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# COASTAL WETLANDS

AN INTEGRATED ECOSYSTEM APPROACH



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From Craig Tobias, Salt Marsh Biogeochemistry – An Overview. In: Gerardo M. E. Perillo, Eric Wolanski, Donald R. Cahoon, Mark M. Brinson, editors, *Coastal Wetlands: An Integrated Ecosystem Approach*.

Elsevier, 2009, p. 445. ISBN: 978-0-444-53103-2

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## SALT MARSH BIOGEOCHEMISTRY – AN OVERVIEW

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### 1. INTRODUCTION

Salt marshes have long been considered important sources, sinks, and/or transformers of biologically important nutrients in the coastal landscape. Macrophyte production contributes autochthonous organic matter to soils. Marsh geomorphology and hydrodynamics lead to trapping of allochthonous organic and mineral particulates. The high rates of respiration in marsh soils create an electron-rich, chemically reduced environment proximal to oxidized surface waters. The subsurface redox environment is further modified by root-mediated

release of O<sub>2</sub> into the rhizosphere, physical mixing by macro-organisms, and water movements caused by tidal infiltration and drainage, factors that vary over tidal to seasonal and interannual scales. As such, marshes provide highly reactive surfaces that modify water quality. High organic matter production rates, variable redox environments, and physically dynamic ecosystems that are regularly pulsed by tides are characteristic features of salt marshes, mangrove swamps, tidal freshwater wetlands, and seagrass systems. Salt marshes differ considerably from nonvegetated mudflats in terms of overall autotrophic productivity and impacts of macrophyte root production on the cycling of macroelements. While there are many commonalities between saline and tidal freshwater wetlands, the chemistry of seawater (notably the presence of sulfate) leads to significant biogeochemical differences in processes such as organic carbon (C) oxidation and the cycling of nitrogen (N), sulfur (S), iron (Fe), and phosphorus (P).

The goal of this chapter is straightforward. We present an overview of the processing and cycling of the major biologically relevant elements (C, N, P, S, and Fe) in salt marshes. In keeping with the ecosystems theme of this book, and to the extent possible, the cycles are parsed into exchanges, pathways of internal cycling, and burial for each element.

## 2. CARBON

### 2.1. Exchanges

#### 2.1.1. Photoautotrophy

Marsh macrophytes serve as a dominant source of new C to marshes, play a key role in stabilizing marsh platforms, trapping sediments, aerating the soil through root O<sub>2</sub> loss (ROL), and influencing biogeochemical cycling (Bodelier, 2003; Hines, 2006). Rates of net primary production (NPP) in *Spartina alterniflora* marshes range from ~100 to >2,500 g/cm<sup>2</sup>/year (Mitsch and Gosselink, 1993; Dame et al., 2000), with highest values in south Atlantic and Gulf coast marshes (Mendelsohn and Morris, 2000). Belowground biomass accumulation often equals or exceeds that of aboveground tissues (Valiela et al., 1976; Schubauer and Hopkinson, 1984; Darby and Turner, 2008). The productivity of other marsh plants including *Spartina patens*, *Distichlis spicata*, and *Juncus roemerianus* can be comparable to that of *S. alterniflora* (Mitsch and Gosselink, 1993). NPP can vary within a single marsh as a function of anoxia, sulfide, and salinity stresses that affect nitrogen uptake and assimilation (King et al., 1982; Mendelsohn and Morris, 2000). Further, sea level anomalies lead to high interannual variability by affecting flooding frequency and thus the salinity of marsh porewaters (Morris, 2000; Morris et al., 2002). The majority of C fixed by plants is atmospheric CO<sub>2</sub> although small amounts (<10% of atmospheric fixation) can come from porewater dissolved inorganic C (DIC) or CO<sub>2</sub> that is recycled in lacunar spaces (Hwang and Morris, 1992).

Relative to rates of macrophyte productivity, less is known about primary productivity by salt marsh benthic microalgae and macroalgae. Benthic microalgal

**Table 1** Net benthic microalgal (BMP) and vascular plant production (VPP) in tidal salt marshes, and the ratio of BMP to net primary production (NPP), where  $NPP = BMP + VPP$ 

State, USA	Productivity (g C/m <sup>2</sup> /year)		BMP NPP	Reference
	Microalgal	Vascular plants		
Massachusetts	53 <sup>a</sup>	212 <sup>a</sup>	0.20	Van Raalte et al., 1976
New York	50	292	0.15	Woodwell et al., 1979
Delaware	61–99	NR	0.25	Gallagher and Daiber, 1974
Virginia	27.8	254	0.10	Anderson et al., 1997
Virginia	67 <sup>b</sup>	161	0.29	Miller et al., 2001
Virginia	235	831	0.22	Buzzelli et al., 1999
South Carolina	98, 234 <sup>c</sup>	534, 296 <sup>c</sup>	0.16, 0.44 <sup>c</sup>	Pinckney and Zingmark, 1993
Georgia	180	732	0.20	Pomeroy, 1959; Teal, 1962
Georgia	208	1127	0.16	Pomeroy et al., 1981
Mississippi	28–151	248–742 <sup>a</sup>	0.90–0.38	Sullivan and Moncreiff, 1988
Texas	71	550–900	0.90–0.11	Hall and Fisher, 1985
California	185–341	243–340	0.43–0.58	Zedler, 1980

Note that this calculation differs from the oft-reported ratio that expresses BMP as a fraction of plant production (i.e., BMP/VPP). Plant production was estimated from aboveground biomass in all studies except Miller et al. (2001) where a CO<sub>2</sub>-based gas flux model was utilized. NR, not reported.

<sup>a</sup> Converted from original estimates, assuming that algal and/or plant biomass is 50% C.

<sup>b</sup> BMP was measured in cleared zones within a dense *Spartina patens*/*Distichlis spicata* canopy; rates in these cleared zones likely overestimate rates beneath the canopy (Sullivan and Daiber, 1975).

<sup>c</sup> Averages for tall and short *Spartina alterniflora* zones, respectively.

productivity ranges from ~30 to 300 g C/m<sup>2</sup>/year (Table 1) and shows a similar latitudinal pattern as for macrophytes. The highest rates are observed along the southeast Atlantic and California coasts (Zedler, 1980). Benthic microalgal production generally accounts for ~10–25% of total ecosystem (i.e., macrophyte + algal) productivity but sometimes exceeds plant productivity (Table 1). Microalgal productivity is often higher during winter when the plant cover is at a minimum. Despite lower rates of productivity, benthic microalgal biomass is generally more labile than that of macrophytes and is preferentially assimilated by secondary consumers (Sullivan and Moncreiff, 1990; Currin et al., 1995; Sullivan and Currin, 2000).

### 2.1.2. Allochthonous C deposition

Tidal flooding provides a mechanism for the delivery and deposition of water column suspended sediments and associated C. Rates of sedimentation depend on suspended sediment concentrations, tidal range, vegetation, creek proximity, and hydroperiod (Friedrichs and Perry, 2001). Thus, sedimentation and organic C deposition vary widely from marsh to marsh, laterally within a single site, and temporally within the year. As an example, deposition rates in Paulina Marsh, the

Netherlands, ranged from  $<100 \text{ g/m}^2/\text{spring-neap cycle}$  near the marsh-upland border to  $2,000 \text{ g/m}^2/\text{cycle}$  at the marsh-mud flat boundary (Temmerman et al., 2003). Across the entire marsh, deposition averaged  $\sim 200 \text{ g/m}^2/\text{cycle}$ . Assuming an organic C content of 5–10% for suspended sediments (Middelburg and Herman, 2007), deposition across this marsh delivers  $250\text{--}500 \text{ g C/m}^2/\text{year}$ . This rate falls within the range of deposition reported for other salt marshes (Cahoon and Reed, 1995; Salgueiro and Caçador, 2007) and for tidal freshwater marshes (Chapter 19). Thus, sedimentation represents a source of C to salt marshes comparable to C fixation by benthic microalgae and chemoautotrophs (Section 2.2.3). Such inputs of allochthonous C have been suggested as a mechanism to explain the 9–12‰ depletion in soil organic matter  $\delta^{13}\text{C}$  values (relative to *S. alterniflora* biomass) that is often observed in mineral-dominated marshes (Middelburg et al., 1997). Marshes in sediment-starved regions or those that are infrequently flooded by tides will have lower inputs of allochthonous C relative to autochthonous C sources.

Considerable quantities of sediment-associated C can be delivered by hurricanes and other large storms (Parsons, 1998; Turner et al., 2006a). Hurricanes Katrina and Rita (Gulf of Mexico coast, USA, August/September 2005) deposited  $22.3 \text{ kg sediment/m}^2$  (Turner et al., 2006a). Assuming that these sediments originated from offshore (as hypothesized by Turner et al., 2006a) with an average organic C content of 2.2% (Mayer et al., 2007), this deposition delivered  $490 \text{ g C/m}^2$  to the marsh surface. The mineral fraction can contribute to significant vertical marsh growth (Turner et al., 2006a), but the fate of the organic fraction is currently unknown.

### 2.1.3. Organic C export

The exchanges of C and nutrients between marshes and tidal waters have been studied for decades, often in the context of the outwelling hypothesis (Kalber, 1959; Odum, 1968; see reviews by Nixon, 1980; Dame, 1994; Childers et al., 2000). High variability in terms of hydrology, basin age, and geomorphological setting, among other features, makes it a futile task to draw broad conclusions with respect to the direction and magnitude of particulate and dissolved organic C (POC and DOC) fluxes that will apply to all marshes at all times. Childers et al. (2000) summarized the salt marsh flux literature that has appeared since Nixon's (1980) influential review of marsh-estuarine exchanges. In their compilation, three of eight studies showed a net annual POC export, with rates of  $11\text{--}128 \text{ g C/m}^2/\text{year}$  (the other five studies had POC imports of  $3\text{--}140 \text{ g C/m}^2/\text{year}$ ). In the North Inlet (South Carolina) system, the entire 3,200 ha marsh basin exported POC, whereas the geologically young Bly Creek sub-basin (66 ha) imported POC (Dame et al., 1986, 1991). In contrast to the high variability in the rates and direction of POC exchange, 11 of the 13 studies reporting DOC fluxes showed net DOC export ( $15\text{--}328 \text{ g C/m}^2/\text{year}$  versus  $<15 \text{ g C/m}^2/\text{year}$  for the two studies that showed DOC import). In North Inlet, the seepage and drainage of DOC-rich marsh porewaters is more important during summer, whereas external inputs related to freshwater discharge play a larger role during winter (Wolaver et al., 1986).

There is some evidence that transient biota (e.g., fishes) can mediate significant C (and N) export from marshes. This mechanism is beyond the scope of this chapter (but see Deegan, 1993; Deegan et al., 2000; Teal and Howes, 2000).

#### 2.1.4. Inorganic C export

Mass balance calculations indicate that a significant fraction of marsh primary production (>90%) must be decomposed or otherwise exported in order to explain long-term C accumulation rates (Howes et al., 1985; Gardner, 1990; Middelburg et al., 1997). Gaseous CO<sub>2</sub> emissions from salt marshes range from 240 to 720 g C/m<sup>2</sup>/year (Blum et al., 1978; Howes et al., 1985; Morris and Whiting, 1986; Morris and Jensen, 1998; Miller et al., 2001) with an additional loss of dissolved inorganic C of 120–240 g C/m<sup>2</sup>/year (Howes et al., 1985; Morris and Whiting, 1986; Nietch, 2000; Wang and Cai, 2004). Across saline and brackish marshes, the export of DIC accounts for ~20–30 of total inorganic C losses (i.e., CO<sub>2</sub> + DIC). Tidal marshes can export significant amounts of DIC to adjacent coastal waters, influence the apparent metabolic state of these waters (i.e., net autotrophic vs. heterotrophic), and affect the magnitude and direction of CO<sub>2</sub> exchange between coastal waters and the atmosphere (Cai and Wang, 1998; Cai et al., 1999, 2000; Raymond et al., 2000; Neubauer and Anderson, 2003; Wang and Cai, 2004; Borges, 2005). Similar estimates for tidal freshwater marshes are reported in this book (Chapter 19).

The CO<sub>2</sub> and DIC that accumulate (and can be lost) from salt marsh soils can be derived from the decomposition of plant roots or bulk soil organic matter. <sup>13</sup>C isotopes indicate that root respiration can account for 21–90% of total soil respiration (Wang et al., in review.), with a higher fractional contribution of roots in more organic marshes. The mineralization of the large pool of soil organic matter can proceed at appreciable rates, even many years after in situ plant primary production has stopped (Morris and Whiting, 1986; Wang et al., in press.).

Emissions of CH<sub>4</sub> from salt marshes are generally lower than fluxes from freshwater wetlands (Bartlett et al., 1987; Bridgman et al., 2006). In a compilation of flux data from North American wetlands, the average CH<sub>4</sub> flux from freshwater wetlands was  $36.0 \pm 5.0$  g C/m<sup>2</sup>/year (average  $\pm$  SE), whereas that from salt marshes was  $3.6 \pm 2.3$  g C/m<sup>2</sup>/year (Bridgman et al., 2006). Sulfate reduction coupled to anaerobic CH<sub>4</sub> oxidation (Martens and Berner, 1977; Boetius et al., 2000) would further reduce CH<sub>4</sub> emissions, but this process has not been explored in salt marsh soils.

