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Benthic primary production and nitrogen cycling in *Spartina alterniflora* marshes: effect of restoration after acute dieback

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Abstract The sudden and massive *Spartina alterniflora* dieback at the turn of the millennium generated numerous unanswered questions regarding its mechanistic causes and consequences. This study, conducted during 2007–2008, aimed to elucidate mechanisms of recovery and determine whether recovery was accelerated by replanting efforts. The onset of a severe drought during the summer of 2007, however, provided a potential glimpse into the mechanisms driving dieback events. Study sites were established in two of the hardest hit states, Georgia and Louisiana. Each site had a replicated block design consisting of the following four treatments: reference, dieback, dieback with low density replanting (90 cm spacing), and dieback with high density replanting (30 cm spacing). To assess biogeochemical cycling and ecosystem functioning, we quantified rates of nitrogen fixation, potential nitrification, potential denitrification, and benthic production biannually. All measured process rates decreased following the drought year of 2007. Nitrogen fixation was positively correlated with benthic production rates in Louisiana, while denitrification was positively correlated with benthic production rates in Georgia and Louisiana. The lack of decreased benthic production during the 2007 drought could indicate that benthic microphytes cope with better with drought than plants, but may be outcompeted during non-drought years. Replanting efforts significantly increased ecosystem recovery in Louisiana and to a lesser extent in Georgia.

Keywords Microphytobenthos · Spartina marsh · Acute dieback · Photosynthesis · N cycling

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Introduction

Intertidal marshes are essential components of coastal ecosystems and provide critical ecosystem services, generating 10.6 of the 33 trillion dollars worth of services globally each year (Costanza 1997). Global climate change and associated sea level rise may jeopardize the crucial ecosystem services provided by marshes (Craft et al. 2009). Compared to the chronic impacts of sea level rise, climate change will likely result in more acute impacts on ecosystem

functioning, such as the sudden marsh dieback observed in US Eastern and Gulf coast states between 1999 and 2001. Record losses of vegetation cover were observed during that period: marsh dieback affected 158,000 ha in Louisiana (McKee et al. 2004) and 800 ha in Georgia (Ogburn and Alber 2006). The dieback events coincided with the most intense drought over the last century in Louisiana (Swenson et al. 2004) and the driest 3 year period ever recorded in Georgia (Alber et al. 2008). Similar but smaller scale dieback events occurred in both states during the exceptionally dry year of 2007 (Alber et al. 2008).

*Spartina alterniflora w*as the only plant species that suffered dieback in Louisiana, while both *S. alterniflora* and *Juncus roemerianus* suffered dieback in Georgia (McKee et al. 2004; Alber et al. 2008). Many causes have been hypothesized for theses plant dieback events, including fungal pathogens (Schneider et al. 2004), grazing of *Littoria irrorata* (Silliman and Bertness 2002; Silliman et al. 2005), and biogeochemical factors such as increased salinity, water deficit, increased acidity, and/or metal toxicity (Gambrell and Patrick 1978; McKee et al. 2004; McKee et al. 2006; Mendelssohn et al. 2006). Mesocosm experiments with Louisiana marsh soil suggested that interaction between increased salinity, decreased pH, and increased release of Fe and Al reduced the capacity of *S. alterniflora* to endure low-impact stressors and led to near complete mortality (Mendelssohn et al. 2006). Since the early millennium massive dieback event, marshes in both Louisiana and Georgia have shown some recovery (McKee et al. 2006; Alber et al. 2008). With extreme droughts expected to become more common in the future (Randall et al. 2007), understanding the causes of mortality and the path to recovery are crucial. In this study, we examined the impacts of dieback on marsh primary production coupled to the cycling of the primary limiting nutrient in these ecosystems, nitrogen (Vitousek and Howarth 1991).

Primary production in marshes arises from both macrophytes and microphytes. Historically, *S. alterniflora* was thought to be the dominant primary producer in salt marsh ecosystems (Odum and de la Cruz 1967; Nixon 1980). Pioneering work by Haines (1977) led to the realization that benthic microalgae (BMA), largely diatoms and cyanobacteria, accounted for a surprisingly large and unrecognized fraction of marsh primary production with temperature and salinity primarily controlling BMA production (Rasmussen et al. 1983; MacIntyre et al. 1996). Marsh consumers, like filter feeders, were thought to be more dependent on phytoplankton than *S. alterniflora* (Haines 1977) but later, microphyte primary production was shown to be an equally important component of the estuarine food web (Pomeroy et al. 1981; Pinckney and Zingmark 1993a, b). The importance of labile BMA production to the food web arises from the fact that *S. alterniflora*-derived organic matter must go through the detrital food web before utilization by higher level consumers; in contrast, BMA-derived organic matter is directly available. Numerous studies have shown that up to 50 % of the carbon in higher trophic levels originates from BMA production (Haines 1977; Peterson and Howarth 1987; Sullivan and Moncreiff 1990) and that BMA production is strongly linked to bacterial respiration (Middelburg et al. 2000).

The diatom-dominated BMA community in Georgia marshes differ greatly from the Louisiana marshes, which hosts extensive, cyanobacteria-dominated microbial mats up to several cm thick (Joye et al. 2003; Joye and Lee 2004). The proliferation of laminated microbial communities, e.g. microbial mats, maintains tight coupling in energy and nutrient cycling between autotrophs and heterotrophs over small (mm) spatial scales (Joye and Paerl 1994). From an ecosystem perspective, the abundance of cyanobacteria is relevant for the following reasons. First, cyanobacterial dominance results in the BMA community being able to sustain both carbon and nitrogen fixation (Joye and Lee 2004) in a generally N-limited habitat (Vitousek and Howarth 1991). Second, despite tight internal cycling, microbial mat communities can export significant amounts of mat derived-material to the coastal and marsh ecosystems, making them a potential source of labile organic carbon to the coastal environment (Bouillon et al. 2000; Joye and Lee 2004).

Given the possibility of increased frequency of severe drought in coastal regions, understanding how recent massive marsh dieback events influence carbon and nitrogen cycling in these key coastal ecosystems is crucial. We examined the relationship between nitrogen cycling and BMA productivity in marshes in Louisiana and Georgia following acute dieback events. By transplanting different densities of *S. alterniflora* into previously barren dieback areas, we assessed the effect of regrowth on BMA production and nitrogen cycling. We estimated N-fixation,

nitrification (NTR), and denitrification (DNF) rates in slurry experiments. We hypothesized that vegetation dieback would increase BMA production, which would subsequently stimulate N cycling processes. The results illustrate the interactions between BMA production, NTR, DNF and N-fixation after recent massive dieback events and shed light on how re-vegetation may affect these interactions.

