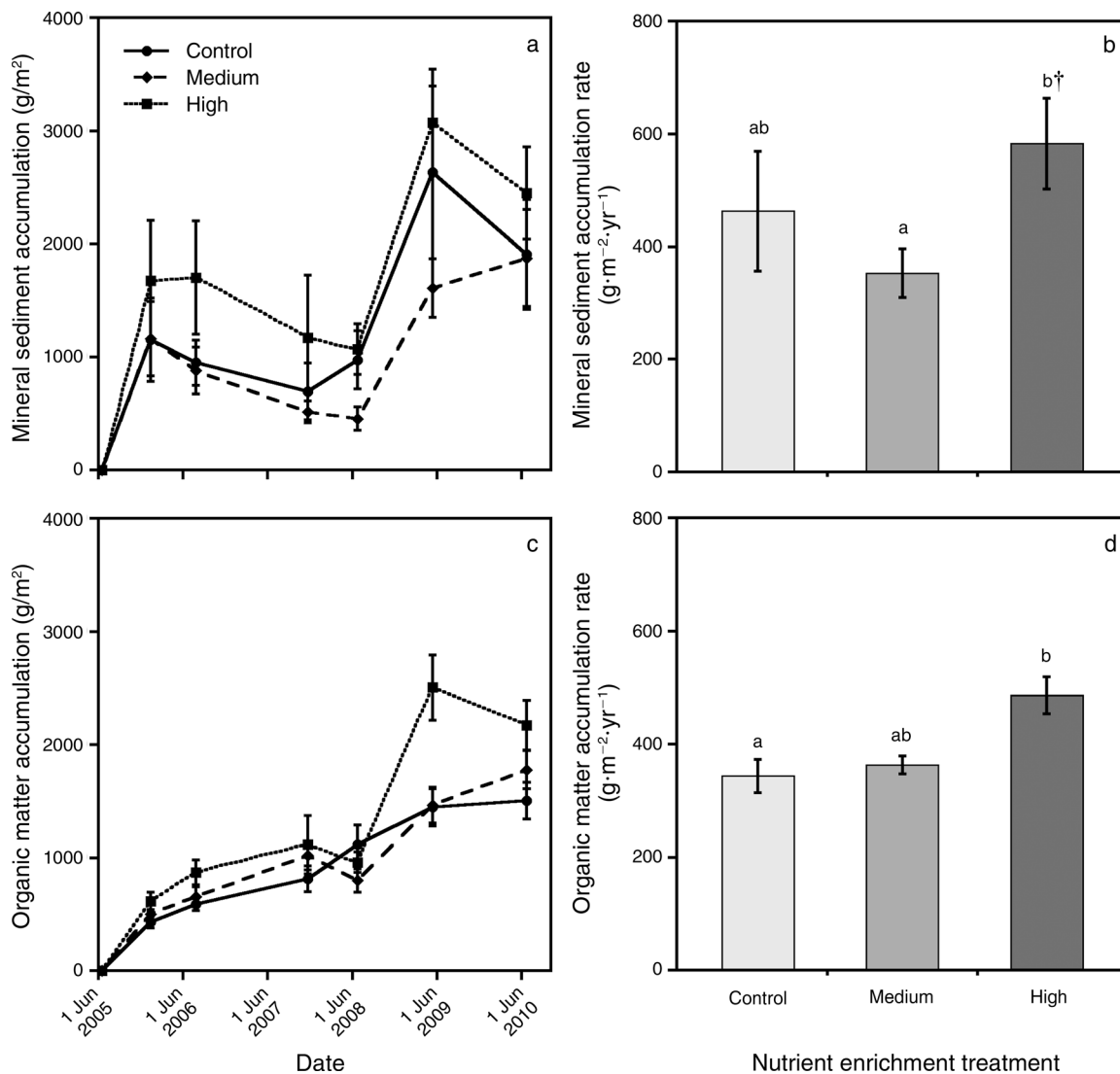


FIG. 4. Temporal trends and linear regression-based rates of (a, b) mineral sediment accumulation and (c, d) organic matter accumulation (mean \pm SE) with respect to whole-plot nutrient enrichment treatments (averaged over split-plot herbivory treatments). In panels (b) and (d), different letters identify differences among means ($P \leq 0.05$, † $0.05 < P \leq 0.10$; Tukey-Kramer multiple comparison test).

nutrient-enhanced accretion did not influence elevation change, which was similar among all plots throughout the study period, with corresponding rates that were not significantly affected by nutrient enrichment (Fig. 5c, d). Rather, shallow subsidence showed a nonsignificant trend ($P = 0.18$), increasing by sevenfold with increasing nutrient enrichment, though high variability across time periods as well as nutrient enrichment treatments was evident (Fig. 5e, f).