## 2.2. Internal cycling

### 2.2.1. Aerobic mineralization

Molecular oxygen is rapidly used in salt marsh soils as an electron acceptor for microbial respiration and an oxidant for reduced chemical species. Marsh O<sub>2</sub> uptake (maximal at low tide) ranges from 5 to 65 mol O<sub>2</sub>/m<sup>2</sup>/year (Howes et al., 1984; Howarth, 1993; Cai et al., 1999). Many plants including *S. alterniflora*, *Spartina anglica*, and *J. roemerianus* can oxidize subsurface soils through ROL

(Mendelssohn et al., 1995; Holmer et al., 2002; Maricle and Lee, 2002; Koretsky and Miller, 2008). The amount of O<sub>2</sub> uptake due to advective air movement into drained pore spaces can be ~50% of the diffusive O<sub>2</sub> uptake across the marsh atmosphere boundary (Morris and Whiting, 1985). Filling pore spaces with fully aerated tidal water (rather than air) contributes a much smaller amount of O<sub>2</sub> due to the lower concentration of O<sub>2</sub> in water and decreased diffusion in water. Infauna can increase soil oxidation through burrowing, bioirrigation, and physical mixing of the substrate (Meile et al., 2001; Gribsholt and Kristensen, 2002; Kristensen and Kostka, 2005). Because there are no in situ methods for quantifying O<sub>2</sub> added during ROL or faunal activity, estimates of aerobic respiration are likely to be seriously underestimated if only O<sub>2</sub> fluxes across the marsh surface are considered. Howarth (1993) estimated that aerobic respiration accounted for 18–30% of total soil respiration but diagenetic simulation results suggest a much smaller contribution (1–5% of the total organic matter decomposition; Furukawa et al., 2005).

Because organic matter can persist above the soil surface as standing dead stems and wrack, measurements of soil processes alone will underestimate the total role of aerobic decomposition. Fungi and bacteria carry out a significant amount of C mineralization subaerially and under aerobic conditions. For example, peak microbial respiration rates on senescent leaves of tall *S. alterniflora* coincided with peak fungal biomass (Buchan et al., 2003). Fungal degradation can remove up to 60% of the original aboveground organic matter (Newell and Porter, 2000) with aerobic degradation continuing to occur as the bacterial standing crop increases during later stages of decomposition (Benner et al., 1986; Newell et al., 1989).

### 2.2.2. Anaerobic mineralization

Thermodynamic theory indicates that the availability of electron acceptors and competition between microbes for electron donors will govern the relative importance of different catabolic processes (Megonigal et al., 2004). Respiration using O<sub>2</sub> as the electron acceptor has the highest energy yield. Following the depletion of O<sub>2</sub>, a predictable sequence of anaerobic processes follows: denitrification, Mn reduction, Fe(III) reduction, SO<sub>4</sub><sup>2-</sup> reduction, and methanogenesis (Ponnamperuma, 1972). There is some recent evidence that humic acids can also be significant electron acceptors. One result of the competition among microbes for electron donors can be vertical redox stratification that reveals itself as gradients in solid phase or porewater geochemistry (Griffin et al., 1989; Taillefert et al., 2007). However, due to fine-scale heterogeneity in distributions of electron donors and electron acceptors, multiple pathways can coexist within the same volume of soil (Højberg et al., 1994).

Despite the importance of denitrification for NO<sub>3</sub><sup>-</sup> removal (Section 3.1.5), denitrification is not significant for organic C turnover in marshes due to relatively low NO<sub>3</sub><sup>-</sup> supply. It accounts for ≤1% of C mineralization in salt marsh soils (Table 2). Additions of NO<sub>3</sub><sup>-</sup> to Georgia marsh soils did not increase total C mineralization rates (Hyun et al., 2007).

To our knowledge, Mn(III, IV) reduction rates have not been measured in salt marshes. However, voltametric (microelectrode) studies have identified dissolved Mn<sup>2+</sup> in vegetated soils (Brendel and Luther, 1995) and in nonvegetated intertidal

**Table 2** Importance of anaerobic to total (aerobic + anaerobic) metabolism in several salt marshes and the partitioning of anaerobic C decomposition through various pathways

	Anaerobic Total	% of anaerobic respiration				Citation
		NO <sub>3</sub> <sup>-</sup> reduction	Metal reduction	SO <sub>4</sub> <sup>2-</sup> reduction	Methanogenesis	
Sippewissett (MA)	0.82	0.2	“Negligible”	99.4	0.4	Howarth, 1993
Jack Bay (MD)	ND	ND	2.7–51.4 <sup>a</sup>	48.6–95.2 <sup>a</sup>	0–2.0 <sup>a</sup>	Neubauer et al., 2005b
Skidaway Island (GA)	ND	ND	0–109 <sup>b</sup>	6–82 <sup>b</sup>	ND	Kostka et al., 2002a
	ND	ND	28–96 <sup>c</sup>	4–72 <sup>c</sup>	ND	Gribsholt et al., 2003
	0.95–0.99 <sup>d</sup>	0.9–1.0 <sup>d</sup>	1.7–61.6 <sup>d</sup>	36.8–97.5 <sup>d</sup>	ND	Furukawa et al., 2004
	ND	ND	0–71.8 <sup>e</sup>	22.1–95 <sup>e</sup>	ND	Hyun et al., 2007
Sapelo Island (GA)	0.70	1.1	“Negligible”	94.4	4.4	Howarth, 1993
	ND	ND	ND <sup>f</sup>	0–106 <sup>f</sup>	ND	Kostka et al., 2002b

The relative importance of each pathway is taken directly from each citation or calculated after summing the measured pathways and assuming that unmeasured pathways did not significantly contribute to total anaerobic metabolism. This is not always a valid assumption since the sum of individual metabolic rates does not always equal total CO<sub>2</sub> + CH<sub>4</sub> production. Mn reduction rates have not been measured in salt marsh soils and sediments, so “metal reduction” refers to biological Fe(III) reduction only. “Negligible” is a quote from Howarth (1993). “ND” indicates that aerobic respiration was not reported or that rates for a specific metabolic pathway were not measured.

<sup>a</sup>Range due to monthly variability in rates measured in June, July, and August.

<sup>b</sup>Range due to spatial variability between a bioturbated, vegetated (*Spartina alterniflora*) levee site and an unvegetated, nonbioturbated creekbank.

<sup>c</sup>Range due to spatial variability with increasing distance from *Uca pugnax* burrows (0–35 cm from burrow wall), as well as variations between rhizosphere and levee bulk soils.

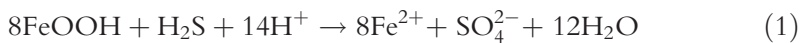
<sup>d</sup>Range due to spatial variability in modeled rates (integrated to 9 cm depth) between locations that are vegetated with *S. alterniflora*, containing abundant bioturbating fiddler crabs (*U. pugnax*) but no plants, and are unvegetated and lack *U. pugnax*.

<sup>e</sup>Range due to lateral variability between tall *S. alterniflora*, short *S. alterniflora*, and creekbank zones, as well as depth-related differences (0–3 cm and 3–6 cm) within each zone.

<sup>f</sup>Range due to lateral variability between a bioturbated unvegetated creekbank, a bioturbated vegetated (*S. alterniflora*) levee, and *S. alterniflora* mid-marsh zones, as well as depth-related differences (0–5 cm and 10–15 cm) within each zone. In this study, Fe(III) reduction was measured. Although no distinction was made between chemical and biological Fe(III) reduction, Kostka et al. (2002b) suggested that abiotic Fe(III) reduction dominated.

creek bank sediments (Taillefert et al., 2007), indicating that Mn(III, IV) reduction was occurring. Based only on the presence/absence of reduced Mn, it is not possible to determine whether the Mn reduction was driven by biological (enzymatic) or strictly chemical reactions. Regardless, Mn(III, IV) reduction will probably be less important than Fe(III) reduction with respect to C mineralization since Mn is generally present at lower concentrations than Fe (Luther et al., 1992). However, Mn reduction can be a dominant pathway in nearsurface subtidal marine sediments (Canfield et al., 1993; Thamdrup, 2000).

Iron(III) reduction can be an important pathway for organic matter turnover in salt marsh soils, accounting for 50–100% of anaerobic metabolism (Table 2). The relatively recent recognition that metal reduction can be a significant biological process contrasts with the historical view that  $\text{SO}_4^{2-}$  reduction dominates anaerobic metabolism in salt marshes (Howarth and Hobbie, 1982; Howarth, 1993). Many early studies were conducted in short *S. alterniflora* or mid-marsh habitats where  $\text{H}_2\text{S}$  accumulates due to low porewater turnover rates. Under these conditions,  $\text{SO}_4^{2-}$  reduction should dominate metabolism and Fe(III) reduction will be a primarily abiotic process where Fe oxides serve as an oxidant for sulfides:



Biological Fe(III) reduction will be more important than chemical reduction when amorphous Fe(III) oxides are plentiful and continually regenerated, or  $\text{H}_2\text{S}$  production is low relative to the Fe(III) concentration (Jacobson, 1994). Indeed, marsh zones with heavy bioturbation activity (especially by fiddler crabs, *Uca* spp.) can have anaerobic metabolism dominated by biotic Fe(III) reduction (Gribsholt et al., 2003; Furukawa et al., 2004; Hyun et al., 2007). Plant-driven inputs of  $\text{O}_2$  (via ROL) and organic C can also lead to significant rates of C turnover coupled to Fe(III) reduction (Neubauer et al., 2005b) although this mechanism appears to be less important than bioturbation in some salt marsh soils (Furukawa et al., 2004). Further, Fe(III) oxides formed in the rhizosphere can be more amorphous (a factor that favors enzymatic Fe(III) reduction) than those in bulk soil (Weiss et al., 2004). Gribsholt and Kristensen (2002) suggested that the highest rates of organic matter decomposition and Fe(III) reduction will occur in substrates that are bioturbated (to regenerate Fe(III) oxides) and vegetated (with plants acting as an organic C source). Hydrology, including diurnal tidal cycles (Taillefert et al., 2007) and seasonal changes in tidal water level (Neubauer et al., 2005b) or groundwater (GW) discharge (Tobias et al., 2001b), may also be important in driving  $\text{O}_2$  penetration into marsh soils and sediments, regulating Fe(III) regeneration, and leading to significant rates of biotic Fe(III) reduction.

Humic acids can be used as terminal electron acceptors for anaerobic metabolism with reasonable thermodynamic efficiency (Cervantes et al., 2000), in addition to their role as electron shuttles for Mn(III, IV) and Fe(III) reduction (Lovley et al., 1996). To date, the potential role of humic acid reduction as a pathway for organic C oxidation has not been directly measured but inferred from an inability to completely account for total rates of microbial respiration (i.e.,  $\Sigma\text{CO}_2 + \text{CH}_4$

production). For example, the sum of individually measured anaerobic pathways accounted for only 43% of total metabolism in a Georgia salt marsh (Hyun et al., 2007) and 20–30% in a Maryland brackish marsh (Neubauer et al., 2005b).

SO<sub>4</sub><sup>2-</sup> reduction is often a dominant pathway for anaerobic C metabolism (Table 2; Howarth and Hobbie, 1982; Howarth, 1984; Hines et al., 1989; Kostka et al., 2002b). SO<sub>4</sub><sup>2-</sup> concentrations typically exceed several millimolar in flooding water so that SO<sub>4</sub><sup>2-</sup> availability will not limit reduction (Boudreau and Westrich, 1984; Roychoudhury et al., 2003b). Instead, competition from other electron accepting processes and the availability of labile organic C regulate the relative importance of SO<sub>4</sub><sup>2-</sup> reduction. Based on considerations presented earlier, SO<sub>4</sub><sup>2-</sup> reduction should have the largest contribution to total anaerobic C metabolism in soils that are unvegetated, largely undisturbed (i.e., low bioturbation), and/or poorly flushed (allowing H<sub>2</sub>S to accumulate and minimizing advective O<sub>2</sub> delivery) – this has been demonstrated in several recent studies (Kostka et al., 2002a,b, Furukawa et al., 2004). Further, SO<sub>4</sub><sup>2-</sup> reduction rates can be limited by an imbalance between the temperature responses of microbes that hydrolyze and ferment complex organic substrates and SO<sub>4</sub><sup>2-</sup> reducers that utilize the resulting simple organic molecules (Weston and Joye, 2005). At low temperatures, the production of low-molecular weight dissolved organic carbon exceeds its consumption, resulting in accumulation. At high temperatures, however, SO<sub>4</sub><sup>2-</sup> reduction becomes limited by the rate at which low-molecular weight electron donors are generated (Weston and Joye, 2005) and by feedbacks from the accumulation of respiratory end products.

There has been little work on rates of CH<sub>4</sub> formation in salt marshes although existing evidence suggests that methanogenesis accounts for less than 5% of anaerobic respiration (Table 2). The paradigm is that methanogenesis in salt marshes is limited because methanogens are out-competed for electron donors (King and Wiebe, 1980a) although CH<sub>4</sub> production can be substantial in some humus-rich salt marsh soils (Giani et al., 1996). In a comparison of tall and short *S. alterniflora* zones, King and Wiebe (1980b) found that rates of CH<sub>4</sub> production were considerably greater in the short *Spartina* zone. At the same time, SO<sub>4</sub><sup>2-</sup> was relatively more depleted in the short *Spartina* zone, which allowed methanogenesis to increase in importance (King and Wiebe, 1980b). Given higher Fe(III) reduction in creek bank *Spartina* zones (Furukawa et al., 2004; Hyun et al., 2007), electron donor availability to methanogens may be limited by metal reducers along creek banks and SO<sub>4</sub><sup>2-</sup> reducers in the marsh interior. Despite the thermodynamic constraints against methanogenesis, some C are mineralized through this process, an indication of microzones in the soil matrix that is depleted in other electron acceptors and/or regions where substrates exist that can be converted to CH<sub>4</sub> but cannot be used by SO<sub>4</sub><sup>2-</sup> reducers (e.g., methanol and methylated amines; Oremland et al., 1982).

### 2.2.3. Chemoautotrophy

Reduced compounds such as Fe(II) and H<sub>2</sub>S contain considerable energy that can be released upon oxidation. When this oxidation occurs through a chemoautotrophic microbial process, the energy in the chemical bonds can be utilized to fix

porewater DIC in marsh soils. Thus, from a C cycling perspective, this C fixation represents primary production. However, from an energetic perspective, chemoautotrophy is a form of secondary production (after Howarth, 1993; Chapin et al., 2006) since the chemical energy in the inorganic compounds was originally released from organic matter (or  $H_2$ ).

