COASTAL
WETLANS
AN INTEGRATED ECOSYSTEM APPROACH

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CHAPTER 19

BIOGEOCHEMISTRY OF TIDAL FRESHWATER WETLANDS

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Contents

1. INTRODUCTION

By virtue of their unique position in coastal landscapes, tidal freshwater wetlands (TFWs) are hot spots of biogeochemical transformation and exchange (Pasternack, 2009). As with all tidal wetlands, they occur in geo-morphic settings that promote exchanges of water, solutes, solids, and gases with adjacent terrestrial and aquatic ecosystems, groundwater, and the atmosphere. However, many features of biogeochemical processes in TFWs are distinct from the nontidal freshwater and saline ecosystems that lie within the coastal landscape because of a unique combination of flushing by tides, the chemical milieu of freshwater, and their position at the limit of tidal influence.

Tidally driven hydrology is expected to produce more open element cycles in TFW than nontidal freshwater wetlands, and is the basis of the Outwelling Hypothesis (Kalber, 1959; Odum, 1968) that has informed a great deal of research in saline tidal wetlands. Low concentrations of sulfate in fresh water make TFWs stronger sources of CH_4 (a potent greenhouse gas) than saline tidal wetlands (Bartlett et al., 1987). Exports of dissolved inorganic carbon (C) and alkalinity from TFWs have relatively dramatic effects on water chemistry because adjacent estuarine waters are relatively poorly buffered compared to saline waters closer to oceans.

The broad outlines of biogeochemical cycles in TFWs are influenced by many of the same factors that constrain element cycles in nontidal and saline tidal wetlands. TFWs support herbaceous marshes, swamp forests, and shrub lands that differ with respect to primary productivity, root–leaf–wood C allocation, and C quality. They occur on both mineral and organic soils, the chemical composition of which is expected to affect a host of ecosystem processes, including the contribution of Fe(III) to anaerobic microbial respiration (Neubauer et al., 2005b). TFWs are found on eutrophic and oligotrophic rivers that place limits on nutrient availability and productivity.

This review focuses on the exchanges, transformations, and storage of the major elements, recognizing that these processes govern the contribution of TFWs to the metabolism of coastal landscapes.

2. CARBON BIOGEOCHEMISTRY

The most complete C budget of a tidal freshwater wetland is for Sweet Hall Marsh on the Pamunkey River in Virginia, USA (Neubauer et al., 2000, 2002; Neubauer and Anderson, 2003; Figure 1). One strength of this C budget is that it is based, in part, on repeated measurements of ecosystem-level CO_2 and CH_4 exchange. This approach avoids several problems with estimating C input from biomass harvests (i.e., how to account for biomass turnover and translocation; see discussion in Neubauer et al., 2000), and is especially insightful for understanding ecosystem-level C cycling. We present the Sweet Hall C budget as a case study and a heuristic device for organizing our review of C cycling in TFWs.

2.1. Carbon inputs

Gas exchange studies are particularly useful for understanding the integrated metabolism of ecosystems. Two-thirds of annual C inputs to Sweet Hall Marsh come from in situ gross primary production (GPP), which represents the photosynthetic CO_2 assimilation of macrophytes and microalgae (Figure 1). About 37% of macrophyte GPP is consumed in growth and maintenance respiration, leaving 625 g C/m^2/year in net primary production (NPP), but also root exudates and possibly mycorrhizae. In a given year, NPP is supported by a combination of current-year photosynthates and C that was translocated from storage organs such as rhizomes. Accounting for both photosynthesis and translocation, macrophyte NPP
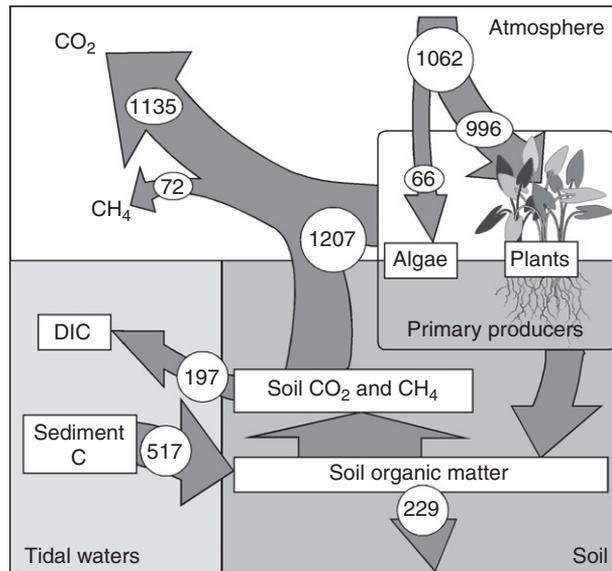
Figure 1 Carbon budget for Sweet Hall Marsh, USA, showing the major pools and fluxes. All fluxes are in units of g C/m^2/year. Ecosystem boundaries for the purpose of this budget are the soil–atmosphere interface, the soil–tidal water interface, and the 30 cm depth contour (which is based on the 1963 ^{137}Cs peak). Most of the belowground biomass and the most active zone of biological activity lies within the top 30 cm of the marsh.