Methods

Study site

Spartina alterniflora marshes that suffered acute, sudden dieback from 1999 to 2001 on Sapelo Island in Georgia (31°24′N, 81°17′W) and near Port Fourchon in Louisiana (29°08′N, 90°13′W) were the focus of this work. Sampling plots on Sapelo Island were selected near the ferry dock at Marsh Landing on the southwest side of the island and near Dean Creek on the southeast side of the island. The sites at Port Fourchon were selected along a small canal parallel to the main port canal. The geomorphology and hydrology of Georgia and Louisiana marshes differs substantially. Louisiana salt marshes are microtidal (0.3 m tidal range) and are subject to diurnal tidal inundation. In contrast, the Georgia coast is subject to semi-diurnal inundation by a mesotidal (2.5 m) regime. The difference in tidal dynamics influenced the development of different benthic microbial primary producer communities: surface sediments in Louisiana were inhabited by well-developed cyanobacterial mats while surface sediments in Georgia were dominated by diatom biofilms.

Experimental design

In the spring of 2006, 6 treatment blocks per site were assigned randomly in areas affected by marsh dieback and boardwalks were constructed to minimize disturbance due to sampling. Each block was divided into 4 plots (60 m^2) for different treatments: a reference plot (hereafter, Ref), which exhibited no evidence of dieback, and three dieback plots. One of the dieback plots was left bare (hereafter B) and the other two were replanted with either high density (30 cm plant spacing; hereafter, HD) or low density (90 cm plant spacing; hereafter, LD) of *S. alterniflora* from the same ecotone as the specific site (Hester et al. 2009). Sampling was done in the spring and fall of 2007 and 2008 for four samplings in total.

Sample collection

On each sampling trip, a 30 cm deep soil core was collected from each plot using a 10 cm diameter Russian Peat Corer. From the cores, two depths were analyzed, the root zone (0–5 cm) and below the root zone (25–30 cm) for estimates of NTR and DNF analyses (stored at 4 °C). The 2008 sampling trips included an additional sampling of the 10–15 cm zone. To estimate rates of BMA production and N-fixation, cores were collected using 4-cm diameter, 5 cm long PVC tubes. These cores were stored at ambient temperature, moisture, and irradiance conditions until BMA production and N-fixation assays were performed. In each plot, random triplicate 1-cm deep sediment samples were collected for chlorophyll (*a–c*) analysis. A few drops of $MgCO_3$ were added to the sediment surface to stabilize the chlorophyll and samples were stored on ice in the field, and subsequently frozen at −20 °C until analysis (Strickland and Parsons 1972). After primary production rate assays were completed, the cores were subsampled to determine N-fixation rates and chlorophyll concentration.

Rate assays

Oxygenic photosynthesis

Oxygen depth profiles and rates of gross oxygenic photosynthesis (GOP) were determined using the light–dark shift technique and UNISENSE® oxygen microsensors (microelectrodes), a picoammeter, and a computer-controlled micromanipulator to position the microsensors (Revsbech and Jørgensen 1983; Revsbech et al. 1983; Jonsson 1991; Joye and Lee 2004). Measurements were conducted immediately upon returning to the laboratory (in less than a week) except for fall 2007 samples due to logistical issues (variable storage for up to 2 months). Benthic chlorophyll concentrations did not change significantly during storage for Louisiana samples but increased slightly for Georgia Ref samples during the fall 2007; chlorophyll normalization of primary production rates corrected for changes in chlorophyll during storage.

Oxygen concentration and GOP rates were estimated in 150 μm steps from roughly 1,000 μm above the sediment surface to the depth of zero oxygen concentration below the sediment water interface; concentrations and rates were integrated from the sediment surface to the depth of zero oxygen concentration via trapezoidal integration. Oxygen production rates were quantified at 0, 100, and 1,000 μmol quanta m^{-2} s^{-1}, reflecting dark conditions, the average daily irradiance, and maximum summer irradiance, respectively. Each core was allowed to equilibrate for 30 min at an individual light intensity and then triplicate profiles were run for each core/light intensity to capture heterogeneity. After the profiles were completed, a cut-off 5 ml syringe was used to collect a 1 cm deep, 1 cm^2 sediment sample for analysis of chlorophyll *a–c*. The cyanobacteria-dominated Louisiana samples were extracted using 5 ml of 45:45:10 (acetone:methanol:water) and sonicated on ice twice for 30 s with a shaking step in between (Strickland and Parsons 1972). Georgia diatom-dominated samples were extracted using 5 ml of 100 % acetone and sonicated on ice once (Strickland and Parsons 1972). Chlorophyll concentrations were quantified using spectrophotometry (Strickland and Parsons 1972); these data were used to estimate the chlorophyll-*a* specific GOP rate. To estimate the total BMA areal production for the different treatments, GOP rates were corrected for their proportional areal coverage (Hester et al. in preparation) (BMA area = 100 % − % *S. alterniflora* cover).The low light intensity and high light intensity represent the range of rates found in the field.

Nitrogen fixation

Rates of nitrogen fixation were measured using the acetylene reduction method (Stewart et al. 1967; Joye and Lee 2004) in treatments that lacked *S. alterniflora* cover (Georgia: LD and B; Louisiana: LD, HD and B) since preliminary results indicated no detectable N-fixation in the Ref treatment for both Georgia and Louisiana and the HD treatment for Georgia. During storage (<2 weeks), samples were kept moist with filter sterilized (0.2 μm) site-specific sea water in an incubator under a representative light intensity (200–400 μmol quanta m^{-2} s^{-1}) with a 10:14 h (light:dark) periodicity. Estimates of N-fixation were made during simulated day and night conditions, as described below. Using a cut-off 5 ml syringe, 4 cores of 1 cm^2 × 1 cm deep were taken from each sample and placed upright in a 20 ml serum vial. Each vial was purged with He for ~5 min to create anoxic conditions. Without disrupting the mat sample, 5 ml of filtered (0.2 μm), He-purged sea water was added. Acetylene (10 % v/v) was added by replacing 2 ml of the vial headspace with purified acetylene gas. One of the four serum vials for each mat was sampled immediately as a time zero by vortexing the vial and displacing the head space into a syringe with 3 M NaCl. The remaining three samples were incubated either during the daytime (at representative light intensity, 200–400 μmol quanta m^{-2} s^{-1}) or at night (covered in aluminum foil to prevent laboratory light interference) and subsequently sampled as described for the time zeros. Gas samples were then transferred into a 5 M NaCl-filled serum vial (by injecting the gas and displacing the brine). Gas samples were stored upside down at room temperature prior to ethylene concentration quantification using flame ionization detection gas chromatography and comparison to certified ethylene standards (Scott Specialty Gases®, Scotty III) (Joye and Lee 2004).