Sulfides produced through  $SO_4^{2-}$  reduction are rapidly incorporated into minerals such as iron monosulfides (FeS) and pyrite ( $FeS_2$ ). Given that >70% of the energy in organic compounds utilized by  $SO_4^{2-}$  reducers ends up in these reduced sulfur compounds, it is apparent that FeS,  $FeS_2$ , and  $H_2S$  in marsh substrates represent a considerable energy source. Mass balance calculations indicate that >90% of the sulfides are ultimately reoxidized or exported (Howes et al., 1984; Gardner, 1990). Rates of S-mediated chemoautotrophy may range from ~20 to 480 g C/m<sup>2</sup>/year (Howarth and Teal, 1980; Howarth, 1984, 1993), a rate that is comparable to benthic microalgal production. However, if these sulfides are oxidized chemically, the energy is diverted from chemoautotrophic production.

Lithoautotrophic Fe(II)-oxidizing bacteria (FeOB) exist in salt marsh (Weiss et al., 2003) and subtidal marine environments (Emerson and Moyer, 2002; Edwards et al., 2003). Below, we calculate Fe(II) supply rates from the turnover of Fe–S minerals and oxidized Fe(III) to estimate potential rates of chemoautotrophic production by FeOB. In *S. alterniflora* soils, rates of  $SO_4^{2-}$  reduction typically range from ~15 to 75 mol S/m<sup>2</sup>/year (daily rates extrapolated to an annual basis; see Table 2 of Kostka et al., 2002b). Since the majority of the iron sulfides produced by  $SO_4^{2-}$  reduction are eventually oxidized, we estimate that 7–75 mol Fe(II)/m<sup>2</sup>/year are generated due to the turnover of reduced S compounds. In a Georgia salt marsh, Kostka et al. (2002a) reported Fe(III) reduction rates (and therefore Fe(II) production rates) of 0–190 mol Fe(II)/m<sup>2</sup>/year (extrapolated from daily rates). Combining these estimates of Fe(II) supply due to Fe–S mineral turnover and Fe(III) reduction, we estimate a total supply of Fe(II) of 7–265 mol Fe(II)/m<sup>2</sup>/year. If this Fe(II) is oxidized microbially with a growth yield of 0.7 g C/mol Fe(II) oxidized (Neubauer et al., 2002b), chemoautotrophic Fe(II) oxidation could contribute a maximum of 2–185 g C/m<sup>2</sup>/year of new production. However, the actual contribution of FeOB to chemoautotrophic production is likely to be considerably lower since FeOB are a very small component (<0.01%) of the total salt marsh microbial community (Weiss et al., 2003) and account for 50% or less of total Fe(II) oxidation (Neubauer et al., 2002b, 2007).

#### 2.2.4. Carbonate mineral formation

In most marine environments,  $Fe^{2+}$  rapidly precipitates with sulfides (Section 4.2.2); however, large concretions containing siderite ( $FeCO_3$ ) have been found in some salt marshes (Pye, 1981). The  $\delta^{13}C$  evidence suggests that these carbonates are partially derived from the degradation of marsh organic matter (Pye et al., 1990), with siderite more likely to form in saline/brackish systems when rates of Fe(III) reduction are high relative to  $SO_4^{2-}$  reduction due to low organic C availability (Adams et al., 2006). Under such conditions or when biological Fe(III) reduction is favored over chemical Fe(III) reduction (see above; Jacobson, 1994), low sulfide

concentrations mean that  $\text{Fe}^{2+}$  and  $\text{Mn}^{2+}$  are more likely to complex with  $\text{CO}_3^{2-}$  than with sulfides (Berner, 1969; Pye et al., 1990; Adams et al., 2006). However, Giblin and Howarth (1984) reported that porewaters of Great Sippewissett Marsh (Massachusetts) were highly undersaturated with respect to both siderite and rhodochrosite ( $\text{MnCO}_2$ ), providing strong evidence that formation of these minerals is limited.

### 2.3. Burial

As determined using  $^{137}\text{Cs}$  and  $^{210}\text{Pb}$  radiotracers, rates of salt marsh C accumulation ranged from  $\sim 100\text{--}200\text{ g C/m}^2/\text{year}$  over the last 50–100 years (Turner et al., 2000; Chmura et al., 2003; Bridgham et al., 2006; Craft, 2007). This range is comparable to that for tidal freshwater marshes (Craft, 2007; Magonigal and Neubauer, 2009; Neubauer, 2008) although C accumulation may be lower in salt marshes than in tidal freshwater and brackish marshes (Craft, 2007). The organic matter that is buried long-term likely represents a combination of in situ production (litter, detritus, aquatic, and subsurface roots) and allochthonous organic materials associated with mineral sediments (Wolaver et al., 1988; Craft et al., 1993; Rooth et al., 2003; Nyman et al., 2006; Neubauer, 2008). Average accretion and accumulation rates decrease over the first  $\sim 1,000$  years following burial due to decomposition and compaction of deeper soil horizons (Neubauer et al. 2002a, Turner et al. 2006b). Ultimately, the magnitude of C (as well as N and P) burial depends on long-term marsh responses to rising sea level.

## 3. NITROGEN

The total salt marsh N pool varies with marsh age and can be 5–30 times larger than the sum of all N cycling reactions within a year, leading to long turnover times for marsh N (Anderson et al., 1997; Rozema et al., 2000). The largest marsh N pool is in bulk soils ( $200\text{--}1,000\text{ g N/m}^2$ ; to a 30 cm depth), with plant biomass containing  $1\text{--}22\text{ g N/m}^2$  (Hopkinson and Schubauer, 1984; DeLaune and Patrick, 1990; Morris, 1991; Anderson et al., 1997; Rozema et al., 2000; Hopkinson and Giblin, 2008). In porewaters, dissolved organic nitrogen (DON) and  $\text{NH}_4^+$  are the dominant species (concentrations often  $\geq 100\text{ }\mu\text{M}$ ) while  $\text{NO}_3^-$  concentrations are generally low ( $\leq 10\text{ }\mu\text{M}$ ). Despite the smaller overall inventory of porewater DIN, it is a common intermediate reservoir for the numerous internal N cycling reactions.

### 3.1. Exchanges

#### 3.1.1. N fixation

N fixation may be important for building N stocks in young marshes, but its importance generally lessens as marshes trap more exogenous N and increase internal recycling. In mature marshes, N fixation ranges from  $<0.5$  to  $6.8\text{ g N/m}^2/\text{year}$

(Teal et al., 1979; Rozema et al., 2000; Moisander et al., 2005). It is usually a small part ( $\sim 10\%$ ) of the total N inputs and is an order of magnitude lower than internal N recycling rates (Valiela and Teal, 1979; Anderson et al., 1997; Rozema et al., 2000). In young or restored marshes, rates can exceed  $35 \text{ g N/m}^2/\text{year}$  and be of sufficient magnitude to support macrophyte N demand (Currin et al., 1996; Tyler et al., 2003). N fixation is concentrated in the marsh surface and performed principally by hetero- and nonheterocystous cyanobacteria (Currin and Paerl, 1998a,b; Piehler et al., 1998). N fixation patterns represent the sum total effects of irradiance, cyanobacterial diversity, tidal inundation, and  $\text{O}_2$  inhibition of nitrogenase (Ubben and Hanson, 1980; Joye and Paerl, 1994; Currin et al., 1996; Moseman, 2007).

### 3.1.2. Atmospheric deposition

Atmospheric deposition, which is typically dominated by  $\text{NO}_3^-$  and DON, can also occur as  $\text{NH}_4^+$  and particulate N (PN) (Russell et al., 1998; Paerl et al., 2002). The dissolved inorganic N (DIN) concentrations in precipitation are comparable to those in coastal tidal waters (Russell et al., 1998; Paerl et al., 2002). However, because precipitation comprises only a small part of the marsh water budget (Morris, 1991; Lent et al., 1997), atmospheric deposition rates are a small part of the N budget. Along the Atlantic coast (USA), atmospheric deposition ( $< 0.5\text{--}1.2 \text{ g N/m}^2/\text{year}$ ) is  $\sim 15\%$  of the water column inputs (Valiela et al., 1978; Morris, 1991; Paerl et al., 2002; Seitzinger et al., 2002; Buzzelli, 2008); higher loadings ( $\sim 3 \text{ g N/m}^2/\text{year}$ ) are seen in marshes of northwestern Europe (Rozema et al., 2000). There is a need for more studies in areas such as East Asia that can have even higher N deposition rates.

### 3.1.3. Groundwater inputs

Groundwater can be an important route of N delivery to salt marshes that are adjacent to N-loaded watersheds with low evapotranspiration, conductive soils, and short flow paths. Discharge occurs at either the marsh-upland border, directly into tidal creek beds, or can flow under the marsh and discharge subtidally offshore (Howes et al., 1996; Portnoy et al., 1997). Groundwater fluxes range from  $< 1.0$  to  $100 \text{ L/m}^2/\text{day}$  (Tobias et al., 2001a). Groundwater N fluxes to salt marshes ( $0.2\text{--}100 \text{ g N/m}^2/\text{year}$ ; Table 3) reflect the net result of discharge, N concentration in groundwater, marsh area, and some influence of porewater drainage. Great Sippewissett Marsh overlies an N-rich, highly conductive aquifer;  $\geq 50\%$  of the new N to the marsh is supplied by GW (Valiela and Teal, 1979). However, Anderson et al. (1997) presented a marsh N budget where inputs of GW N were trivial despite close proximity to an N-rich aquifer. In other cases, GW N delivery is low due to N-poor GW (despite high flow rates) or because GW bypasses (i.e., flows under) marsh substrates (Portnoy et al., 1997; Tobias et al., 2001a–c). Because discharge typically decreases with distance from the upland-marsh border (Howes et al., 1996), the GW N flux can be less important in large marshes with short stretches of marsh-upland border than in fringing marshes. Flux estimates provided by watershed-scale numerical models

**Table 3** Selected groundwater nitrogen (GW N) fluxes estimated for a range of salt marshes

Marsh	GW N flux (gN/m <sup>2</sup> /year)	Dominant N species	Method	References
Ringfield, VA, USA	0.2	NO <sub>3</sub> <sup>-</sup>	Salt balance, hydraulic head	Tobias et al., 2001a
Philips Creek, VA, USA	<1.7	NO <sub>3</sub> <sup>-</sup>	Spring discharge	Anderson et al., 1997
Bly Creek, SC, USA	0.4	DON	Hydraulic head	Dame et al., 1991; Wolaver et al., 1988
Nauset Marsh, MA USA	0.4	NO <sub>3</sub> <sup>-</sup>	Simulation model	Colman and Masterson, 2008
Nauset Marsh	2–28	NO <sub>3</sub> <sup>-</sup>	Multiple methods	Giblin and Gaines, 1990; Nowicki et al., 1999
Great Sippewissett, MA	26	NO <sub>3</sub> <sup>-</sup>	Flood-ebb salt balance	Valiela et al., 1978
Pamet River Estuary, MA	23.8–99.4	DIN	Radium budget	Charette, 2007
North Inlet, SC	12	NH <sub>4</sub> <sup>+</sup>	Radium budget	Krest et al., 2000

Method denotes the technique used to calculate the water flux component of the GW N flux.

(Colman and Masterson, 2008) may provide a better-constrained estimate of GW-N flux when compared to small-scale direct measurements extrapolated to the whole ecosystem. The direct-measure flux estimates, particularly those based on geochemical tracers (e.g., radium budgets; Krest et al., 2000), include some component of recycled porewater N that can lead to an overestimate of GW-N delivery. More recent studies have used radium isotopes to parse out the contribution of “fresh” groundwater from that of recycled porewaters (Charette, 2007). Despite some of the uncertainties associated with radium-based estimates of GW-driven exchanges of N, this approach operates at expanded scales not afforded by other techniques (Krest et al., 2000; Charette et al., 2003; Charette, 2007).

### 3.1.4. Tidal inputs/outputs

Tidal exchange usually dominates the mass fluxes of N between salt marshes and adjacent ecosystems (Morris, 1991; Rozema et al., 2000). Thirty years of tidal flux studies show that marshes transform N, sometimes acting as a net importer or exporter of dissolved or PN. The magnitude, and in some cases the direction, of such exchanges can reverse on short timescales within a single marsh (Dankers et al., 1984; Wolaver et al., 1988; Whiting et al., 1989; Anderson et al., 1997) and it remains difficult to predict whether a particular marsh will import or export various N species at any given time.

**Table 4** A representative subset of reported tidal exchange fluxes (g N/m<sup>2</sup>/year)

N fraction	Net import				Net export			
	Range	Mean	std	<i>n</i>	Range	Mean	std	<i>n</i>
NO <sub>3</sub> <sup>-</sup>	0.6–2.7	1.6	0.8	8	0.2–6.3	2.1	2.1	11
NH <sub>4</sub> <sup>+</sup>	0.4–4.8	2.9	1.9	6	1.6–8.7	4.2	2.8	7
DON	0.9–24.1	7.4	11.2	4	0.3–9.2	3.3	17.3	4
PN	0.9–31	8.7	15.2	4	4.5–42	10.7	16.1	5

The range, mean flux, number of studies, and standard deviation (std) of the flux magnitudes are reported. Exchange data from Jordan et al. (1983), Anderson et al. (1997), Chambers et al. (1994), and compilations of previous work presented in Dame (1994), Childers (1994), Childers et al. (2000), and Valiela et al. (2000).