DISCUSSION

Belowground standing crop, decomposition, and soil shear strength

As expected, increasing nutrient availability decreased live root standing crop to where it was significantly

lower in the top 5 cm of soil, and nonsignificantly lower on average in the top 30 cm of soil. The negative effect of nutrient enrichment on living roots similarly influenced live (root + rhizome) standing crop, but only in the top 5 cm of soil. Nonetheless, these results support a growing body of scientific literature that has shown eutrophic conditions can reduce living belowground standing crop, and more specifically root standing crop, with significant rhizome standing crop reductions occurring less frequently (Valiela et al. 1976, Hines et al. 2006, Darby and Turner 2008a, b, Davey et al. 2011, Ket et al. 2011, Deegan et al. 2012). Thus, reduced root biomass appears to be a likely consequence when nutrients are available in excess, because plants can acquire the nutrients necessary to sustain maximum

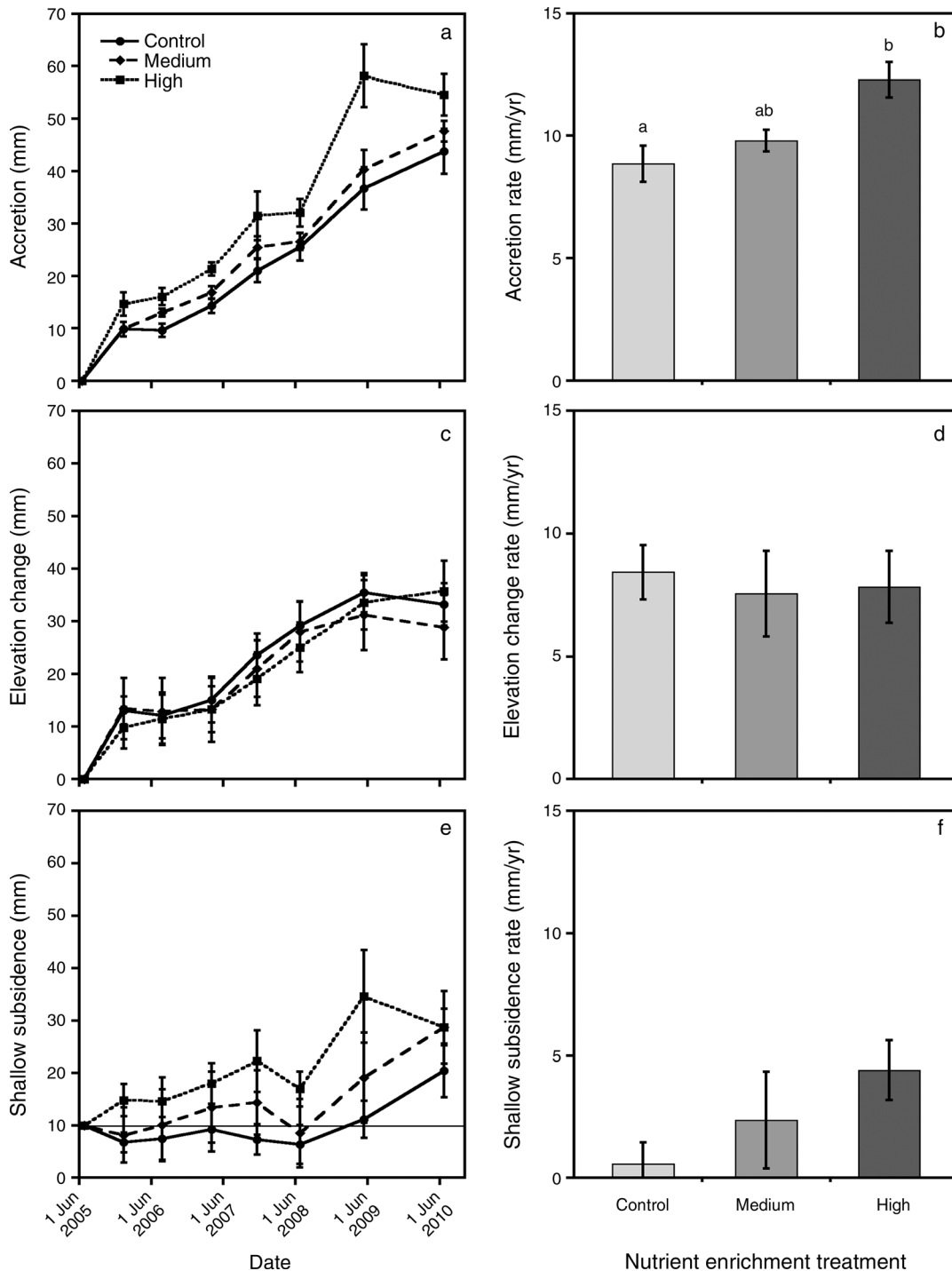


FIG. 5. Temporal trends and linear regression-based rates of (a, b) soil accretion, (c, d) elevation change, and (e, f) shallow subsidence (mean \pm SE) with respect to whole-plot nutrient enrichment treatments (averaged over split-plot herbivory treatments). In panel (b), different letters identify differences among means ($P < 0.05$; Tukey-Kramer multiple comparison test). The letters do not appear in panels (d) and (f) because there were no statistical differences among means.

growth with fewer roots compared to nutrient-limited conditions, where root proliferation is essential for nutrient acquisition (Hodge 2004, Cahill and McNickle 2011). In contrast, total (live + dead) standing crop is

generally unaffected by nutrient enrichment within the time frame of most investigations (Gallagher 1975, Haines 1979, Buresh et al. 1980, Wigand et al. 2004, Hunter et al. 2008, Anisfeld and Hill 2012), and we are

aware of only two negative responses in coastal wetlands (Morris and Bradley 1999, Ket et al. 2011). However, a more recent interpretation of the Morris and Bradley (1999) results suggests that the significant reduction in total belowground standing crop observed after 13 years of fertilization may have been due to dilution of soil organic matter resulting from enhanced mineral sedimentation caused by a fertilization-induced increase in aboveground stem density (Morris et al. 2002).