Potential nitrification

Potential nitrification assays (pNTR) were conducted the part in yellow is correct within 24 hours of collection using the amended slurry method (Bodelier et al. 1996) in the spring and fall of 2008. Five ml of sediment collected from the 0–5 cm depth horizon were mixed in a 50 ml serum vial with 25 ml of oxygenated (bubbled with air for ~30 min) of filtered sea water amended with 0.33 g/l $(NH_4)_2SO_4$ to bring the NH_4^+ concentration to 5 mM and the buffering agents 0.14 g/l K_2HPO_4 and 0.027 g/l KH_2PO_4. Each serum vial was wrapped in aluminum foil and plugged with a cotton ball and Al foil cap to prevent evapotranspiration and light inhibition of ammonia-oxidizing bacteria. High sulfide concentrations in Louisiana marsh soils during required that vials be shaken with unamended sea water for 10 h before the adding the ammonium to start the assay (this was done in spring attempting to reduce variability observed in the fall). Oxic conditions were confirmed using a polarographic oxygen sensor. After the addition of ammonium, vials were shaken at 150 rpm at 25 °C and aqueous sub-samples (2 ml) were collected using a cut-off pipette tip at time 0 and after 1, 18 and 36 h of

incubation. Water samples were centrifuged for 10 min and subsequently frozen at −20 °C until analysis for NO_x using Antek Instruments® model 745 with a vanadium reduction manifold coupled to a model 7050 nitrite oxide detector.

Potential denitrification

Potential denitrification rates (pDNF) were measured using the acetylene block method (Joye et al. 1996) using sediment samples that stored at 4 °C for (at most) 2 weeks. Slurries were generated by transferring 2 ml of sediment to a 20 ml serum vial and then purging the vial headspace with helium for 5 min. Next 5 mL of filtered site-specific seawater amended with glucose (200 μM) and nitrate (100 μM) and purged with He was added to each vial. Assays were initiated by replacing 2 ml of the vial headspace with acetylene (10 % v/v) generated from calcium carbide and passed through a water trap to remove contaminants. Samples were incubated at 15 °C while shaking gently (50 rpm) for 6 h. Time zero samples were terminated immediately after acetylene addition. To end the experiment, an 8 mL headspace subsample was collected after vortexing the sample and by adding 3 M NaCl to the vial and collecting the displaced headspace into a syringe. The gas phase was then transferred into a 5 M NaCl-filled serum vial by injecting the gas and displacing the brine. Gas samples were stored upside down at room temperature prior to analysis for N_2O concentration using electron capture gas chromatography; a precolumn and a 10 port Valco valve allowed venting of acetylene so that it did not reach the detector (Joye and Paerl 1994).

Statistical analyses

Statistical analyses were conducted in JMP 9. All data were tested for normal distribution before one-way ANOVA analyses were done (non-parametric Wilcoxon test in case of non-normal distribution) for the different treatments, collection depths, different sites and blocks with nested effects of replicates and using Tukey post-hoc's (or pairwise Wilcoxon) for pairwise comparison. Regression analysis was done between all processes measured. For Louisiana multivariate regression analysis was conducted to explain denitrification rates by all GOP rates (normalized, non-normalized, high light and low light) and N-fixation. Unless otherwise stated, significant differences indicate $p < 0.05$.

Results

Chlorophyll and gross oxygenic photosynthesis

Chlorophyll *a* concentrations were significantly higher in marsh soils from Louisiana (85.74 ± 114.5 mg m^{-2}) than Georgia (24.56 ± 18.39 mg m^{-2}). While no treatment effects were observed between Georgia plots, Ref plots in Louisiana exhibited lower chlorophyll *a* concentrations compared to all other plots. Chlorophyll *b* concentrations (Georgia: 3.86 ± 5.07 mg m^{-2}; Louisiana: 7.73 ± 23.7 mg m^{-2}) and *c* (Georgia: 6.88 ± 4.87 mg m^{-2}; Louisiana: 4.78 ± 10.5 mg m^{-2}) were consistently low.

Rates of GOP were low in Georgia marsh soils, while GOP rates were high in Louisiana marsh soils at both light intensities (Fig. 1). Overall, treatment effects were different at each sampling time and depended on the light intensity. At low light intensities in Georgia, the spring and fall of 2007 showed significantly higher GOP rates for HD and LD, respectively, than for B or Ref. Conversely, GOP rates in B plots were higher than Ref in both the spring and fall of 2008 (Fig. 1). Chlorophyll normalized GOP rates in Georgia show a similar pattern, except for the fall 2007, when normalized rates in B plots were higher than Ref (Fig. 2). In the spring of 2007 in Louisiana, GOP rates in the Ref treatment were lower than all others with LD having the highest rates (Fig. 1). In the fall 2007, Ref and LD had the lowest rates with the highest rates observed in B. In both fall and spring 2008, LD (spring: $p < 0.06$) and HD proved significantly higher than B and Ref. The chlorophyll normalized rates (Fig. 2) showed the same pattern as non-normalized rates for spring and fall 2007. However, in spring 2008 the normalized rates were lower in B than both HD and Ref. No significant treatment effects were observed for the normalized rates in fall 2008.

Under high irradiance, GOP rates in Georgia exhibited a slightly different pattern (Fig. 1) with higher activity in Ref plots than in HD or B in fall 2007. This pattern was not apparent in the chlorophyll-normalized rates (Fig. 2). The only significant difference in normalized rates was in spring 2008 with B