Over twenty salt marsh N studies provide an accounting of N exchanges as DIN, DON, and particulate organic N (PON)/PN (Table 4). In this data set, 40% of the marshes were net annual importers of NH<sub>4</sub><sup>+</sup>, 35% imported NO<sub>3</sub><sup>-</sup>, 27% imported DON, and 26% imported PON/PN. The exchanges (either import or export) of NH<sub>4</sub><sup>+</sup> tended to be larger than those of NO<sub>3</sub><sup>-</sup>. The magnitude of import/export of DON and PON were higher than those of the DIN fractions but were highly variable. The developmental phase or “age” of the marsh seems to play a role in exchanges. Relative marsh age has been inferred by its location along the marsh estuarine continuum where young marshes lie closest to the upland border (Dame and Gardener, 1993; Dame, 1994) or have been defined by the ratio of vegetated to open water areas and the extent of tidal creek connections, where young marshes possess large areas of open water and few inlet/outlets (Valiela et al., 2000). When tidal exchanges are broken down as a function of marsh age (Dame, 1994; Valiela et al., 2000), younger marshes tend to import total N (although DON is often exported), whereas older marshes often export N as both DIN and DON. Some of the NO<sub>3</sub><sup>-</sup> export from these mature marshes may be explained by NO<sub>3</sub><sup>-</sup>-rich groundwater discharge (Howes et al., 1996) or rapid oxidation (i.e. nitrification) of porewater that drains into exposed creekbeds during ebb tide. Mid-aged marshes generally import PN and export dissolved N (Dame, 1994). Tidal amplitude is superimposed on marsh age as an added control on tidal fluxes – younger marshes are more sensitive to changes in tidal amplitude – a response that reflects changes in hydraulic conductivity, porewater chemistry, and rates of porewater drainage as marshes age (Whiting and Childers, 1989; Childers, 1994; Howes and Goehringer, 1994). Using data exclusive of flume studies, Childers et al. (2000) showed that tidal amplitude alone accounted for 40% of the variance in NO<sub>3</sub><sup>-</sup> exchanges. At tidal amplitudes above 1.2 m, marshes tended to switch from NO<sub>3</sub><sup>-</sup> import to export. This switch is consistent with higher tidal ranges delivering more direct drainage of high NH<sub>4</sub><sup>+</sup> porewater that can be rapidly oxidized and exported as NO<sub>3</sub><sup>-</sup>.

The largest PON (and POC) import is observed in younger marshes (Childers, 1994; Dame, 1994; Osgood, 2000; Valiela et al., 2000). Tidal range positively

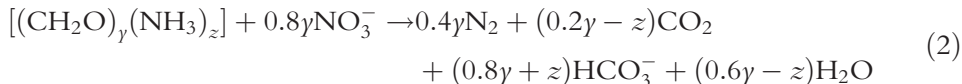
influences PON import in younger systems, but does not affect older marshes, which tend to be net exporters (Childers, 1994; Dame, 1994). Across a range of marsh types, net annual import of PON is observed about as often as net export of PON (Table 4). Stoichiometric PON flux estimates ( $\text{POC flux} \times \text{N} : \text{C}_{\text{POM}}$ ) agree reasonably well with other direct estimates of PON import and range from 0.9 to 42 g N/m<sup>2</sup>/year.

### 3.1.5. Gaseous losses

Denitrification is the primary route for losses of gaseous N from salt marshes. In addition to N<sub>2</sub>, several intermediate N gases are produced during denitrification (e.g., N<sub>2</sub>O). Denitrification in saturated soils/sediments usually yields <10% N<sub>2</sub>O as an end product (Smith et al., 1983; Seitzinger and Kroeze, 1998). Under exceptionally high NO<sub>3</sub><sup>-</sup> loads, Tobias et al. (2001c) reported a N<sub>2</sub>O : N<sub>2</sub> ratio closer to 0.40 and suggested denitrification as a source of N<sub>2</sub>O in heavily N-loaded marshes. Although NH<sub>4</sub><sup>+</sup> is abundant in porewaters, soil pHs are typically low enough (NH<sub>3</sub> pK<sub>a</sub> = 9.7) to prevent significant volatilization of NH<sub>4</sub><sup>+</sup> to NH<sub>3(g)</sub> (Morris, 1991).

Organic carbon is the principal electron donor for denitrification; the importance of alternate electron donors (e.g., reduced sulfur or iron) to marsh denitrification remains open.

#### *Denitrification coupled to organic matter oxidation*

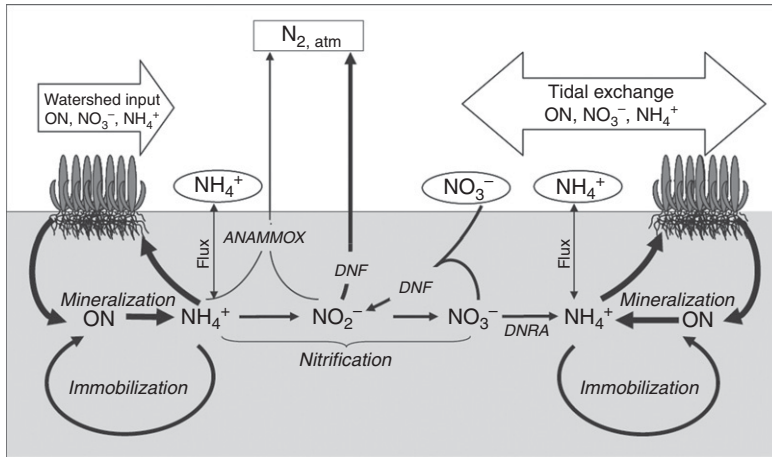


Denitrification rates range from 0 to 60 g N/m<sup>2</sup>/year (Table 5) and comparisons are hampered by methodological differences (see discussion in Seitzinger et al., 2006). Nevertheless, the differences in rates (Table 5) cannot be explained solely by different methods. Total denitrification depends on O<sub>2</sub> concentrations in the subsurface, NO<sub>3</sub><sup>-</sup> supply, quantity and quality of organic carbon, and the presence of inhibitors (e.g., sulfide). The source of NO<sub>3</sub><sup>-</sup> for denitrification comes from allochthonous sources (direct denitrification) or is supplied from mineralization–nitrification (coupled denitrification; Figure 1). Seitzinger et al. (2006) suggested a breakpoint around 20 μM NO<sub>3</sub><sup>-</sup> in a variety of freshwater and saline environments where coupled denitrification dominates at lower NO<sub>3</sub><sup>-</sup> concentrations and direct denitrification dominates when NO<sub>3</sub><sup>-</sup> exceeds 20 μM. This assertion has not been well-tested in marshes. While O<sub>2</sub> in high abundance inhibits direct denitrification, its delivery into the NH<sub>4</sub><sup>+</sup>-rich subsurface promotes the high rates of coupled nitrification–denitrification observed in close proximity to root channels and infaunal burrows (Howes et al., 1981; Dollhopf et al., 2005). Hammersley and Howes (2005) attributes several-fold higher coupled denitrification rates measured in situ versus laboratory rates to the enhancement of denitrification by plants. Seasonal variations in direct denitrification reflect changes in the external NO<sub>3</sub><sup>-</sup> loading (Koch et al., 1992). Coupled denitrification is enhanced by external inputs of

**Table 5** Select salt marsh denitrification rates

Reference	g N/m <sup>2</sup> /year	Geographic Region	Location	Ambient NO <sub>3</sub> <sup>-</sup>
Anderson et al., 1997	0.6	Mid Atlantic, VA	Philips Creek, VA	Low
Smith et al., 1985	1.7	Gulf Coast, LA	Four League Bay, LA	Moderate to high
Kaplan et al., 1979, Valiela and Teal, 1979	0–44	New England, MA	Great Sippewisset, MA	High
Aziz and Nedwell, 1986	0.3–0.8	UK	Colne Pt., UK	Moderate to high
Koch et al., 1992	0.3–0.7	UK	Torridge Marsh, UK	Moderate to high
Thompson et al., 1995	0–1.8	Southeastern NC	Newport River, NC	Low
Eriksson et al., 2003	0–19.6	Mediterranean	Venice Lagoon, Italy	High
Poulin et al., 2007	2.3–5.5	Canada	St. Lawrence River, Canada	Low to moderate
Tobias et al., 2001b	102	Mid Atlantic, VA	Ringfield, VA	Very high
Hammersley and Howes, 2003	30	New England, MA	Mashapaquit, MA	High
Hammersley and Howes, 2005	2–60	New England, MA	Great Sippewisset, MA	High
Compilation by Morris, 1991	0.4–14.3	East Coast, USA, Europe	several	Variable
DeLaune et al., 1989	7	Gulf Coast	Barataria Bay, LA	Moderate

Rates encompass various laboratory and in situ techniques including N<sub>2</sub> accumulation, <sup>15</sup>N<sub>2</sub>, <sup>15</sup>N<sub>2</sub>O dilution, isotope pairing, acetylene block, and mass balance methods.



**Figure 1** Summary of the major N cycling pathways in salt marshes. DNF = denitrification; DNR A = dissimilatory nitrate reduction to ammonium; ANAMMOX = anaerobic ammonium oxidation. The sizes of the arrows denote the relative magnitudes of the processes.

reduced N (Hammersley and Howes, 2005) and responds to increased  $\text{NH}_4^+$  supply from mineralization. Positive relationships have been observed between mineralization and denitrification in freshwater systems (Seitzinger, 1994; Mulholland et al., 2008). This pattern is mirrored in some salt marshes where higher denitrification is coincident with seasonally high mineralization rates (Anderson et al., 1997). For marshes dominated by either type of denitrification, the highest rates are encountered in surface soils that are exposed at low tide, in closest contact with  $\text{NO}_3^-$  in overlying water at high tide, nearest the zone of nitrification, and closest to nearsurface labile organic matter supplies (Koch et al., 1992; Tobias et al., 2001b).

Because denitrification exports N, it plays an important role in overall N residence time. Competition for N between plants and denitrification is a regulator of long-term N retention, with denitrification reported at roughly 20% of plant uptake (White and Howes, 1994b). There are examples of marshes where plant growth far outcompetes denitrification for N (Anderson et al., 1997) and those where denitrification and plant N demand are roughly equal (Morris, 1991). Studies in several mature marshes put losses of N through denitrification approximately equivalent to inputs via N fixation, suggesting that the balance between these two pathways are important for overall marsh N balance (Valiela and Teal, 1979; Morris, 1991; White and Howes, 1994b; Anderson et al., 1997; Rozema et al., 2000). Denitrification ranges between 15% and 100% of N burial, with most marshes showing similar magnitudes for each pathway. There are only a few examples of systems where denitrification vastly exceeds burial and are likely explained by high  $\text{NO}_3^-$  loading that fuels high rates of direct denitrification (Kaplan et al., 1979). As with all other input and removal pathways, the magnitude of denitrification is small relative to internal N cycling.

Anaerobic ammonium oxidation (ANAMOX) is an alternate pathway by which N can be exported from ecosystems. ANAMOX uses ammonium to reduce nitrite to produce N<sub>2</sub>. It is chemoautotrophic and, unlike denitrification, does not require organic carbon. ANAMOX can rival rates of denitrification in a variety of marine sediments but is less important in high organic carbon systems (like salt marshes), where it accounts for less than 10% of the N<sub>2</sub> production (Dalsgaard et al., 2005). It is not currently considered an important route of N loss from salt marshes.

### 3.2. Internal cycling

#### 3.2.1. Photoautotrophy

Except for some very young marshes, autotroph N demand exceeds inputs and primary production is fueled by recycled N. Macrophyte N uptake is one of the larger N flux terms ranging from 1 to 33 g N/m<sup>2</sup>/year (Gallagher et al., 1980; Hopkinson and Schubauer, 1984; Morris, 1991; Blum, 1993; Dai and Weigert, 1996; Anderson et al., 1997; Rozema et al., 2000; Hopkinson and Giblin, 2008). Microalgal uptake in marshes is ~10–15% of emergent macrophyte demand (Anderson et al., 1997; Rozema et al., 2000; Tyler et al., 2003). Aboveground plant N content ranges from <0.2% to 3% (Buresh et al., 1980; Anderson et al., 1997). Nitrogen frequently limits plant production; plants respond to nitrogen additions with increased N content and enhanced biomass production (Deegan et al., 2007; Drake et al., 2008; and others).

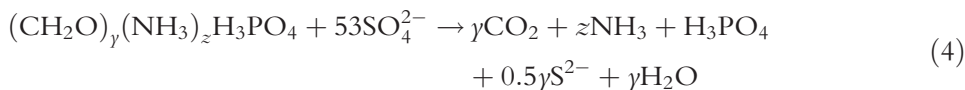
#### 3.2.2. Mineralization and immobilization

The sum of new N inputs to salt marshes is on the order of 0.5% to <5% of the total N necessary to support macrophyte production (Hopkinson and Schubauer, 1984; DeLaune et al., 1989; Dame et al., 1991; Anderson et al., 1997). The difference is made up by the mineralization of organic N into the NH<sub>4</sub><sup>+</sup> pool that has a high rate of turnover (Figure 1). Both aerobic and anaerobic (e.g., sulfate reduction) mineralization pathways yield NH<sub>4</sub><sup>+</sup>.

*Aerobic mineralization ( $\gamma/z = C : N$  ratio of the organic matter)*



*Sulfate reduction*



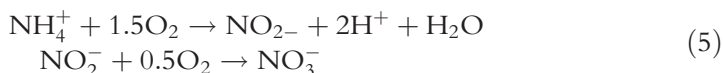
Consequently, porewater NH<sub>4</sub><sup>+</sup> concentrations in well-developed marshes are high. Mineralization rates vary widely between marshes (3.0–122 g N/m<sup>2</sup>/year; Morris, 1991; Anderson et al., 1997; Rozema et al., 2000; Thomas and Christian, 2001; Tobias et al., 2001a). Mineralization rates decrease exponentially with depth due to decreasing organic matter quantity and lability (Bowden, 1984; Howes et al., 1985; Tobias et al., 2001a).

For a variety of marshes, mineralization meets between 50% and 200% of autotrophic N requirements. Even in systems that appear to have mineralization

rates that exceed uptake by N sinks (e.g., plants or denitrification), no large exports of N are observed (Anderson et al., 1997). Several lines of evidence indicate that microbial immobilization plays an important role in retaining a significant fraction (15–50%) of mineralized N (Anderson et al., 1997; Hopkinson and Giblin, 2008). Increases in the N content of macrophyte detritus during diagenesis are consistent with the immobilization of porewater  $\text{NH}_4^+$  (Benner et al., 1991). Significant retention of  $^{15}\text{N}$  tracers within marsh soils over 100 days (93%; DeLaune et al., 1983) to 7 years (40%; White and Howes, 1994a,b) indicates that the  $\text{NH}_4^+$  pool acts as a common substrate for exchanges among plant assimilation, microbial recycling, and removal via denitrification and burial.