at Sweet Hall Marsh was 557–736 g C/m^2/year (1,150–1,500 g biomass/m^2/year), which is about double the peak aboveground biomass of the site (Neubauer et al., 2000). NPP in TFWs was reviewed recently by Whigham (2009).

Sediment deposition is an important vehicle for importing allochthonous particulate organic C into TFW soils, and it enhances organic C preservation and nutrient removal through burial. TFWs that keep pace with sea-level rise are net C sinks, at least on an areal basis, because organic matter is buried in accreting sediments (Stevenson et al., 1988; Craft, 2007; Neubauer, 2008). Sweet Hall Marsh imports 517 g C/m^2/year via sediment deposition (Neubauer et al., 2002), a full one-third of all organic C inputs to the site (Figure 1). However, the magnitude of this flux varies dramatically according to the geomorphic setting of the TFW (Pasternack, 2009). For example, proximity to the turbidity maximum that forms at the freshwater–saltwater interface of tidal rivers has a profound effect on C deposition rates (Darke and Megonigal, 2003; Morse et al., 2004).

The sources of allochthonous C compounds imported with TFW sediment deposits have not been well characterized, but presumably include upland soils, dissolved organic carbon (DOC) sorbed to mineral particles, and plankton. The age and chemical composition of these sources varies, affecting the extent to which they are ultimately decomposed or preserved as soil organic matter. A meta-analysis of the ^{13}C signature of >300 bulk organic samples from salt marshes, mangroves, and seagrass beds suggested that the organic matter preserved in coastal sediments is

dominated by allochthonous sources at sites with ≤10% organic soil C (Boullion and Boschker, 2006). Because allochthonous C represents ∼33% of all C inputs to Sweet Hall but only ∼10% of microbial soil respiration (54–71 g C/m^2/year; Neubauer et al., 2002), it seems that allochthonous C compounds are generally more recalcitrant to decomposition than autochthonous, mainly plant-derived, compounds. Buried organic matter is also a sink for N, P, and other elements in organic tissues (see Sections 4 and 5).

2.2. Carbon outputs

The collective respiration of plants, microbes, and animals at Sweet Hall Marsh is supported by total organic C inputs (GPP + sediment-associated C) of 1,579 g C/m^2/year (Figure 1). As discussed above, roughly one-third of GPP is consumed by the plants themselves in growth and maintenance respiration, processes that release CO_2 directly to the atmosphere, soil atmosphere, or soil solution. Most of the remaining GPP takes the form of plant biomass that supports the heterotrophic respiration of bacteria, fungi, insects, grazing snails, and a variety of other organisms (Hines et al., 2006). An uncertain fraction of GPP may be lost from plants as root exudates.

Organic C inputs from plants and sediments are eventually subjected to decomposition and microbial degradation, producing soil organic matter, dissolved inorganic carbon (DIC) and DOC, and CH_4. At Sweet Hall Marsh, 15% (229 g C/m^2/year) of all organic C inputs are buried by accreting soil and enter a very slowly decomposing soil organic matter pool. The remaining 85% is cycled in timeframes of hours to months via plant, animal, and microbial respiration, and other microbial degradation processes such as fermentation. Rates of organic C burial in TFWs along the Atlantic and Gulf coasts of North America, and on the Scheldt River, EU, ranged from 10 to 930 g C/m^2/year (Table 1, Neubauer, 2008 and references therein). In addition to sequestering organic C, sediment accumulation adds elevation to wetlands soils at approximately the rate of sea-level rise (Morris et al., 2002).

2.2.1. Exports of CO_2, DIC, DOC, and POC

C compounds exported from tidal wetlands influence the chemical composition of the atmosphere and adjacent estuaries. The plant and microbial respiration that takes place in saturated or flooded soils generates DIC, which partitions into CO_2, HCO_3^-, and CO_3^{2-} according to pH. At Sweet Hall Marsh, 12% of all organic C added to the marsh is exported as DIC. A portion of the DIC pool is emitted directly to the atmosphere as CO_2, while the remainder is exported to the York River (Figure 1; Neubauer and Anderson, 2003).