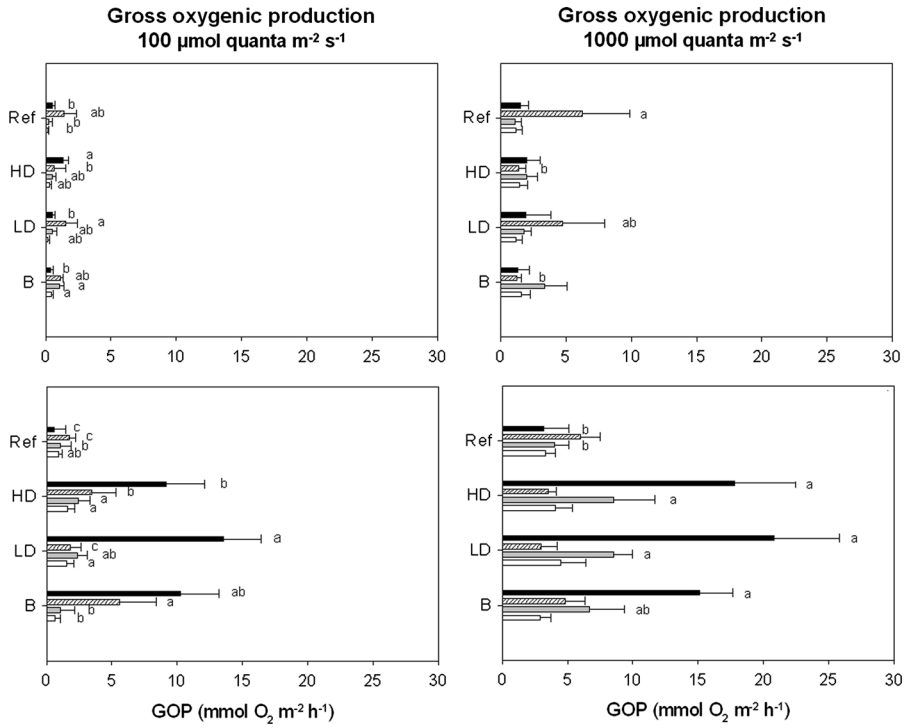

Fig. 1 Gross oxygenic production (GOP) incubated at 100 (*left*) and 1,000 (*right*) µmol quanta m^{-2} s^{-1}. The labels on y-axis represent reference (Ref), high density replanting (HD), low density replanting (LD) and dieback (B). The *top panels* represent Georgia (GA) and the bottom panels represent Louisiana (LA). The *bars* represent the mean for spring 2007 (*black*), fall 2007 (hatched), spring 2008 (*grey*) and fall 2008 (*white*). The *error bars* represent standard errors and *letters* indicate significant differences between treatments

being lower than Ref. No other treatment effects were significant in Georgia under high light conditions. In Louisiana, under high light conditions rates in B, LD and HD exceeded those in Ref in spring 2007 (Fig. 1). In spring 2008, however, only LD and HD were significantly higher than Ref. Chlorophyll normalized rates in LD were higher than Ref in spring 2007; while in spring 2008, LD and B were lower than HD and Ref. Surprisingly, in fall 2007, the Ref plots had the highest normalized rates (Fig. 2). The GOP rates for both light intensities showed differences between 2007 and 2008 with significantly lower rates in the spring of 2008 compared to 2007. In addition, the chlorophyll normalized rates were lower in 2008 than in 2007 (low light: $p = 0.0141$; high light: $p = 0.0002$) and fall (low light: $p = 0.0571$; high light: $p = 0.0020$).

Normalizing GOP rates by coverage area resulted in many similar patterns (Table 1). However, it revealed additional significant differences between treatments. At low light intensities, different patterns were found in every sampling time, except for spring 2007. For Georgia, B is larger than HD in fall 2007, while HD is not larger than LD in Louisiana. In the spring of 2008, B was found to be larger than HD and LD in addition to Ref while in Georgia B was smaller than LD instead of HD in Louisiana (2007). During the fall of 2008, LD was smaller than B for Georgia, while HD was no longer smaller than B (2007). At high light intensities, LD was larger than HD in both springs and fall 2008 for Louisiana. In the fall of 2007, Ref was not larger than any other treatment and even was smaller than B in Louisiana.

Nitrogen fixation

Nitrogen fixation rates observed in Georgia marsh soils were much lower than those observed in Louisiana (Fig. 3), with rates in the LD plots exceeding those in B plots ($p = 0.063$). Louisiana N-fixation rates exhibited no treatment effects during day or night time incubation. Daytime rates were significantly higher in spring 2007 compared to both fall 2007 and

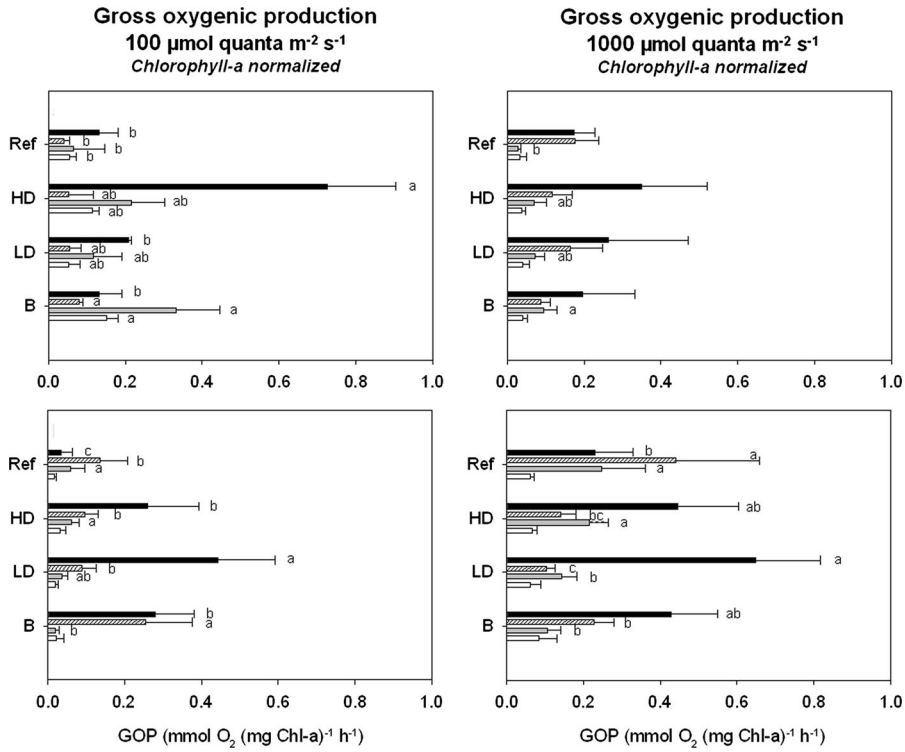

Fig. 2 Chlorophyll-*a* normalized gross oxygenic production incubated with 100 (*left*) and 1,000 (*right*) µmol quanta m^{-2} s^{-1}. The labels on y-axis represent reference (Ref), high density replanting (HD), low density replanting (LD) and dieback (B). The *top panels* represent Georgia (GA) and the *bottom panels* represent Louisiana (LA). The *bars* represent the mean for spring 2007 (*black*), fall 2007 (*hatched*), spring 2008 (*grey*) and fall 2008 (*white*). The *error bars* represent standard errors and *letters* indicate significant differences between treatments

spring and fall 2008. Rates from spring 2008 were higher than those in fall 2008. Nighttime rates showed no treatment effect and higher rates in spring 2007 compared to all other sampling times.