### 3.2.3. Nitrification

Nitrification is the oxidation of ammonium to nitrate. It consumes molecular  $\text{O}_2$  and links mineralization to N export via denitrification. Nitrification is the rate-limiting step for subsequent denitrification of mineralized N out of marshes.



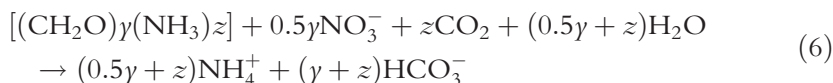
Nitrification occurs in the presence of adequate supplies of  $\text{O}_2$  and  $\text{NH}_4^+$ ; because porewaters are typically rich in  $\text{NH}_4^+$ , nitrification is generally limited by  $\text{O}_2$  availability. It is restricted either to surface soils or oxic microzones, declines with depth, and is influenced by tidal wetting and drying in close proximity to root channels or burrows (Howes et al., 1981; Tobias et al., 2001a; Eriksson et al., 2003; Dollhopf et al., 2005; Costa et al., 2007). Nitrification activity is inhibited by elevated sulfide levels (Joye and Hollibaugh, 1995), high salinities (Seitzinger et al., 1991; Rysgaard et al., 1999), and low pH (<4.50) characteristic of drained marshes undergoing acidification due to high rates of sulfur oxidation (Portnoy and Giblin, 1997). Under anaerobic conditions,  $\text{NO}_3^-$  is quickly reduced so concentrations are low in the absence of large external  $\text{NO}_3^-$  inputs.

Annual rates of nitrification range from 0.26 to 52 g N/m<sup>2</sup>/year (Abd Aziz and Nedwell, 1986; Anderson et al., 1997; Tobias et al., 2001b; Eriksson et al., 2003; Hammersley and Howes, 2003; Dollhopf et al., 2005; Costa et al., 2007). Eighty percent of the reported rates are <10 g N/m<sup>2</sup>/year, with higher rates observed during warmer months (Thompson et al., 1995; Anderson et al., 1997). Some of the highest estimates come from marshes that are heavily N loaded (Eriksson et al., 2003; Hammersley and Howes, 2005) suggesting that competition for N can occur between nitrifiers and autotrophs. In marsh N budgets, nitrification is 4- to 20-fold lower than mineralization (Abd Aziz and Nedwell, 1986; Anderson et al., 1997; Neubauer et al. 2005a) and is roughly equivalent to coupled denitrification. In situ estimates of nitrification following a whole ecosystem  $^{15}\text{NH}_4^+$  release showed that rapid nitrification on the marsh surface accounted for 30% of the  $\text{NH}_4^+$  transformations (Gribsholt et al., 2005, 2006). This in situ technique yielded nitrification rates four- to eightfold higher than those measured in the laboratory and illustrated the importance natural gradients of  $\text{O}_2$  and  $\text{NH}_4^+$  in maintaining this reaction. This type of approach shows promise in addressing nitrification (and other processes) at the ecosystem scale.

### 3.2.4. Dissimilatory nitrate reduction to ammonium

Dissimilatory nitrate reduction to ammonium (DNRA) retains N (Figure 1). The reaction is largely mediated by facultative anaerobic fermentative bacteria (Tiedje, 1988; Nijburg and Laanbroek, 1997; Megonigal et al., 2004) although chemolithoautotrophic DNRA has been proposed as an additional DNRA pathway (Brunet and Garcia-Gil, 1996).

*DNRA – complete stoichiometry – from Canavan et al. (2007)*



Temperature, salinity, sulfide, redox, labile organic carbon, and  $\text{NO}_3^-$  concentration have all been suggested as potential controls on DNRA (King and Nedwell, 1985; An and Gardner, 2002; Laverman et al., 2007). DNRA appears to be favored at high- and low-temperature extremes (Kelly-Gerreyn et al., 2001) and seems to be enhanced by a high organic carbon :  $\text{NO}_3^-$  ratio or when ample sulfide provides an alternate electron source (Gardner et al., 2006). DNRA can be further coupled to sulfur cycling through sulfide inhibition of denitrification which allows DNRA to dominate (Brunet and Garcia-Gil, 1996; Christensen et al., 2000; An and Gardner, 2002; Senga et al., 2006) or by inducing some sulfate-reducing bacteria to switch to  $\text{NO}_3^-$  as the terminal electron acceptor and produce  $\text{NH}_4^+$  (Dalsgaard and Bak, 1994; An and Gardner, 2002). Different sulfide and carbon loads may also influence microbial community controls on DNRA and contribute to variations in observed rates (Burgin and Hamilton, 2007; Scott et al., 2008).

DNRA effectively competes with denitrification for  $\text{NO}_3^-$  across a range of “wet” ecosystems where it often accounts for over 50% of the  $\text{NO}_3^-$  reduction (Kelly-Gerreyn et al., 2001; Megonigal et al., 2004). DNRA is currently believed to be most prevalent in marine sediments where rates range from 0 to 40 g N/m<sup>2</sup>/year (Gilbert et al., 1997; Bonin et al., 1998; Christensen et al., 2000; Kelly-Gerreyn et al., 2001; An and Gardner, 2002; Gardner et al., 2006; Thornton et al., 2007). It has been measured only a few times in salt marshes (King and Nedwell, 1985; Tobias et al., 2001a,c) and fresh water wetlands (Bowden, 1986; Neubauer et al., 2005a; Scott et al., 2008). DNRA in mesohaline marsh soils, measured in the laboratory and in situ using a <sup>15</sup>NO<sub>3</sub><sup>-</sup> tracer release, yielded “annualized” rates ranging from 1.2 to 92 g N/m<sup>2</sup>/year. These rates ranged from 0.3 to 2 times that of denitrification (Tobias et al., 2001a,c). DNRA appears to be an important fate for  $\text{NO}_3^-$  in salty, high-sulfide, organic-rich sediments, yet this pathway remains understudied in salt marshes (Poulin et al., 2007). The positive relationship between DNRA and increasing salinity/sulfide suggests increasing N retention in tidal fresh and mesohaline marshes as seawater encroaches up estuaries due to sea level rise (SLR).

### 3.3. Burial

Long-term nitrogen burial rates in salt marshes have been estimated directly using sediment traps, horizon markers, radioisotope profiles (<sup>210</sup>Pb, <sup>137</sup>Cs), and extrapolated from SLR estimates (Hutchinson et al., 1995; Merrill and Cornwell, 2000;

Craft, 2007; Goodman et al., 2007). N (and P) burial combines contributions from allochthonous suspended sediments and autochthonous organic matter. N is recycled multiple times within marsh soils, porewater, and biota before it ultimately becomes sequestered primarily in belowground organic matter (White and Howes, 1994b). Nitrogen burial rates along the Atlantic and Gulf coasts (USA) range from 1 to 23 g N/m<sup>2</sup>/year (Craft, 2007 and references therein). For Wadden Sea salt marshes, net sedimentation of N is on the order of 10–50 g N/m<sup>2</sup>/year (Rozema et al., 2000). For systems that lack direct measurements, a SLR proxy can be used to estimate N burial. With some exceptions (Chmura and Hung, 2004), there is good agreement between marsh accretion and SLR (Donnelly et al., 2004). By combining typical bulk density and N content estimates for marsh soils with local measures of SLR, one can broadly generalize that marshes keeping pace with SLR are burying N on the order of 2–6 g N/m<sup>2</sup>/mm SLR. In rapidly accreting marshes (>5 mm/year), N burial can be comparable to the rate at which new N is delivered. For most other systems, N burial is on the order of 50–60% of the total N inputs (Anderson et al., 1997; Neubauer et al., 2005a). Network analysis of three salt marshes (New England, Georgia, and Mid Atlantic, USA) indicated that burial is second only to tidal export as the fate of imported PN across these marsh types (Thomas and Christian, 2001). N burial is inversely related to salinity due to a lower soil N content at euryhaline sites and enhanced decomposition of belowground organic matter at higher salinity marshes (Craft, 2007).

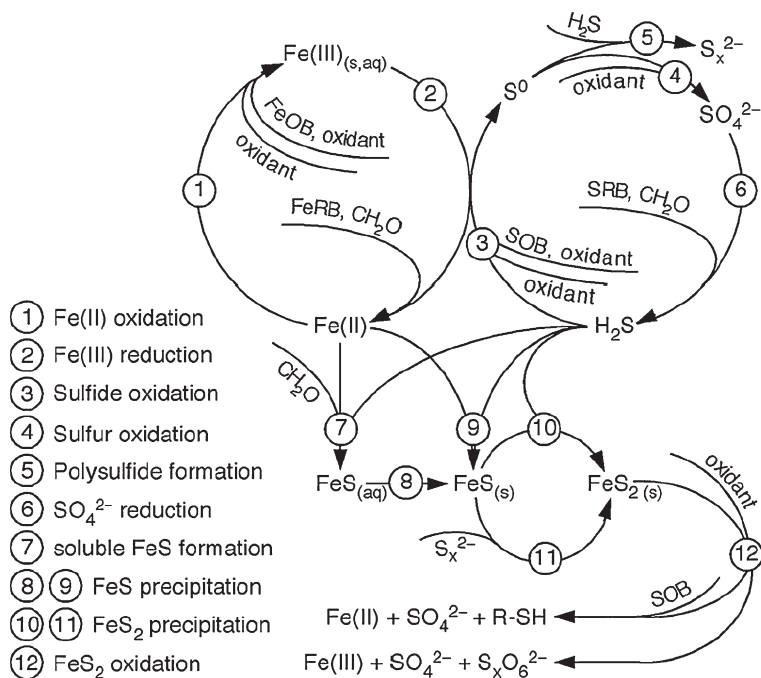
## 4. IRON AND SULFUR

The biogeochemical cycles of iron and sulfur are tightly linked in salt marsh soils (Figure 2), primarily through the abiotic reduction of Fe(III) by sulfides and via the reactions that control the formation and dissolution of Fe–S minerals such as iron monosulfides (FeS) and pyrite (FeS<sub>2</sub>). Further, both elements undergo active redox cycling, play a role in organic C catabolism (Section 2.2), and may also contribute to significant chemoautotrophic production (Section 2.2.3).

### 4.1. Exchanges

#### 4.1.1. Dissolved Fe and S exchanges

If water infiltrating marsh soils to replace the 5–20 L/m<sup>2</sup>/day lost to seepage and evapotranspiration (Morris, 1995) has near-oceanic SO<sub>4</sub><sup>2-</sup> concentrations (~28 mM SO<sub>4</sub><sup>2-</sup>), there is a potential SO<sub>4</sub><sup>2-</sup> source of 4.5–18 g SO<sub>4</sub><sup>2-</sup>-S/m<sup>2</sup>/day. These tidal SO<sub>4</sub><sup>2-</sup> inputs often exceed rates of sulfate reduction (Morris, 1995; Kostka et al., 2002b). SO<sub>4</sub><sup>2-</sup> delivery rates vary with soil depth, distance from tidal creeks, and location within the estuary. Sulfate concentrations in marsh porewaters are typically depleted (relative to a conservative tracer), indicating net SO<sub>4</sub><sup>2-</sup> utilization (Gardner et al., 1988; Hines et al., 1989; Hsieh and Yang, 1997). We do not know of any estimates of dissolved Fe delivery to salt marshes although this flux is probably insignificant in the total marsh Fe budget.



**Figure 2** The Fe and S cycles are linked in salt marsh soils through a series of biologically mediated and abiotic reactions. This figure focuses on inorganic forms of Fe and S. With the exception of thiol (R-SH) formation during biological pyrite oxidation, the complexities of the organic Fe or S cycles are not considered here. For simplicity, the oxidation of FeS is not shown although the products of this reaction are similar to those of pyrite oxidation (i.e.,  $\text{SO}_4^{2-}$ , Fe(II), and/or Fe(III)). FeOB and SOB = Fe(II) and sulfide-oxidizing bacteria, respectively; FeRB and SRB = Fe(III) and  $\text{SO}_4^{2-}$ -reducing bacteria, respectively. Oxidants are compounds including  $\text{O}_2$ ,  $\text{NO}_3^-$ ,  $\text{MnO}_2$ , and Fe(III) oxides that can oxidize reduced compounds.  $\text{CH}_2\text{O}$  generically refers to organic C, which can be in the form of organic molecules that are catabolized by heterotrophic microbes such as FeRB and SRB or as ligands that play a key role in solubilizing and/or reducing Fe minerals (e.g., Luther et al., 1992; Carey and Taillefert, 2005).

The advection of marsh porewater and diffusive fluxes each play a role in exporting dissolved S and Fe. Estimates of the export of  $\text{H}_2\text{S}$  ( $20 \text{ g S/m}^2/\text{year}$ ) and thiosulfate ( $1,504 \text{ g S/m}^2/\text{year}$ ) from Great Sippewissett Marsh are considerable, representing the energetic equivalent of 23% of total NPP (Howarth and Teal, 1980). Using a  $\text{H}_2\text{S}$  concentration of  $100 \mu\text{M}$  for tall *S. alterniflora* soils (King et al., 1982) and applying a porewater replacement rate of  $5\text{--}20 \text{ L/m}^2/\text{day}$  (as above), we estimate an export of  $6.4\text{--}22 \text{ g H}_2\text{S-S/m}^2/\text{year}$ , a rate that is comparable to the value calculated by Howarth and Teal (1980). Luther et al. (1982b) observed that the  $\text{SO}_4^{2-} : \text{Cl}^-$  ratio over the tidal cycle decreased during ebb tide in two marsh creeks but increased dramatically in a third creek, indicating that total S import/export depends on spatially distinct balances between sulfate reduction and oxidation of metal sulfides. Guo et al. (2000) reported a  $\text{Fe}^{2+}$  flux of  $0.9\text{--}1.9 \text{ g Fe/m}^2/\text{year}$

from saline and brackish marsh microcosms. The loss of  $\text{Fe}^{2+}$  due to porewater drainage will be greater at creek banks than in mid- and high-marsh locations due to a higher  $\text{Fe}^{2+}$  supply [more Fe(III) reduction and a lower degree of pyritization (DOP)] and more rapid rates of porewater turnover in creek bank marshes. Given the kinetics of Fe(II) oxidation, it is likely that a significant fraction of  $\text{Fe}^{2+}$  in tidal waters will be rapidly reoxidized and may settle back onto marsh surfaces. However, reactions with organic ligands may keep the resulting Fe(III) in a soluble form (Luther et al., 1996) and allow  $\text{Fe}_{(\text{aq})}$  to be exported.