In our study system, the vast majority of total belowground standing crop was categorized as dead biomass, which was an order of magnitude greater than live biomass. Thus, the effect of nutrient enrichment on belowground decomposition potentially represented a major pathway for altered ecosystem function. However, as predicted, soil organic matter decomposing in litterbags for two years was unaffected by nutrient enrichment when compared to the control. These results were corroborated by our dead belowground standing crop results, which showed no changes in biomass after 13 years of nutrient additions.

Similar results showing no effect were found by other coastal wetland fertilization studies utilizing the litterbag method as a direct measure of organic matter decomposition in nutrient-amended soil (Valiela et al. 1985, Jordan et al. 1989, Feller et al. 1999, Rybczyk et al. 2002, McKee et al. 2007, Anisfeld and Hill 2012). However, of these studies, only Valiela et al. (1985), Feller et al. (1999), and Anisfeld and Hill (2012) used organic matter that was internally enriched with nutrients, while the remainder, including the present study, incubated unenriched organic matter in nutrient-enriched soil (i.e., external enrichment). A previous review of wetland decomposition experiments concluded that external nutrient enrichment generally has no effect on rates of organic matter decomposition, while internal enrichment of plant tissue can accelerate decay rates, but only during the initial stages of decomposition (Rybczyk et al. 1996). For example, aboveground *Spartina alterniflora* and *Spartina patens* tissue grown in N-fertilized plots lost more mass during the first year of decomposition when excess nutrients were provided, but mass losses were similar to control treatments at the end of the 700-day study (Valiela et al. 1985). These results correspond with a more recent meta-analysis showing that external N enrichment stimulated high-quality organic matter decomposition, but inhibited recalcitrant tissue breakdown, with no overall significant effect (Knorr et al. 2005). Further, N enrichment consistently altered microbial community structure, depressed microbial activity, and reduced the ability of extracellular enzymes to decompose recalcitrant organic matter in soils from a broad range of ecosystems, including wetlands and coastal environments (Ramirez et al. 2012).