Evidence is mounting that freshwater and low-salinity tidal wetlands are dominant sources of DIC to estuarine waters. Extrapolating DIC export from Sweet Hall Marsh (197 g C/m^2/year) to all tidal marshes of the York River Estuary suggests that 47% of excess water column DIC (i.e., DIC unexplained by conservative mixing of freshwater and marine end members) is imported from wetlands (Neubauer and Anderson, 2003). Several other studies suggest there is significant

Table 1 Vertical accretion and nutrient burial rates in tidal freshwater and oligohaline wetlands in the United States

Location	Method	Accretion (mm/year)	(g C, N, or P/m²/year) C burial[a]	N burial	P burial	Reference
North River, MA	Model[b]	(1.3–3.6)	ND	(3.1–8.6)	(0.3–0.8)	Bowden et al. (1991)
Tivoli Bay, Hudson River, NY	^{210}Pb	4.5 ± 1.4 (3.6–6.9)	142 ± 90 (33–285)	11.6 ± 3.6 (8.0–15.9)	2.3 ± 1.0 (1.1–3.6)	Merrill (1999)
Two sites, Delaware River, NJ	^{137}Cs, ^{210}Pb	(6–12)[c]	(139–204)	(7.1–8.8)	(3.2–6.1)	Church et al. (2006)
Otter Point Creek, MD	^{210}Pb	5.0 ± 4.5 (2.1–10.2)	163 ± 153 (65–339)	(2.7–11.7)	(0.5–2.1)	Merrill (1999), Merrill and Cornwell (2000)
Three sites, Choptank River, MD	^{210}Pb	9.2 ± 2.7 (6.1–10.9)	366 ± 103 (265–470)	(19.2–27.1)	(0.2–2.0)	Merrill (1999), Merrill and Cornwell (2000)
Eight sites, Choptank River, MD	^{210}Pb	8.4 ± 4.7 (3.2–21.5)	ND	21 ± 11 (7–44)	1.7 ± 1.1 (0.5–4.3)	Malone et al. (2003)
Twenty-five sites[d], Patuxent River, MD	^{210}Pb	8.5 ± 6.0 (1.1–21.9)	358 ± 258 (9–930)	16.9 ± 11.9 (0.5–36.1)	4.3 ± 3.9 (0.1–12.6)	Merrill (1999)
Jug Bay Marsh, Patuxent River, MD	Pollen[e]	(3.7–8.9)	(70–249)	(8–26)	(0.6–2.3)	Khan and Brush (1994)
Sweet Hall Marsh, Pamunkey River, VA	^{137}Cs	8.5	229 ± 45	18.1 ± 3.1	ND	Neubauer et al. (2002, 2005a)

Table 1 (*Continued*)

Location	Method	Accretion (mm/year)	(g C, N, or P/m^2/year)			Reference
			C burial[a]	N burial	P burial	
Carr's Island, Altamaha River, GA	^{137}Cs	(3.5–4.6)	(103–122)	(7–8)	(0.4–0.8)	Craft (2007)
Barataria Basin, Mississippi River, LA	^{137}Cs	(6.5–10.6)	(153–239)	(9–16)	(0.5–1.0)	Hatton et al. (1983)
Barataria Basin, Mississippi River, LA	^{137}Cs	7.5	198	12	ND	DeLaune et al. (1986)

Values are presented as means $\pm$ 1SD, with reported ranges in parentheses. Studies that did not contain burial rates for at least two of the three elements (C, N, P) are not shown. ND, no data.

[a] As needed, organic matter (OM) accumulation rates were converted to C assuming % C = 0.5 (% OM).

[b] Ranges calculated from a mechanistic model of sediment decomposition. P burial determined from soil P content in Bowden (1984).

[c] Cores (1 per site) were dated using both ^{137}Cs and ^{210}Pb. At one site, accretion rates from the two methods were identical. At the other site, this table reports the midpoint for the ^{137}Cs (14 mm/year) and ^{210}Pb methods (9 mm/year), as was done by Church et al. (2006).

[d] Seventeen sites for N burial.

[e] Range in rates estimated since 1900 for high and low marsh cores.

export of DIC from freshwater and low-salinity tidal wetlands to estuaries and coastal oceans (Smith and Hollibaugh, 1993; Frankignoulle and Bourges, 1996; Cai and Wang, 1998; Frankignoulle et al., 1998; Nietch, 2000).