#### 4.1.2. Atmospheric exchanges

The deposition of atmospheric  $\text{SO}_4^{2-}$  ( $<1 \text{ g SO}_4^{2-}\text{-S/m}^2\text{/year}$ , NADP, 2008) and Fe ( $\sim 0.1 \text{ g Fe/m}^2\text{/year}$ ; Duce et al., 1991) in the coastal zone is much lower than other inputs of these elements. However, atmospheric fluxes may be locally elevated in close proximity to industrial emissions (Lecoanet et al., 2001).

Saline and brackish marshes emit  $\text{H}_2\text{S}$ , dimethyl sulfide [DMS,  $(\text{CH}_3)_2\text{S}$ ], carbonyl sulfide (COS), methanethiol ( $\text{CH}_3\text{SH}$ ), carbon disulfide ( $\text{CS}_2$ ), and dimethyl disulfide [ $(\text{CH}_3\text{S})_2$ ] (Morrison and Hines, 1990; DeLaune et al., 2002). Most salt marshes are net sources of S gases to the atmosphere (Cooper et al., 1987; Dacey et al., 1987; Morrison and Hines, 1990; Crozier et al., 1995; DeLaune et al., 2002) although there are reports of uptake of specific gases (e.g., COS; Morrison and Hines, 1990). DeLaune et al. (2002) reported an average total gaseous emission rate of  $0.6 \text{ g S/m}^2\text{/year}$  for a salt marsh and  $0.3 \text{ g S/m}^2\text{/year}$  for a brackish marsh.

The production of sulfur-containing gases is positively correlated with  $\text{SO}_4^{2-}$  concentrations (Crozier et al., 1995), a pattern that was observed for total gaseous S emissions along a salinity gradient (DeLaune et al., 2002). Because the production of these gases is biologically driven, emission rates are generally greater with higher plant biomass and growth (Morrison and Hines, 1990; DeLaune et al., 2002). DMS dominates emissions ( $>50\%$ ) in *S. alterniflora* marshes with low emissions as  $\text{H}_2\text{S}$  ( $<10\%$ ; Cooper et al., 1987; DeLaune et al., 2002b). A *S. patens* brackish marsh emits primarily  $\text{H}_2\text{S}$  and COS (DeLaune et al., 2002). High DMS emission rates from *S. alterniflora* versus *S. patens* brackish marshes reflect some differences in plant physiology; *S. alterniflora* contains high concentrations of dimethylsulfoniopropionate (DMSP), the precursor to DMS, whereas *S. patens* does not (Dacey et al., 1987). The differential emissions along salinity gradients also show the effect of sulfide sequestration in metal S complexes in euryhaline marshes. Despite emission of several S gases, it is not an important loss term for individual marshes relative to burial and tidal export. While S gas emissions are important for atmospheric chemistry and radiative balance (Shaw, 1983; Kelly and Smith, 1990), salt marshes contribute little as a global source/sink.

#### 4.1.3. Sedimentary Fe and S deposition

Recently deposited sediments and nearsurface marsh soils often have Fe contents in the range of 1–2% (mass basis; DeLaune et al., 1981; Gardner et al., 1988; Merrill and Cornwell, 2000) and S contents of 0.5–2% (although values up to 5% can occur; Cutter and Velinsky, 1988; Gardner et al., 1988; Giblin, 1988). Using these

Fe and S concentrations and mass deposition rates for Paulina Marsh (Section 2.1.2), annual deposition of these elements is  $\sim 50\text{--}100\text{ g Fe/m}^2\text{/year}$  and  $\sim 25\text{--}100\text{ g S/m}^2\text{/year}$ . These deposition rates roughly overlap with long-term accumulation (burial) rates of these elements (Section 4.3).

## 4.2. Internal cycling

### 4.2.1. Iron and sulfur reduction

Iron(III) reduction can be biotic or abiotic (Figure 2). Microbial and geochemical analyses have suggested a significant, if not dominant, role for microbial Fe(III) reduction although there is spatial variability in the importance of each pathway (Section 2.2.2). Large populations of Fe(III)-reducing bacteria (FeRB) can be found in vegetated soils and around roots (Lowe et al., 2000; Kostka et al., 2002a; Koretsky et al., 2003; Weiss et al., 2003), proximal to  $\text{SO}_4^{2-}$ -reducing bacteria and aerobic microbes (Koretsky et al., 2005). Microbial Fe(III) reduction accounts for 80–100% and 39–53% of total reduction in mineral- and organic-rich marsh soils, respectively (Kostka et al., 2002a; Gribsholt et al., 2003; Neubauer et al., 2005b; Hyun et al., 2007). Koretsky et al. (2003) proposed that seasonal changes in rates of  $\text{H}_2\text{S}$  production cause oscillation between chemically dominated Fe(III) reduction in summer and biologically dominated Fe(III) reduction in other seasons.

The reduction of  $\text{SO}_4^{2-}$  is primarily a biological process coupled to the oxidation of simple organic compounds including volatile fatty acids and acetate (Hines et al., 1994, 1999; Boschker et al., 2001). The  $\text{H}_2\text{S}$  produced tends to rapidly convert to pyrite although some fraction ( $< 5\text{--}23\%$ ) appears as organo-sulfur compounds (Howarth, 1979; Neubauer et al., 2005b). Seasonal patterns of  $\text{SO}_4^{2-}$  reduction tend to follow temperature patterns and are also influenced by marsh primary production (Howarth and Teal, 1979; Hines et al., 1999; Koretsky et al., 2003). Sulfate reduction decreases when plants allocate more C to flowering/reproductive structures and less C leaks into the soil (Lytle and Hull, 1980; Hines et al., 1999). The relative abundance of  $\text{SO}_4^{2-}$ -reducing bacteria (SRB) ribosomal ribonucleic acid (rRNA) associated with plant roots increased in parallel with changes in  $\text{SO}_4^{2-}$  reduction activity (Hines et al., 1999). Similarly, the SRBs *Desulfobacter* and *Desulfovibrio* were more prevalent in summer than winter (Koretsky et al., 2005). However, Hines et al. (1999) reported that the rRNA that could be ascribed to SRB did not change significantly over the year (relative to bacterial rRNA) even though rates of  $\text{SO}_4^{2-}$  reduction did show seasonal variability.

### 4.2.2. Formation and oxidation of Fe–S minerals

Solid phase sulfides are operationally divided into acid volatile sulfides (AVS, consisting of  $\text{H}_2\text{S}$  and FeS) and chromium (II)-reducible sulfides (CRS:  $\text{FeS}_2$  and  $\text{S}^0$ ). Early work measuring  $\text{SO}_4^{2-}$  reduction rates demonstrated that a large fraction of the added  $^{35}\text{SO}_4^{2-}$  tracer appeared as solid phase sulfides, indicating that Fe–S minerals form rapidly in salt marsh soils (Howarth, 1979). In terms of concentration, pyrite is a 10-fold more important end product than iron monosulfides

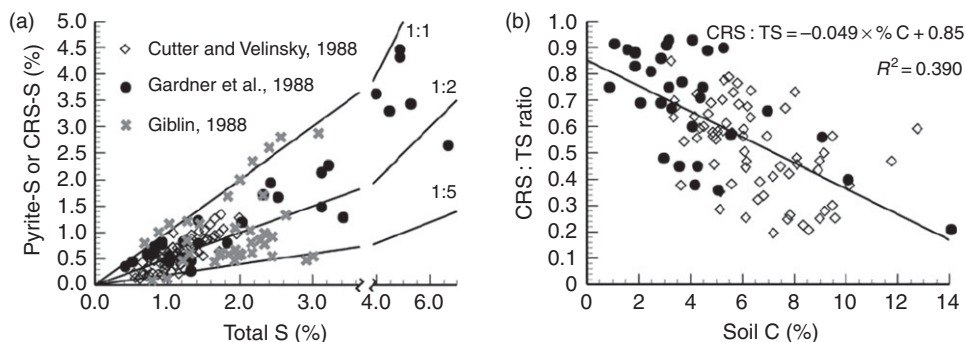
although the mechanisms of pyrite formation involve an FeS intermediary (Figure 2; Giblin and Howarth, 1984; Cutter and Velinsky, 1988; Gardner et al., 1988). The reaction of Fe(II) and H<sub>2</sub>S leads to the formation of a soluble FeS phase when suitable organic ligands are present (Taillefert et al., 2000; Carey and Taillefert, 2005) or to direct precipitation of FeS minerals. Reaction with additional reduced S (as H<sub>2</sub>S or polysulfides, S<sub>x</sub><sup>2-</sup>) then leads to FeS<sub>2</sub> precipitation (Canfield et al., 1998; Rickard and Luther, 2007).

Inorganic sulfide minerals are not always the dominant form of S in salt marsh soils (Figure 3a). Across a range of salt marshes, CRS accounts for 20–100% of total soil S [average CRS:TS (total sulfur) ratio = 0.57 ± 0.25 SD]. The nonpyritic sulfur is likely dominated by organic S forms (Giblin, 1988). Organic S accounted for 45 ± 19% of the total S pool in the top 30–50 cm of Great Marsh, Delaware (Cutter and Velinsky, 1988). Similarly, the soil C content is inversely correlated with the fraction of CRS-S (Figure 3b) in Great Marsh, Delaware (Cutter and Velinsky, 1988), and North Inlet, South Carolina (Gardner et al., 1988). In this same data set, there was a positive relationship between the DOP and the CRS : TS ratio for Great Marsh but not for North Inlet (data not shown).

The DOP (Berner, 1970), an index of how much of the available Fe has reacted with sulfides to form pyrite, is calculated as

$$\text{DOP} = \frac{\text{Fe}_{\text{pyrite}}}{\text{Fe}_{\text{pyrite}} + \text{Fe}_{\text{reactive}}} \quad (7)$$

where Fe<sub>pyrite</sub> is the amount of Fe in pyrite and Fe<sub>reactive</sub> is the amount of reactive or amorphous Fe in the sample. In salt marshes, DOP values for interior/high marsh sites are generally higher than for creekbank/levee sites (King et al., 1982; Gardner et al., 1988; Giblin, 1988; Otero and Macias, 2003; Roychoudhury et al., 2003a;



**Figure 3** Soil pyrite relationships in salt marsh soils. Most data are from *Spartina alterniflora* marshes although the Giblin (1988) study also included data from sites vegetated with *Spartina patens*, *Scirpus*, and *Typha*. Data points are individual samples and reflect temporal and spatial (lateral and depth related) variability in solid phase soil chemistry. (a) Chromium(II)-reducible sulfur (CRS) versus total sulfur (TS) in marsh soils. Solid lines indicate contours where CRS = TS, CRS = 0.5TS, and CRS = 0.2TS. (b) Relationship between the CRS : TS ratio and the soil C content. The regression line is fit through all data.

Roychoudhury, 2007). Sulfide production in interior marsh sites is  $\sim 1$ – $2$  orders of magnitude greater than the rate of Fe delivery (Gardner et al., 1988), and DOP values can approach 1.0 at these sites (DOP  $\sim 0.6$ – $1.0$ ). The lower DOP in creek bank marshes ( $\sim 0.2$ – $0.7$ ) indicates an enhanced supply of reactive Fe (Section 2.2.2), decreased sulfide availability (King et al., 1982), and/or processes that limit the formation/accumulation of pyrite.

Gross rates of pyrite formation are considerably greater than net rates of pyrite accumulation (Gardner, 1990), indicating that pyrite is actively oxidized or exported from marsh soils. Net pyrite oxidation exists during the spring/summer growing season while net pyrite formation occurs in winter (Giblin and Howarth, 1984; Cutter and Velinsky, 1988). Variations in the timing and frequency of flooding of marsh surfaces can override some of this seasonal generality (see discussion in Giblin, 1988). Hsieh and Yang (1997) speculated that roots play a major role in rates of pyrite accumulation by oxidizing the soil and providing labile organic C to fuel Fe(III) reduction and  $\text{SO}_4^{2-}$  reduction. Below the rooting zone, pyrite concentrations do not show large seasonal or spatial variability, again emphasizing the role of plants in both  $\text{FeS}_2$  formation and oxidation (Cutter and Velinsky, 1988; Hsieh and Yang, 1997).

Diagenetic model results suggest that rhizosphere oxidation (with either  $\text{O}_2$  or organic compounds as oxidants) was responsible for the majority of  $\text{FeS}_2$  oxidation (Gardner, 1990). Bioturbation near creek banks can remove 18% of subsurface pyrite by bringing it to the surface where it could be oxidized and/or washed away (Gardner et al., 1988). Advection of  $\text{O}_2$ -rich tidal water through soils contributes to subsurface  $\text{FeS}_2$  oxidation, and the seepage of water out of creek banks provides advective removal of  $\text{H}_2\text{S}$ . This tidal flushing, rather than effects of macro-organisms and plants, was most significant in affecting pyritization in creek bank soils (Roychoudhury et al. 2003a). Away from creek banks, where infaunal densities and porewater flushing are low, rhizosphere oxidation is likely to be the most significant mechanism for pyrite turnover. Thermodynamically,  $\text{FeS}_2$  can be oxidized anaerobically with  $\text{NO}_3^-$ ,  $\text{MnO}_2$ , or Fe(III) as oxidants. With some exceptions (Schippers and Jørgensen, 2002; Carey and Taillefert, 2005), the significance of these reactions has not been fully assessed.