To some extent, litterbag results contrast with nutrient-enhanced decomposition indirectly measured as soil respiration (Morris and Bradley 1999, Wigand et

al. 2009, Anisfeld and Hill 2012) and loss of cotton-strip tensile strength (Feller et al. 1999, Laursen 2004, Turner 2011). However, these distinct responses likely result from a number of methodological artifacts. For instance, soil respiration is a cumulative measure of CO₂ efflux produced by both microbes and plant roots. In forest soils, the contribution of root respiration to total soil respiration ranged from as little as 10% to as much as 90% (Hanson et al. 2000), and thus could potentially account for a sizable portion of soil respiration in wetland soils as well. Furthermore, soil CO₂ efflux from wetland microcosms was found to be primarily associated with the decomposition of labile carbon sources (Entry 2000), which typically represent a small but active fraction of the soil carbon pool (Zou et al. 2005, Dodla et al. 2012). Therefore, cotton strips composed almost entirely of cellulose, a relatively labile carbon source (Slocum et al. 2009), do not reflect the heterogeneity of substrate quality in soil organic matter undergoing decomposition. Feller et al. (1999) demonstrated this inconsistency in a mangrove swamp where nutrient enrichment accelerated cotton strip decomposition but had no effect on plant tissue simultaneously decomposing in litterbags. Nonetheless, results obtained using both indirect methods (i.e., soil respiration and cotton strips) do reinforce findings that suggest a shift in microbial activity to the preferential decomposition of labile organic matter occurred with nutrient enrichment (Ramirez et al. 2012).

Based on the assumption that belowground biomass and organic matter decomposition directly affect soil shear strength, we expected the nutrient-induced reduction in live root standing crop to correspond with a concomitant reduction in the force required to induce soil failure. Unlike mineral sediment, roots and rhizomes form an interconnected network that can effectively distribute shear stress over a larger volume of soil. For instance, our results show that regardless of nutrient enrichment treatment, significant reductions in soil shear strength with depth occurred where living roots and rhizomes decreased to negligible quantities between 15 and 25 cm beneath the soil surface. Furthermore, soil strength was relatively constant at depths below 25 cm where living biomass was either absent or present in such small quantities as to likely have little influence on soil matrix integrity. Therefore, soil shear strength appears to be directly related to the quantity of living belowground biomass, since the depth distribution of dead standing crop was relatively uniform throughout the soil column to a depth of 50 cm, and there was no significant effect of nutrient enrichment on the rate of organic matter decomposition. Yet, in contrast to our prediction, nutrient enrichment had no negative effect on soil shear strength despite reduced live root standing crop. In fact, the opposite occurred; the force required to induce soil failure tended to increase with increasing nutrient enrichment over the depth-averaged 50 cm profile. These results suggest that even though fewer

roots were present in fertilized plots, the root system tended to be stronger, which correlated significantly with increased rooting depth.

The tendency for nutrient enrichment to enhance soil shear strength was unexpected and in opposition to the results of others. Turner et al. (2009) and Turner (2011) concluded that greater nutrient availability reduces soil shear strength, and thereby increases the vulnerability of coastal wetlands to erosion. However, in both studies, significantly lower soil shear strength due to nutrient enrichment was identified only at depths where living roots and rhizomes were likely present in minimal quantities, or not at all, compared to surface depths (i.e., 25–30 cm and 60–100 cm, respectively for the two studies). Hence, their results suggest that nutrient enrichment affects the strength of dead biomass by stimulating recalcitrant organic matter decomposition. While this is contrary to our findings and those of others, we acknowledge that different processes may be occurring at deeper depths.

In an oligohaline marsh receiving nutrient-laden Mississippi–Atchafalaya River water, lower soil shear strength coincided with a more decomposed substrate, compared to a similar marsh not receiving diverted river water (Swarzenski et al. 2008). However, in their study, marsh soils with lower shear strength had higher porewater sulfide concentrations and lower soil redox potential in addition to having higher porewater N and P concentrations. Thus, in this case, reduced soil strength may more likely be attributable to changes in hydrology caused by river water influx, the effect of increased sulfate loading on soil organic matter dynamics, or sulfide-induced impacts on root growth rather than greater N and P availability. Likewise, in eutrophic salt marshes in Jamaica Bay, New York, USA, lower soil strength occurred where lower intertidal elevations produced more saturated soil conditions (Wigand et al. 2014), which again indicates that local hydrology is an important regulator of soil shear strength.