Potential nitrification

Potential nitrification rates were significantly higher for LD compared to all other treatments in the fall of 2008 in Georgia (Fig. 4). Potential nitrification rates were high and extremely variable (81.5 ± 122 nmol N $g^{-1}_{drysoil}$ h^{-1}) and, therefore, few significant treatment or temporal effects were noted. However, when comparing different sampling times, spring 2008 rates in Georgia showed the highest rates. Further, rates in the Georgia Ref plots in spring 2008 were higher than rates observed in Louisiana. Georgia fall pNTR rates were consistently higher than those measured in Louisiana.

Potential denitrification

Overall, pDNF were fairly low, but exhibited site, season and treatment specific patterns (average rates = Georgia: 1.4 ± 4.6 µmol N_2O $g^{-1}_{drysoil}$ h^{-1}; Louisiana: 1.6 ± 6 µmol N_2O $g^{-1}_{drysoil}$ h^{-1}) (Fig. 5). Rates of pDNF were higher in the root zone (0–5 cm) compared to the deep sediment (25–30 cm) for both Georgia and Louisiana. However, in Louisiana during spring 2007, higher pDNF rates were observed at 25–30 cm compared to 0–5 cm. Spring pDNF rates were consistently and significantly higher than fall rates for both Georgia and Louisiana. pDNF rates in Georgia were significantly higher than rates in Louisiana except for spring 2007 (only at 25–30 cm). Spring and fall pDNF rates proved to be significantly higher for both Louisiana and Georgia in 2007 compared to 2008. Treatment effects were observed in Louisiana only during fall 2007 at 25–30 cm depth

Table 1 BMA production for 2007 and 2008 (mmol O_2 m^{-2} h^{-1}) corrected for total bare area

Treatment	2007				2008			
	Spring		Fall		Spring		Fall	
	Low	High	Low	High	Low	High	Low	High
GA–B	0.37 ± 0.12b	1.25 ± 0.41	0.95 ± 0.45ab	1.27 ± 0.33	1.22 ± 0.30a	3.94 ± 1.14a	0.43 ± 0.11a	1.62 ± 0.31
GA–LD	0.47 ± 0.10b	1.98 ± 1.03	1.41 ± 0.50a	4.42 ± 1.64	0.49 ± 0.21b	2.06 ± 0.44ab	0.17 ± 0.06b	1.01 ± 0.24
GA–HD	1.17 ± 0.35a	1.78 ± 0.40	0.59 ± 0.18c	1.32 ± 0.37	0.40 ± 0.12b	1.35 ± 0.38b	0.24 ± 0.06ab	1.17 ± 0.29
GA–Ref	0.28 ± 0.08b	0.83 ± 0.24	0.74 ± 0.26c	3.2 ± 1.02	0.24 ± 0.10b	1.20 ± 0.25b	0.13 ± 0.03b	0.97 ± 0.21
LA–B	10.22 ± 1.51ab	15.09 ± 1.32ab	4.69 ± 1.59a	4.23 ± 0.87a	1.05 ± 0.35be	6.71 ± 1.38ab	0.64 ± 0.18b	2.93 ± 0.40ab
LA–LD	12.71 ± 1.35a	19.56 ± 2.26a	1.54 ± 0.33be	2.60 ± 0.56b	2.24 ± 0.43a	8.14 ± 1.09a	1.43 ± 0.28a	2.47 ± 0.38a
LA–HD	6.67 ± 0.80b	13.56 ± 2.03b	2.03 ± 0.59b	2.34 ± 0.43b	1.45 ± 0.23ab	5.22 ± 0.84b	0.95 ± 0.15ab	4.45 ± 0.90b
LA–Ref	0.24 ± 0.11c	1.34 ± 0.39c	0.73 ± 0.19c	2.50 ± 0.64b	0.33 ± 0.14c	1.23 ± 0.17c	0.41 ± 0.07b	1.38 ± 0.22b

"BMA low" represents yearly average benthic production at 100 µmol photons m^{-2} s^{-1} and "BMA high" represents yearly average production at 1,000 µmol photons m^{-2} s^{-1}. GA indicates Georgia, LA indicates Louisiana and B, LD, HD and Ref represent the treatments (respectively bare, low density, high density and reference). The error represents the standard deviations

(B, HD > LD). In Georgia, spring 2007 rates were significantly higher in Ref plots, compared to all others for both depths assessed. However, fall 2007 showed no treatment effects in Georgia. In 2008, different patterns were observed in Georgia, with significantly higher rates for Ref plots compared to HD and LD plots in the spring and higher rates for Ref plots compared to LD plots in the fall.

Benthic-nitrogen cycling feedbacks

Regression analysis between nitrogen cycling (pDNF and N-fix) and GOP rates revealed a number of significant positive relationships (Table 2). No correlations were found between GOP and denitrification rates in Georgia. The normalized GOP rates in Georgia, however, were positively correlated with shallow denitrification in Ref and HD at low light (r^2 0.46–0.55), while a positive relationship was found between GOP and pDNF in B and LD at high light (r^2 0.41–0.67). In Louisiana GOP rates correlated positively with denitrification in B (r^2 0.55–0.59). Regression analysis between N-fixation (for Louisiana) and normalized benthic production showed significant correlations in B and LD plots (r^2 0.57–0.59). pDNF was positively correlated to N-fixation at depth 0–5 cm ($r^2 = 0.18$, $p < 0.05$) and 25–30 cm ($r^2 = 0.20$, $p < 0.05$). Multivariate regression analysis for Louisiana showed that pDNF at 0–5 cm was correlated to GOP (low light) rates and N-fixation rates ($r^2 = 0.28$), while denitrification at 25–30 cm was significantly correlated with GOP (high light) ($r^2 = 0.21$).