#### 4.2.3. Iron oxidation

Oxidized Fe, in the form of root plaques or other accumulations (Luther et al. 1982a, Mendelsohn et al., 1995; Weiss et al., 2003), can serve as an electron acceptor for anaerobic metabolism (Lowe et al., 2000; Kostka et al., 2002a; Neubauer et al., 2005b) and as a sink for trace metals and  $\text{PO}_4^{3-}$  (Scudlark and Church, 1989; Chambers and Odum, 1990; Weis and Weis, 2004; Neubauer et al., 2008). In tidal wetlands, the solid phase Fe in the upper portions of the soil profile is generally rich in Fe oxides whereas iron sulfide minerals dominate at lower depths (Griffin et al., 1989). In shallow soils,  $\text{O}_2$  is the likely oxidant that drives both chemical and biologically mediated Fe(II) oxidation. Microbial Fe(II) oxidation linked to anaerobic photosynthesis (Widdel et al., 1993),  $\text{NO}_3^-$  reduction (Straub

et al., 1996), and perchlorate reduction (Chaudhuri et al., 2001) may also play a role. Plant roots are hotspots for oxidation, forming Fe oxide-rich plaques tens of micrometers up to 0.4 cm in thickness (Taylor et al., 1984; Vale et al., 1990). Sundby et al. (2003) proposed that rapid rates of biological and/or chemical Fe(II) oxidation (and therefore plaque formation) occurred in spring as new highly active roots invaded anoxic sediments with high Fe<sup>2+</sup> concentrations. Over multiple years, the oxidizing activity of plant roots can increase extractable Fe(III) pools relative to unvegetated sites (Kostka and Luther, 1995; Roden and Wetzell, 1996; Weiss et al. 2004). Tidal delivery of O<sub>2</sub> also influences temporal patterns of Fe(II) oxidation (Neubauer et al., 2005b). Because Fe(II) availability is low in mid- and high-marsh areas (i.e., DOP is high, see above), overall rates of Fe(II) oxidation are likely to be lowest in these parts of marshes. However, lower pH (Gardner et al., 1988) may lead to biological Fe(II) oxidation being relatively more important in these areas since chemical Fe(II) oxidation rates decrease as pH decreases (Singer and Stumm, 1970).

### 4.3. Burial

Howarth (1984) reported a net rate of S accretion of 13 g S/m<sup>2</sup>/year in the Great Sippewissett and Sapelo Island marshes although this estimate does not include the burial of organic-bound S. Assuming that the S is primarily buried as pyrite (but see below), Fe burial is estimated at ~11 g Fe/m<sup>2</sup>/year. Data from organic-rich brackish and salt marshes show higher rates of total S accumulation (24–46 g S/m<sup>2</sup>/year; Krairapanond et al., 1992). Further, in these marshes, the majority of the S accumulated as C-bonded S (56–65%) and ester sulfates (21–23%) with <3% due to the preservation of pyrite. Based on soil data from Cutter and Velinsky (1988) and an accretion rate of 0.47 cm/year (Church et al., 1981), the S accumulation rate has averaged 29 g S/m<sup>2</sup>/year over the last 75–100 years at Delaware's Great Marsh, with the accumulation split roughly evenly between pyrite and organic S. In the same data set, the long-term accretion rate of 21 g Fe/m<sup>2</sup>/year was driven by pyrite (62% of total Fe accumulation) and oxidized Fe (27%). The accumulation of pyrite increased with depth whereas that of reactive oxides generally decreased with depth. Data from other salt marshes are similar in terms of the magnitude of Fe burial, with rates ranging from ~11 to 60 g Fe/m<sup>2</sup>/year (DeLaune et al., 1981; Gardner et al., 1988).

## 5. PHOSPHORUS

Phosphorus (P) in salt marshes is diversely speciated in the solid and dissolved phases. P cycling is affected by iron and sulfur reactions and thus differs considerably in salt marshes versus tidal freshwater marshes. In salt marshes, less P is adsorbed to soils, and porewaters contain more dissolved inorganic P (DIP) (Paludan and Morris, 1999). N limitation of primary production in salt marshes versus P limitation in freshwaters arises in part from this P

speciation. The resultant four- to fivefold drop in the DIN : DIP ratio of salt marsh porewater prevents P limitation of autotrophs although marsh bacteria remain P-limited due to scarcity of organic P substrates (Sundareshwar et al., 2003).

Solid phases (including sorbed  $\text{PO}_4^{3-}$ ) dominate P inventories. Soil-bound P (0.05–0.08%) plus that in plant detritus is the largest reservoir ( $\sim 30\text{--}100\text{ g P/m}^2$ ), exceeding that of live plant biomass ( $\sim 10\text{--}20\text{ g P/m}^2$ ; 0.05–2% by weight) and porewater  $\text{PO}_4^{3-}$  ( $< 0.5\text{ g P/m}^2$ , 0–100  $\mu\text{M}$ ; Buresh et al., 1980; Sundareshwar and Morris, 1999; Zhou et al., 2007). Large fractions of total phosphorus (TP) are associated with organic matter; marshes low in organic content tend to show lower overall TP and porewater  $\text{PO}_4^{3-}$  (Zhou et al., 2007). The various P fractions in soils are defined as follows: (1) loosely exchangeable (salt extractable) which includes both the dissolved  $\text{PO}_4^{3-}$  pool and the dissolved nonreactive organic P (DNRP); (2)  $\text{PO}_4^{3-}$  bound to oxidized iron and aluminum (of which the iron fraction is redox sensitive); (3) soil organic (humic) P which is removable following sequential NaOH/HCl treatment; (4) calcium (carbonate)-bound P which is liberated following acidification; and (5) residual refractory P (Sundby et al., 1998; Paludan and Morris, 1999; Coelho et al., 2004; Zhou et al., 2007). The amount of TP through the soil profile can either be relatively constant or decline with depth, but TP inventories change little throughout the year (Stribling and Cornwell, 2001; Coelho et al., 2004; Weston et al., 2006). Increases in the refractory P content with depth are consistent with organic matter diagenesis during burial (Lillebø et al., 2007). Approximately 20 to >40% of the bound P is organic (humic + nonreactive + refractory fractions; Coelho et al., 2004; Álvarez-Rogel et al., 2007). Approximately 40% of the TP in soils is readily exchangeable and available for equilibrium maintenance of porewater  $\text{PO}_4^{3-}$  (Lillebø et al., 2007). Spatial and temporal variability in porewater  $\text{PO}_4^{3-}$  coincides with changes in biological activity (e.g., mineralization and plant demand) and physicochemical conditions that affect (de)sorption to/from mineral phases. The highest  $\text{PO}_4^{3-}$  concentrations are seen in soils where mineralization is high and low Eh reduces  $\text{PO}_4^{3-}$  sorption to iron oxides (Chambers et al., 1992; Chambers, 1997; Sundareshwar and Morris, 1999; Stribling and Cornwell, 2001; Lillebø et al., 2007). Exchanges between solid and aqueous phases maintain porewater  $\text{PO}_4^{3-}$  concentrations, and spatial/temporal differences represent adjustments to that dynamic equilibrium rather than large changes in net P import/export.

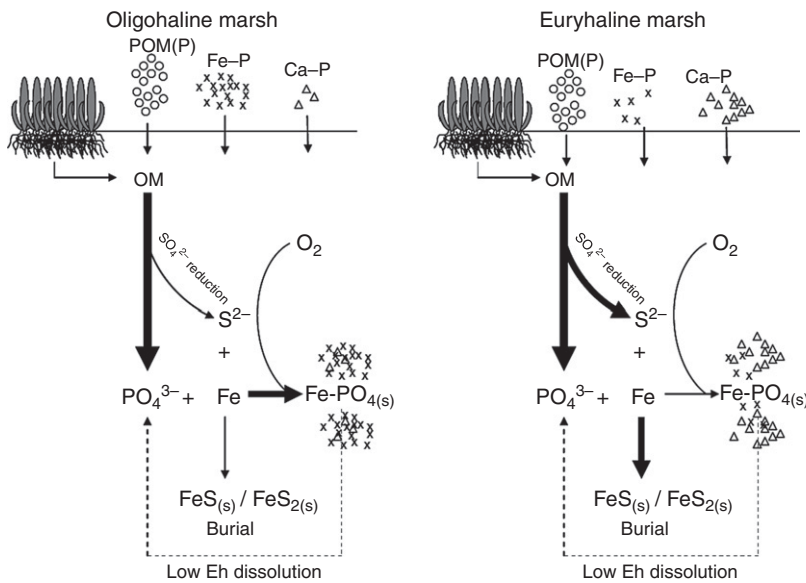
## 5.1. Exchanges

Aside from some instances of groundwater inputs in areas of P-rich geology (Weston et al., 2006) and rainfall scouring of marsh soils (Mwamba and Torres, 2002; Cundy et al. 2007), tides are the principal routes for delivering and removing P. These exchanges are small, however, relative to the size of the marsh P reservoir (Paludan and Morris, 1999; Coelho et al., 2004). While marshes accumulate P over their lifespan as they accrete, they can act at any given time as sinks or sources for particulate and/or DIP.

5.1.1. Tidal inputs/outputs

Settling of particulate P (organic and inorganic bound) represents a major source of P for most salt marshes. There are robust examples of both net import and export of particulate P (Dankers et al., 1984; Childers, 1994; Dame, 1994). The magnitude and distribution of particulate P delivery is controlled by settling patterns of suspended P as a function of water column load, partitioning of P between organic and mineral phases, hydroperiod, and flooding frequency (Friedrichs and Perry, 2001). The mineral-attached fraction of particulate P depends on the geochemical composition of suspended sediments. Changes in ionic strength, pH, and availability of different sorptive minerals along salinity gradients cause differences in the magnitude and form of P delivery to mesohaline and euryhaline marshes (Sundby et al., 1992; Paludan and Morris, 1999; Jordan et al., 2008). Contributions of P associated with Fe and Al oxides are greatest in low salinity environments where Fe and Al minerals are in ample supply (Fox et al., 1986; Froehlich, 1988; Sundareshwar and Morris, 1999). At euryhaline salinities with higher pHs, the Fe- and Al-bound fractions decrease as does the TP adsorbed per unit soil. The calcite-bound/sorbed fraction of P becomes a more important source of settling P to euryhaline marshes (Coelho et al., 2004; Alvàrez-Rogel et al., 2007; Figure 4).

Relative to tidal flux studies of POC or PON, there are fewer estimates of organic particulate P fluxes to marshes. However, one can derive estimates of particulate organic P fluxes from previously measured PON and POC fluxes. Using existing compilations of POC/PON flux data (Dame, 1994; Rozema



**Figure 4** Summary of P dynamics in marsh sediments contrasting freshwater and salt marsh ecosystems. Salt marshes receive and contain more Ca-P relative to Fe-P. Less PO<sub>4</sub><sup>3-</sup> is sorbed to iron in salt marshes due to sulfur cycling.

et al., 2000), we assigned a conservative C : P ratio of 120 to the POC fluxes and an intermediate N : P ratio of 20 (Craft, 2007) to reported PON fluxes. Using these stoichiometries, the range of net particulate organic P (POP) fluxes ranged from  $-0.2$  to  $0.79$  g P/m<sup>2</sup>/year (from POC data, negative sign indicates export; Dame, 1994) and  $-3.0$  to  $2.0$  g P/m<sup>2</sup>/year (from PON data; Rozema et al., 2000). For studies that showed net POP import, average rates were  $\sim 0.6$  g P/m<sup>2</sup>/year (from both POC and PON stoichiometry). The export of POP averaged  $0.2$  and  $1.0$  g P/m<sup>2</sup>/year from POC and PON data, respectively. Tidal flux estimates of net P import tend to be at the low end of measured long-term P accumulation rates (Section 5.3), probably because buried P contains mineral-bound P that is not included in the POP flux calculations.

Younger to middle-age marshes are more likely to show net import of particulate P (Dame, 1994). Marsh flume studies conducted across systems with tidal amplitudes  $\leq 1$  m showed a close balance between P import and export (i.e., insignificant-low net particulate P exchanges). There was a small, but significant net export of sediment-bound P in higher tidal range environments (Childers, 1994). An opposite tidal amplitude effect was reported for organic particulate P. This disparity between inorganic bound and organic particulate P likely reflects asymmetry in flood versus ebb energy and/or density differences between organic versus inorganic particles. Export over mean tidal conditions probably underestimates the total annual particulate P efflux. While large import of sediments and associated P (and N) from offshore can result from storm events (Reed, 1989; Turner et al., 2007), rainfall scouring of exposed marsh sediments followed by export to coastal waters has also been observed (Dankers et al., 1984; Mwamba and Torres, 2002). Sporadic and/or extreme events remain difficult to adequately quantify.

Net tidal exchanges of DIP tend to be two- to threefold smaller than particulate P fluxes. The majority of tidal marsh flux studies, particularly when they include measures of porewater drainage, indicate that salt marshes are small net exporters of PO<sub>4</sub><sup>3-</sup> ( $0.03$ – $2.25$  g P/m<sup>2</sup>/year; Chambers et al., 1992; Childers, 1994; Dame, 1994; Lillebø et al., 2007). Of the 11 studies on whole tidal creeks reviewed by Dame (1994), only two document a net import of PO<sub>4</sub><sup>3-</sup> although there can be seasonal reversals of import/export at individual sites (Jordan and Correll, 1991). Both marshes showing annual PO<sub>4</sub><sup>3-</sup> import were geologically/ecologically young systems. Even young marshes will export PO<sub>4</sub><sup>3-</sup> when porewater PO<sub>4</sub><sup>3-</sup> is high and its exchange is dominated by advection (Osgood, 2000). Phosphate effluxes are most prevalent at the early stages of the flooding tide when low Eh porewater pools are flushed of PO<sub>4</sub><sup>3-</sup> recently produced from organic matter mineralization (Lillebø et al., 2004). At larger tidal ranges, some marshes respond with enhanced PO<sub>4</sub><sup>3-</sup> export (Childers, 1994), while others show a switch from export to import (Childers et al., 2000). These opposite patterns probably represent trade-offs at higher tides between enhanced tidal drainage and an expanded oxidized unsaturated zone favorable to PO<sub>4</sub><sup>3-</sup> sorption to iron oxides.