Accretion, elevation change, and subsidence

Previous research at the present site, using the same fertilized plots, established that nutrient enrichment increased aboveground standing crop by as much as 41% (Slocum and Mendelsohn 2008), while additional research at a nearby site, within the same contiguous marsh, further established that net aboveground primary production increased 36–54% with increasing N enrichment (Graham and Mendelsohn 2010). Therefore, it was not surprising that organic matter accumulation at the soil surface was also significantly higher when additional nutrients were supplied. Similarly, greater aboveground plant growth corresponded with greater accretion in fertilized salt marshes (Anisfeld and Hill 2012, Fox et al. 2012). In contrast, the vegetation's ability to trap mineral sediment did not show a clear response to nutrient enrichment in the present study; there were no significant differences in the rate of

mineral sediment accumulation between fertilized plots and control plots, although plots receiving high nutrient enrichment had the greatest rates of sediment accumulation. Rather, sediment accumulation was strongly influenced by two hurricanes that made landfall near the site (Katrina in 2005 and Gustav in 2008), which could have masked the effects of nutrient enrichment. However, periods of high sediment accumulation did correspond with high organic matter accumulation, particularly in plots receiving high nutrient enrichment after Hurricane Gustav. Thus, fertilization may have enhanced the vegetation's ability to trap storm-induced allochthonous organic matter, or alternatively, nutrient enrichment in combination with storm-induced mineral sediment deposition may have further stimulated aboveground plant growth and litterfall. Regardless of the mechanism, these results, in combination with those showing reduced root standing crop and unaffected organic matter decomposition (relative to the control) following nutrient enrichment, indicate that organic matter accumulation was the dominant process driving nutrient-enhanced soil accretion in this oligohaline marsh.

Interestingly, enhanced soil accretion in nutrient-amended plots did not coincide with enhanced surface elevation change. Anisfeld and Hill (2012) observed a similar response in nutrient-amended salt marsh plots, although a nonsignificant increasing trend was apparent in their results. In contrast, there were no elevation trends across nutrient enrichment treatments in the present study; elevation change was comparable during all sampling periods, and overall rates of change were not significantly different. Instead, we observed a nonsignificant trend resulting in a sevenfold increase in shallow subsidence rates with increasing nutrient enrichment, which offset the nutrient-enhanced accretion rates.

Since no other measured processes were negatively affected by nutrient enrichment, the most likely mechanism driving what appeared to be greater rates of shallow subsidence was lower root standing crop in the surface soil of fertilized plots. Living roots are turgid structures, and even small reductions in biomass can have potentially important implications for soil volume, especially in coastal wetlands with organic soil (Nyman et al. 1990). In fact, root volume was directly related to shallow subsidence in mangrove forests (McKee et al. 2007). Others have calculated that a single gram of soil organic matter is volumetrically equivalent to 4–22 g of mineral sediment in coastal wetland soil (Turner et al. 2000, Neubauer 2008). Thus, the loss of root biomass and consequent effect on soil volume is a likely contributor to apparent changes in shallow subsidence rates following nutrient enrichment.

CONCLUSIONS

By the end of this century, global mean sea level is projected to increase by 26–82 cm (IPCC 2013), and

warmer sea surface temperatures combined with greater atmospheric moisture content are anticipated to increase average storm intensity by 2% to 11% (Knutson et al. 2010). For coastal wetlands, it has been suggested that anthropogenically enhanced nutrient supply may intensify the effects of global climate change by contributing to altered ecosystem function that facilitates instability (e.g., Turner et al. 2009, Kearney et al. 2011, Deegan et al. 2012). However, in contrast to these predictions, we observed an apparent compensatory effect of nutrient-enhanced organic matter accumulation at the soil surface that negated shallow subsidence associated with reduced root standing crop. As a result, the capacity to maintain an intertidal elevation did not diminish, even after more than a decade of experimental nutrient additions. Furthermore, we observed no evidence that elevated nutrient conditions negatively affect soil matrix integrity, even though nutrient enrichment reduced live root standing crop. The root system was evidently stronger, as soil strength tended to increase rather than decrease after additional nutrients were provided. In sum, we observed no negative changes in the stability of this oligohaline marsh after 13 years of nutrient enrichment, which is among the longest coastal wetland fertilization experiments to date. Based on these results, the ability of this marsh, and possibly others, to keep pace with sea level rise and resist the erosive forces of high-energy meteorologic events will likely not be compromised by enhanced nutrient loading. However, before broad-based, general conclusions concerning the effects of nutrient enrichment on ecosystem stability can be made with a high degree of certainty, similar long-term research will be required in a diverse range of coastal wetlands that differ by salinity, species composition, hydrology, morphology, and specific nutrient inputs, among other factors.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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