Discussion

The impacts of acute vegetation dieback on marsh benthic primary production and nitrogen cycling were evaluated by comparing rates and patterns of biogeochemical processes in reference plots and plots impacted by dieback with different densities replanted. The years of extreme drought (Louisiana: 1999–2000; Georgia: 1999–2002) as indicated by very low Palmer Severity Drought Index (PSDI) values, were associated with massive dieback events (McKee et al. 2004; Alber et al. 2008). The 2007 drought was severe for Georgia (Mean 2007 PSDI: −2.84 ± 0.72; NOAA Climate Data Center) while more mild for

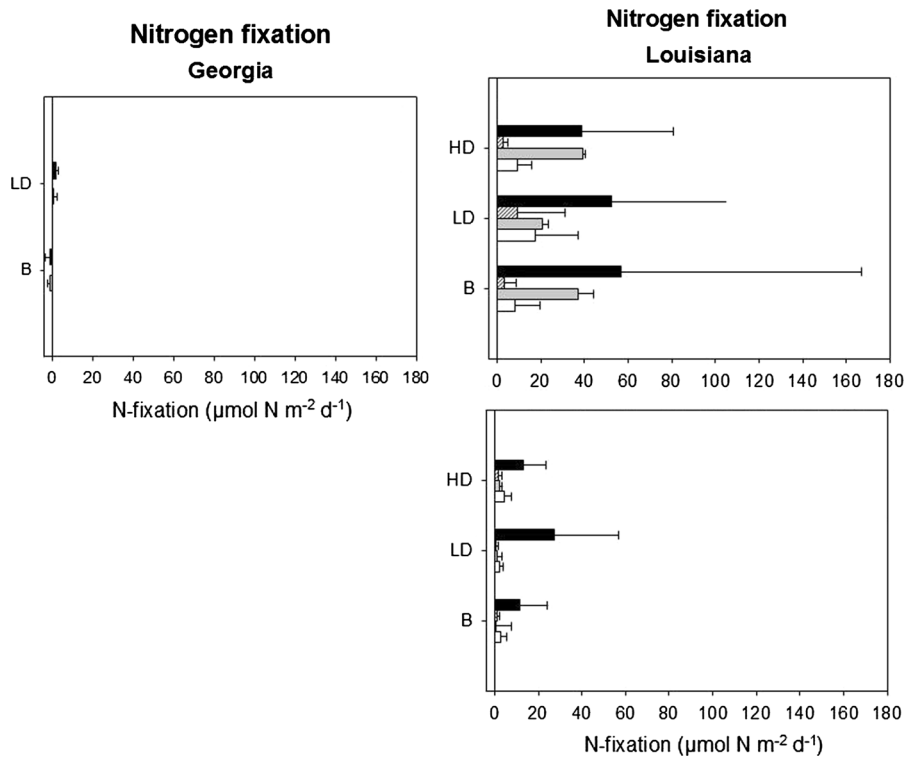

Fig. 3 Nitrogen fixation rates measured in Louisiana (*right*) and Georgia (*left*) during daytime and during nighttime. The labels on y-axis represent high density replanting (HD), low density replanting (LD) and dieback (B). The *bars* represent means and the *error bars* represent standard deviations. The *bars* represent the mean for spring 2007 (*black*), fall 2007 (*hatched*), spring 2008 (*grey*) and fall 2008 (*white*). The *error bars* represent standard

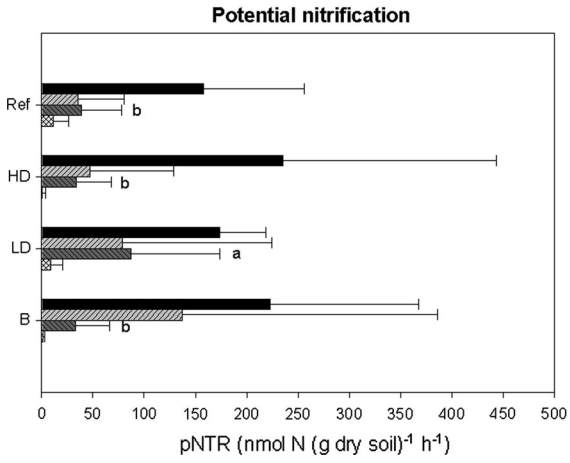

Fig. 4 Potential nitrification rates measured in 2008. The labels on y-axis represent Reference (Ref), high density replanting (HD), low density replanting (LD) and dieback (B). The *bars* represent the mean for spring 2008 (GA: *black*; LA: *hatched dark grey*) and fall 2008 (GA: *hatched light grey*; LA: *double hatched*). The *error bars* represent standard errors

Louisiana (Mean 2007 PSDI: -0.38 ± 1.05; NOAA Climate Data Center), thus, providing a unique opportunity to study drought impacts on biogeochemical processes. The objective of this work was to evaluate the effect of dieback history and *S. alterniflora* replanting and density on biogeochemical processes.

Benthic production

Benthic production can contribute substantial to marsh ecosystem production, accounting for up to 50 % of total production (Haines 1977; Pomeroy et al. 1981; Pinckney and Zingmark 1993a, b). In this study we investigated (1) how benthic primary producers responded to dieback and (2) the degree to which microbial benthic production compensated for reductions in *S. alterniflora* production. Generally lower benthic production rates in Georgia compared to Louisiana were likely explained by differences in tidal regimes, with more frequent inundation and a higher tidal range in Georgia resulting in reduced light intensity at the sediment surface and, thus, resulted in less benthic biomass accrual (Pinckney and Zingmark 1993a, b; MacIntyre et al. 1996).

Experimental treatment effects on benthic production were observed in both Georgia and Louisiana. In field plots, light intensity at the sediment surface was a function of plant canopy density. To simulate this in