Far less DOC is exported from tidal wetlands to estuaries compared to DIC, yet DOC is arguably the most important form of C exported from these systems. Saline tidal marshes generally export DOC to estuaries (Nixon, 1980 and references therein, Chapter 16) where it influences estuarine microbial metabolism, nutrient cycling, and ultraviolet (UV) light penetration of the water column (Epp et al., 2007). There is no evidence of DOC export from Sweet Hall Marsh (Neubauer, 2000), but DOC is exported from TFWs on the Hudson River, USA (Findlay et al., 1998) and the Patuxent River, USA (Figure 2). Raymond and Bauer (2001) proposed that TFWs are 30% of all DOC sources to the comparatively pristine York River, USA.

The chemical composition of DOC influences the effects it will have on receiving estuaries. Features such as the aromatic ring content affect UV radiation adsorption (Tzortziou et al., 2007) and perhaps the ability of DOC to support microbial respiration. Chromophoric dissolved organic matter (CDOM) is the light-adsorbing component of DOC and a dominant fraction of the DOC pool in estuaries. The CDOM exported from a TFW on the Patuxent River, USA has a shallow spectral slope (S_{CDOM}) (Figure 2), indicating the marsh is a source of relatively complex, high molecular weight, and aromatic-rich DOC. Presumably the S_{CDOM} of this TFW marsh reflects the relatively high lignin content and complexity of organic C compounds in emergent wetland plants compared to phytoplankton (Enriquez et al., 1993; Tzortziou et al., 2008).
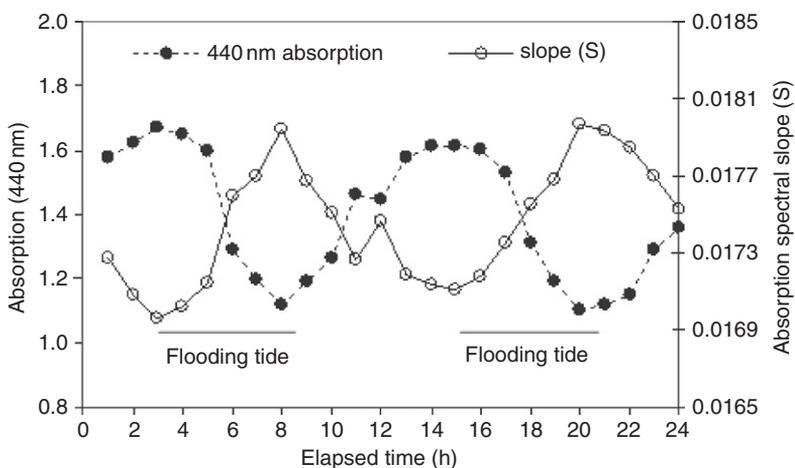
Figure 2 Tidal cycle variation in CDOM optical properties as a function of elapsed time since the first measurement (h) for the tidal cycle sampled at Jug Bay, USA on 7–8 September 2005. Left axis: CDOM absorption magnitude at 440 nm, aCDOM(440), Right axis: CDOM absorption spectral slope (S). The data were collected by M. Tzortziou, unpublished. Two horizontal lines mark the period of flooding tide when waters are dominated by estuarine CDOM sources.

There are relatively few studies of particulate organic carbon (POC) export from TFWs, but the process is expected to be dominated by seasonal and episodic events such as storms (Findlay et al., 1990). Findlay et al. (2005) estimated that TFWs of the Hudson River, USA, either import POC or have a near-zero POC balance. As with DIC and DOC, the contribution of terrestrial sources to POC is highest at the freshwater end of tidal rivers (Hoffman and Bronk, 2006). However, it is difficult to separate the POC contribution of TFWs from upland vegetation and upland soils on the basis of stable C and N isotopes, C:N ratios, or other biomarkers (Hoffman and Bronk, 2006).

2.2.2. Export of methane

A portion of organic matter decomposition in saturated soils yields methane (CH_4) rather than CO_2. In a recent review of wetland CH_4 emissions in the conterminous United States, fluxes from five TFW sites were 32 ± 37 g $CH_4/m^2/year$ (mean $\pm$ SD; Bridgham et al., 2006). This compares to 36 ± 47 g $CH_4/m^2/year$ from all freshwater wetlands in the review and only 10 ± 22 g $CH_4/m^2/year$ from saltwater wetlands, apparently due to suppression by sulfate reduction. Although wetlands are 40% of all CH_4 sources globally, the global contribution of TFWs to atmospheric CH_4 is negligible because of their limited area (Bridgham et al., 2006).