Several factors contribute to seasonality in PO<sub>4</sub><sup>3-</sup> export. Mineralization is the ultimate source of PO<sub>4</sub><sup>3-</sup>, and higher PO<sub>4</sub><sup>3-</sup> effluxes occur during warmer months with up to fourfold increases reported in the summer (Lillebø et al., 2004). Seasonal plant dynamics also influence PO<sub>4</sub><sup>3-</sup> exchange with lower PO<sub>4</sub><sup>3-</sup> effluxes from

vegetated soils (Lillebø et al., 2004). Both vegetated and unvegetated regions of a Portuguese marsh were net sources of  $\text{PO}_4^{3-}$  to the water column through the year except when autotrophic demand by plants and epiphytes was maximal (Lillebø et al., 2004, 2007). The plant modulation of  $\text{PO}_4^{3-}$  efflux over diel and seasonal scales (Lillebø et al., 2004) is attributed to both plant assimilation and to  $\text{O}_2$  pumping into the soils that induces changes in Fe and S cycling and promotes mineral (Fe and carbonate) scavenging of P. The two- to fourfold greater  $\text{PO}_4^{3-}$  adsorption capacity observed in vegetated soils translates to 50% less  $\text{PO}_4^{3-}$  export compared to mudflats. Plant effects are seen on seasonal and diel timescales.

Although the Ca-bound P pool dominates the mineral-bound P reservoir, water column-sediment  $\text{PO}_4^{3-}$  fluxes may be controlled in just a thin layer of soil at the surface through redox-sensitive Fe oxide-P sorption dynamics (Chambers et al., 1992; Lillebø et al., 2007). It is not clear whether or how the Ca-P fraction is involved in  $\text{PO}_4^{3-}$  fluxes. Theoretically, localized pH decreases, for example, due to sulfide oxidation in surface soils (Giblin and Howarth, 1984; Kostka and Luther, 1995) could release this Ca-bound fraction. The extent to which this mechanism might contribute surface P sorption dynamics and subsequent  $\text{PO}_4^{3-}$  fluxes to overlying water is not well characterized.

## 5.2. Internal cycling

### 5.2.1. Photoautotrophy and mineralization

Is the import of P sufficient to support macrophyte production in mature salt marshes? Using the range of macrophyte N uptake presented earlier in this chapter and a plant N : P of 10–20, we estimate macrophyte P demand of 0.1–6.0 g P/m<sup>2</sup>/year. Direct  $\text{PO}_4^{3-}$  uptake is small, as most marshes export DIP, and particle settling supplies  $\sim 0.6 \pm 0.8$  g P/m<sup>2</sup>/year (Section 5.1.1). Comparing this supply rate with a median estimate of plant demand (3 g P/m<sup>2</sup>/year) shows that incoming particulate P is about 20% of plant P demand. Although some marshes can import P at rates nearly sufficient to support macrophyte production (Wolaver and Ziemann, 1984), autotrophy in many marshes must be supported by internal recycling of P. Based on the size of the bioavailable P pool and macrophyte P demand, useable P turns over on the order of 15 years (Paludan and Morris, 1999). Mineralization of organic matter is an important source of  $\text{PO}_4^{3-}$ , but its subsequent availability for plant uptake is controlled by geochemical speciation reactions.

P release during mineralization is consistent with the rates of organic matter respiration (aerobic and anaerobic) and C : N : P stoichiometry presented earlier in this chapter. Using the range of reported N mineralization rates and N : P ratios for plants and marsh soils of 10–25 (Buresh et al., 1980; Craft, 2007; Zhou et al., 2007), P mineralization ranges from 0.3–12 g P/m<sup>2</sup>/year with the majority of mature marshes in the range of 1.0–8.0 g P/m<sup>2</sup>/year. These values are on the order of 5- to 10-fold higher than P import rates and are comparable to macrophyte demand. Bacteria strongly prefer organic P (Sundareshwar et al., 2003), so only a small fraction of any excess  $\text{PO}_4^{3-}$  created during mineralization is microbially immobilized. Instead, it is geochemically sorbed and respiciated. These processes represent

exchanges between sorbed P and porewater  $\text{PO}_4^{3-}$  that help to regulate bioavailability and affect the resultant exchanges of DIP with tidal waters.

### 5.2.2. Geochemical cycling

Bacteria perform the initial mineralization of organic matter to release  $\text{PO}_4^{3-}$ . This  $\text{PO}_4^{3-}$  sorbs readily to humics and oxidized mineral phases and gets incorporated into solid organic fractions of variable lability. Ranges of sorbed P are 0.15–1 mg P/gdw in both vegetated and nonvegetated marsh soils. Exchangeable fractions of sorbed P are on the order of 20–50% depending on mineral composition. Based on radiolabeled  $^{32}\text{P}$  experiments, the dissolved  $\text{PO}_4^{3-}$ , DNRP, Al-, and Fe-bound P pools are potentially available for maintaining equilibrium with porewater  $\text{PO}_4^{3-}$  and thus available for biological uptake but the Ca–P fraction shows little exchangeability (Jensen and Thamdrup, 1993).

Salt marsh soils (relative to oligohaline systems) have lower organic N:P, higher porewater  $\text{PO}_4^{3-}$ , less Fe oxide-bound P, and more Ca-bound P (Paludan and Morris, 1999; Coelho et al., 2004; Zhou et al., 2007). Despite the smaller contribution of Fe oxide-bound P, this fraction remains an important mediator of P dynamics in salt marshes. Zones of Fe-bound P occur in the uppermost soils in contact with the atmosphere and around oxidized root channels (Krom and Berner, 1980). These zones limit upward diffusion of  $\text{PO}_4^{3-}$  (Chambers and Odum, 1990; Coelho et al., 2004). The Fe-bound fraction is the most bioavailable of the sorbed P fractions because of its redox sensitivity and reactivity with sulfur (Figure 4). Salt marshes retain more P in macrophyte-dominated soils where high rates of photosynthesis enhance soil oxidation. Increased Fe oxide formation sorbs more P and draws down porewater  $\text{PO}_4^{3-}$ , leading to greater retention of  $\text{PO}_4^{3-}$  in vegetated soils (Mendelsohn and Postek, 1982; Sundby et al., 1998; Lillebø et al., 2004). Maximum Fe oxide formation and P sorption was observed in a Delaware, USA, marsh in summer when photosynthesis was highest (Kostka and Luther, 1995). Coelho et al. (2004) measured decreased daytime  $\text{PO}_4^{3-}$  export in excess of that attributable to direct plant assimilation, and the formation of P-rich root plaques associated with Ca and Fe oxides in vegetated marsh soils has been widely observed (Caetano and Vale, 2002; Lillebø et al., 2007). Some P-rich plaques are retained on long timescales while others appear to be more transient. The reduction of Fe(III) oxides due to biological processes or chemical reactions with sulfides (Sections 2.2.2 and 4.2.1) can liberate  $\text{PO}_4^{3-}$  and thus reduce the amount of potential P burial (Anschutz et al., 1998; Rozan et al., 2002).

$\text{PO}_4^{3-}$ –Fe interactions are heavily modified by S. Sulfides from  $\text{SO}_4^{2-}$  reduction bind tightly to Fe forming pyrite and/or iron monosulfides (Figures 2 and 4), which inefficiently sorbs  $\text{PO}_4^{3-}$ . Additionally,  $\text{SO}_4^{2-}$  competes for P-binding sites on Fe oxides. Iron sulfide minerals isolate Fe from further redox cycling and limit future binding with  $\text{PO}_4^{3-}$  (Sundby et al., 1992). The net result of a high S environment is that less  $\text{PO}_4^{3-}$  sorbs to solid mineral phases and more remains in porewaters. Redox variations with seasons, tides, and daily photosynthesis generate patterns of Fe and S cycling that modify the P speciation and subsequent release of  $\text{PO}_4^{3-}$  on the ecosystem scale (Giblin and Howarth, 1984; Scudlark and Church, 1989; Kostka and Luther, 1995).

Ca-bound P represents a large fraction (40–80%) of the mineral-bound soil P, yet is less well characterized than other pools (Paludan and Morris, 1999; Coelho et al., 2004; Alvàrez-Rogel et al., 2007; Zhou et al., 2007). Sedimentation of Ca–P particles at the seaward end of estuaries traps P that might otherwise migrate upstream to more P-limited ecosystems. High  $\text{Ca}^{2+}$  (e.g., seawater) competes for P with organics. P-rich root plaques are also carbonate rich, and Ca–P is soluble at low pH. However, Ca–P is not considered readily exchangeable and is not thought to participate in exchanges with porewater  $\text{PO}_4^{3-}$ . On the one hand, the Ca–P fraction appears to be dynamic, while on the other hand, it may represent an essential step toward P burial. Given the magnitude of P bound to Ca in salt marshes, its dynamics may represent a relatively unknown but potentially important component of salt marsh P dynamics.

### 5.3. Burial

Burial is the dominant mechanism of P loss for all salt marshes. The amount of residual-bound P (0–0.26  $\mu\text{g P/gdw}$ ) provides a lower limit on the extent of P burial (Paludan and Morris, 1999; Coelho et al., 2004; Zhou et al., 2007). Assuming that marsh accretion reflects SLR, a conservative P burial rate of  $\sim 0.2 \text{ g P/m}^2/\text{mm SLR}$  can be estimated. If the Ca–P-bound fraction (assumed to be relatively bio-unavailable) is added to the burial inventory, the rate of P sequestration by salt marshes increases by a factor of 2–3. Measured rates of P burial for a variety of salt marshes range between 0.36 and 2.0  $\text{g P/m}^2/\text{year}$  (Craft, 2007 and references therein). These burial rates are generally lower than P burial in freshwater and oligohaline marshes due to higher sediment availability and a greater sedimentary P content in up-estuary environments, as well as increased decomposition rates in higher salinity systems (Merrill and Cornwell, 2000; Craft, 2007; Jordan et al., 2008).

## 6. MARSHES IN TRANSITION AND DIRECTIONS FOR FUTURE WORK

Salt marshes are dynamic in terms of geomorphology, biogeochemistry, and their role in the coastal landscape. They are subject to the synergistic effects of global-scale climate forcings and local-scale human impacts. Our understanding needs improvement of how salt marshes respond to increasing  $\text{CO}_{2,\text{atm}}$ , rising sea level, and increased continental nutrient loading in terms of C, N, and P cycling, storage, or burial. Salinity encroachment accompanying SLR will have its most pronounced effect on mesohaline marshes altering the balance of oxidants (e.g.,  $\text{O}_2$  and  $\text{SO}_4^{2-}$ ) and forms of N and P delivered to marshes. To a large extent, current marsh distribution, accretion, and biogeochemistry reflects the effects of SLR since the last glacial maximum, but future responses are now compounded by additional anthropogenic factors. Human loading of  $\text{CO}_2$  and nutrients to marshes induces responses in plant dynamics; however, the resultant effects on marsh

biogeochemistry and long-term maintenance remain to be determined. The effect of combined global and local stressors on the capacity of marshes to transform biologically important elements and subsequently retain or export them within the coastal landscape is the biggest challenge for future salt marsh biogeochemistry work. We advocate an approach for examining coupled elemental cycling when possible to address these challenges. Based on this review, we offer a few specific directions for future work.

- Improve characterization of the pathways through which organic C is decomposed. Despite decades of studying  $\text{SO}_4^{2-}$  reduction (and, more recently, Fe(III) reduction), there are still instances where these “major” processes account for <50% of total C catabolism. Processes such as Mn(III, IV) reduction and the utilization of humic compounds may be more important than previously assumed.
- Develop a better understanding of DNRA in marshes, its magnitude, and controls. In particular, a better characterization of its synergy with the sulfur cycle is needed. Changes in these pathways are of particular importance for N retention versus export in mesohaline marshes subject to increasing  $\text{SO}_4^{2-}$  loads as SLR accelerates and freshwater withdrawals from rivers induce salinity encroachment upstream in estuaries.
- Explore anaerobic oxidation pathways of Fe(II),  $\text{H}_2\text{S}$ , and Fe–S minerals (FeS,  $\text{FeS}_2$ ). Thermodynamically, a variety of compounds including  $\text{NO}_3^-$ ,  $\text{MnO}_2$ , and Fe(III) can be used as oxidants for various reduced Fe and S species, but the significance of these anaerobic reactions/processes have not been fully assessed. Because the reduction of these oxidants can also be coupled with organic matter catabolism, there are feedbacks and interactions between the cycling of C, Fe, and S.
- Generate a more comprehensive picture of Ca–P dynamics. This is the largest inorganic-bound P fraction. It should be pH sensitive, but it is assumed to be recalcitrant. It may be more dynamic than previously thought, or it may be the pathway to P burial. An insufficient amount of information exists at present to conclude either.
- Continue to pursue techniques that examine “nutrient” fluxes out of marshes to the coastal landscape at expanded spatial scales. Various geochemical tracer approaches (e.g., radium) show promise in this regard, but there needs to be a clearer picture of exactly which fluxes the tracers quantify.

## ACKNOWLEDGMENTS

We thank Robert Twilley, Don Cahoon, and Mark Brinson for their helpful reviews, which significantly improved this chapter. This is contribution no. 1484 from the University of South Carolina's Belle W. Baruch Institute for Marine and Coastal Studies. This work was supported in part by NSF-DEB 0542635, the DOD-DCERP Program, and the UNCW Center for Marine Science.

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