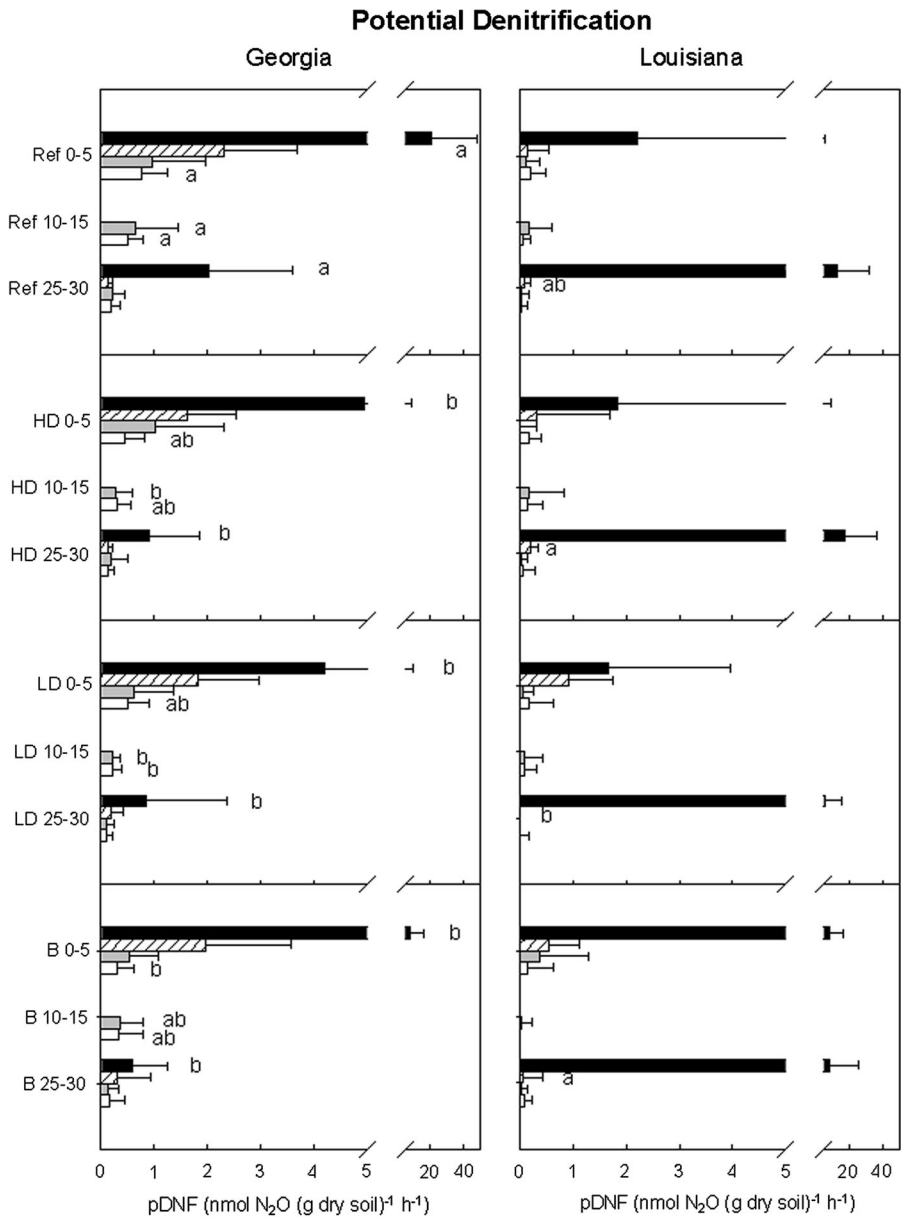

Fig. 5 Potential denitrification rates measured in Georgia (*left*) and Louisiana (*right*). The labels on y-axis represent reference (Ref), high density replanting (HD), low density replanting (LD) and dieback (B). The *bars* represent the mean for spring 2007 (*black*), fall 2007 (*hatched*), spring 2008 (*grey*) and fall 2008 (*white*). The *error bars* represent standard errors and *letters* indicate significant differences between treatments

the laboratory, benthic production rates were determined at low and high light levels. In Georgia, higher light conditions in B and LD plots in the field supported increased biomass accrual of benthic microphytes, which led to higher rates of BMA production rates, specifically, when measured at high light conditions.

Under low light conditions, Georgia LD and HD plots exhibited the highest rates of benthic production in 2007, while B had the highest rates in 2008 (Fig. 2). The chlorophyll-normalized rates under low light conditions were highest in LD in the spring of 2007 (Fig. 2), while rates in B were highest on all other sampling dates. Light limitation appeared to become more important for regulating biomass accrual in Georgia in 2008, potentially explaining the relatively higher rates in B. The 2007 drought could have given the bare dieback sites a greater advantage in producing benthic biomass due to the potential superior microbial drought tolerance of organisms such as benthic algae (Stanley et al. 2004; Schimel et al. 2007) compared to *Spartina* (Mendelssohn et al. 2006). Our

Table 2 Regression analysis between gross oxygenic production (GOP) and nitrogen cycling processes (potential denitrification (0–5 and 25–30 cm) and N-fixation (N-fix)) for different treatments (B, LD, HD and Ref) and light intensities (100 and 1,000 μmol quanta m^{-2} s^{-1})

GOP	pDNF 0–5		pDNF 25–30		N-fix	$GOP_{chlorophyll}$	pDNF 0–5		pDNF 25–30		N-fix
Treatment	GA	LA	GA	LA	LA	Treatment	GA	LA	GA	LA	LA
B-100	X	0.30	X	0.55	0.38	B-100	X	0.29	X	0.20	X
LD-100	X	0.20	X	0.13	X	LD-100	X	X	X	X	0.57
HD-100	X	X	X	X	X	HD-100	0.46	0.16	X	X	X
Ref-100	X	X	X	X	NA	Ref-100	0.55	X	0.21	X	NA
B-1000	X	X	X	0.59	0.28	B-1000	X	0.23	0.67	0.20	X
LD-1000	X	0.17	X	0.25	X	LD-1000	0.24	X	0.41	0.24	0.59
HD-1000	X	X	X	0.31	X	HD-1000	X	X	X	X	X
Ref-1000	X	X	X	X	NA	Ref-1000	X	X	X	X	NA

Gross oxygenic production (GOP) on the left and chlorophyll-normalized GOP on the right. All significant regressions are positively related. The values indicate *r*-squared values ($p < 0.05$). Regression analysis between GOP and N-cycling

GA Georgia, *LA* Louisiana

understanding of benthic stress tolerance and resilience is poorly understood (Davison and Pearson 1996; Schimel et al. 2007). These data, however, indicate a potential advantage of BMA over *Spartina*. A different pattern occurred in Louisiana, where higher light intensities within the B, LD, and HD plots fueled higher benthic production rates in those treatments relative to Ref. Higher light intensities at the sediment surface likely caused higher benthic biomass accrual and, thus, higher benthic production rates. The lack of any significant drought in 2007 for Louisiana showed no major differences in treatment patterns between 2007 and 2008. The higher GOP rates in the spring of 2007 for Louisiana were likely kinetically controlled by the higher temperatures observed that year (GCE-LTER 2007–2009, LUMCON 2007–2009).

Nitrogen cycling and benthic feedbacks

Most nitrogen cycling processes responded most strongly to seasonality (high in spring, low in fall) and to the composition of benthic primary producers, which drove N-cycling feedbacks. Diatoms depend completely on nitrogen mineralization or exogenous sources to provide their inorganic nitrogen requirements, while cyanobacteria can have their own N-source via N-fixation. N-fixation was a small component of the benthic N budget in the diatom-dominated sediments of coastal Georgia. In contrast, high rates of N-fixation were observed in cyanobacteria-dominated microbial mats of coastal Louisiana. The dominance of cyanobacteria in Louisiana marshes was most likely driven by the microtidal inundation regime. However, similar to the pattern observed for GOP rates, all rates of N-cycling processes examined were significantly lower in 2008 compared to 2007.

Patterns of N-fixation exhibited no significant treatment-related differences. The extremely low N-fixation rates compared to potential nitrification and denitrification in Georgia suggest that N-fixation plays a small role in overall ecosystem N dynamics. In contrast, in Louisiana, N-fixation rates were relatively higher compared to potential nitrification and denitrification and both seasonal and spatial patterns were observed. Transplanting *Spartina* has been found to shift a balanced nitrogen cycle to a unbalanced ecosystem with higher N-fixation rates than denitrification rates (Currin et al. 1996). This study, however, found similar pDNF those previously documented in coastal environments (Joye and Paerl 1994; Currin et al. 1996; Joye et al. 1996) and did not find an increase in the N-fixation rate with transplantation.

Lower N-fixation rates were observed during the fall, correlating with reduced light availability and lower temperatures (Tyler et al. 2003; GCE-LTER 2007–2009; LUMCON 2007–2009). In Louisiana, N-fixation rates correlated well with GOP rates in B (r^2 0.28–0.38) and normalized GOP rates in LD (r^2 0.57–0.59) (Table 1). This pattern could result from the increased light availability in B and LD plots, which would stimulate cyanobacterial biomass

accrual. In fact, the generally higher rates of N-fixation observed in day versus night incubations, suggests photosynthetic cyanobacteria are the dominant N-fixers in Louisiana marshes. Hydrogen sulfide can feed electrons directly to ferredoxin to fuel N-fixation activity and the higher rates of N-fixation observed in 2007 could reflect that H_2S-driven N-fixation, possibly by anoxygenic phototrophs, was important (Baas and Joye in preparation). Such H_2S-fueled N-fixation could drive the observed relationship between GOP and N-fixation, since an increase in N supply would potentially increase the benthic photosynthesis (Piehler et al. 1998; Tyler et al. 2003).

Nitrification rates are largely dependent ammonium and oxygen supplies and its activity is inhibited by H_2S (Joye and Hollibaugh 1995). Potential nitrification rates played a much more important role in the N cycle of Georgia sediments than Louisiana sediments, especially during the fall ($\sim 10\times$ higher in Georgia than Louisiana). Lower H_2S concentrations and deeper oxygen penetration depths most likely explain the higher potential nitrification rates observed in Georgia (Joye and Hollibaugh 1995; Baas and Joye in preparation); high H_2S concentrations in Louisiana marsh soils may have inhibited this process (Baas and Joye in preparation). Macrophyte mediated oxygen diffusion into the sediment can control nitrification rates (Bodelier et al. 1996). However, the lack of treatment differences in potential nitrification could indicate that macrophyte mediated oxygen is not controlling nitrification rates.

pDNF were also generally higher in Georgia (except spring 2007, 25–30 cm) and rates in both Georgia and Louisiana dropped precipitously in 2008 relative to 2007. The higher rates in 2007 could be explained by higher benthic production as stimulated by lower abundance and production of Spartina or by reduced plant uptake of nitrate and, thus, increased nitrate availability for denitrifying bacteria. Further, the 2007 drought may have increased Spartina stress, resulting in more plant dead biomass and, thus, increased carbon availability for denitrification. Furthermore, reduced plant productivity in 2007 could have reduced the organic matter available for decomposition in sediments and, therefore, reduced organic carbon availability for denitrification in 2008.

It is important to realize that potential rates cannot be directly extrapolated to the field and represent the enzymatic potential for activity. Assessment of denitrification using the acetylene block method has several possible artifacts. First, acetylene inhibits nitrification and, therefore, measured pDNF rates do not reflect coupled nitrification–denitrification (Hynes and Knowles 1978; Knowles 1990). Secondly, sulfide alleviation of the acetylene block (Sorensen et al. 1987) and diffusion of N_2O to low nitrate microsites (Seitzinger et al. 1994) can result in N_2O consumption and underestimation of the denitrification rate.

Benthic production can control nitrification and denitrification rates (Joye and Paerl 1994; An and Joye 2001; Joye and Lee 2004). We found few significant correlations between shallow denitrification and GOP for both Georgia (none) and Louisiana (weak for LD and B) indicating benthic production is not an important driver for shallow denitrification. We observed strong and significant correlations for deep denitrification and GOP rates in the B treatment in Louisiana. However, it is likely not mechanistic but coincidental because it is difficult to imagine that denitrification in the strongly anoxic deep sediment was affected by benthic-producer-derived DOC, which is sourced at the top of the sediment column. It is more likely that GOP was stimulated by the increased light availability (due to the lack of plants) while increased carbon supply from the decomposition of the vast amount of *Spartina* roots during derived from the original dieback events could have stimulated denitrification rates in the deeper sediments. Chlorophyll normalized GOP rates showed only weak correlations in Louisiana, but strong correlations for Georgia at 0–5 cm for Ref and HD and at 25–30 cm for LD and B. The relationship at 0–5 cm could indicate the importance of priming by labile carbon produced by microphytes as an important mechanism for carbon decomposition of *S. alterniflora* carbon inputs (Valiela et al. 1984; Groffman 1994; Addy et al. 2005).

Overall, these patterns suggest that leaky benthic producers—either BMA or *Spartina*—influence the organic carbon pool available for denitrification and/or that photosynthetic production stimulates nitrification (Georgia) or N-fixation (Louisiana) and subsequently denitrification.

Conclusions

Many questions regarding sediment biogeochemistry remain unanswered following the acute sudden

dieback events observed during the beginning of this millennium. The results of this study indicate that a legacy of the early millennium dieback events is increased contribution of benthic primary production to whole ecosystem productivity. N-fixation was of negligible importance in Georgia, while being important in stimulating benthic production in low density treatments (B, LD) in Louisiana. Due to the more oxygenated soils in Georgia, potential nitrification rates were much higher in Georgia than Louisiana. pDNF depended most on *S. alterniflora* density in Georgia with microphytes mediated priming being an important potential mechanism, whereas in Louisiana dieback sites appear to be stimulated by benthic production. Even though the mechanisms are not completely clear, following the drought in 2007, all processes measured were suppressed during the 2008 sampling year. The high benthic production with the 2007 drought creates the hypothesis that benthic microphytes can deal better with drought than plants, but may be outcompeted during non-drought years. Replanting efforts significantly increased ecosystem recovery with higher levels of success in Louisiana, compared to Georgia.

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