CH_4 emissions from TFWs vary widely, as expected for any broad class of wetland ecosystems (van der Nat and Middelburg, 2000; Bridgham et al., 2006). Rates of CH_4 emission underestimate the contribution of methanogens to overall microbial respiration by 30–90% because they do not account for microbial CH_4 oxidation to CO_2 (Megonigal and Schlesinger, 2002), export of CH_4 in ground-water (Kelley et al., 1995), or ebullition (Chanton et al., 1989, van der Nat and Middelburg, 1998a).

3. PROCESSES GOVERNING ORGANIC CARBON METABOLISM

The fate of organic matter in wetland ecosystems is regulated by complex interactions between plant processes that affect electron donor and electron acceptor availability, and microbial processes that degrade and modify organic matter (Megonigal et al., 2004). Here we review the TFW literature on C cycling processes, focusing on plant–microbe interactions.

A major initial constraint on C metabolism in wetlands is the chemical composition of plant material, a topic that was recently reviewed by Findlay et al. (2009) and is not considered here. Tissue quality interacts strongly with physiochemical factors such as O_2 availability, nutrient availability, temperature, and pH (Day, 1982; Benner et al., 1985). Perhaps the most important of these is O_2, which severely limits decomposition in saturated soils. Aerobic respiration yields more free energy than anaerobic respiration, and is less dependent on highly constrained chemical interactions among microorganisms. Yet, there are virtually no estimates of aerobic respiration in wetlands (but see Howes et al., 1984) because there are no methods for measuring in situ O_2 flux that account for O_2 introduced through root

O_2 loss (ROL). (We prefer this term to radial O_2 loss because it is more intuitive and, arguably, more precise). O_2 diffusion across the soil surface is much easier to quantify and is usually limited to a few millimeters in saturated soils. However, O_2 can penetrate much deeper if the water table drops for an extended period of time. An advantage of studying microbial processes in TFW soils, compared to nontidal soils, is that the depth of O_2 penetration is relatively stable across seasons (Megonigal and Schlesinger, 2002). At aerobic-anaerobic interfaces, reduced forms of elements are oxidized by O_2, regenerating oxidized forms that then support anaerobic respiration.

3.1. Anaerobic respiration

Microorganisms derive energy by transferring electrons from an external electron donor to an external electron acceptor. Most respiration in wetland soils depends directly or indirectly (in the case of H_2) on organic C as the electron donor. Generally, C limits microbial respiration because demand for electron donors exceeds the supply. This is true even in organic soils because most of the organic C is recalcitrant from the perspective of anaerobic respiration. Competition for electron donors among anaerobic microorganisms favors the respiration pathway that yields the greatest free energy in the order denitrification > manganese reduction > iron reduction > sulfate reduction > methanogenesis. There is some evidence that humic substances are common terminal electron acceptors, falling perhaps between iron and sulfate reduction in this sequence (Megonigal et al., 2004).

Many TFWs occur in urbanized watersheds and are exposed to high NO_3^- in floodwater. However, the relative contribution of the denitrification pathway to organic C mineralization, compared to other respiration pathways, has not been quantified in TFW soils to our knowledge. In tidal freshwater river sediments from the Altamaha River, USA, denitrification supported about 10% of anaerobic C mineralization (Weston et al., 2006). The NO_3^- concentrations in this study were 20 μM, which is similar to NO_3^- concentrations in the Hudson River and many other TFW systems. Although it seems unlikely that denitrification is ever a dominant pathway of microbial respiration in TFW soils, it can nonetheless be an important NO_3^- sink in TFW-dominated estuaries (see Section 4.2).

Iron oxide minerals can be the dominant electron acceptor in anaerobic mineral soils (Roden and Wetzel, 1996; Megonigal et al., 2004). The first studies to conclusively establish that Fe(III) reduction supports microbial growth were done in tidal freshwater river sediments (Lovley and Phillips, 1986, 1987). Over a decade later, van der Nat and Middelburg (1998a) suggested that Fe(III) reduction explained up to 80% of anaerobic respiration in mesocosms constructed with TFW soils and plants. The contribution of Fe(III) reduction to anaerobic metabolism appeared to be far higher in mesocosms planted with *Scirpus lacustris* than *Phragmites australis*, suggesting that species-specific plant characteristics influence Fe(III) reduction rates. A field study in a *Peltandra virginica*-dominated TFW showed that Fe(III) reduction mediated 20–98% of anaerobic C metabolism (Neubauer et al., 2005b, Figure 3). The importance of Fe(III) reduction declined throughout
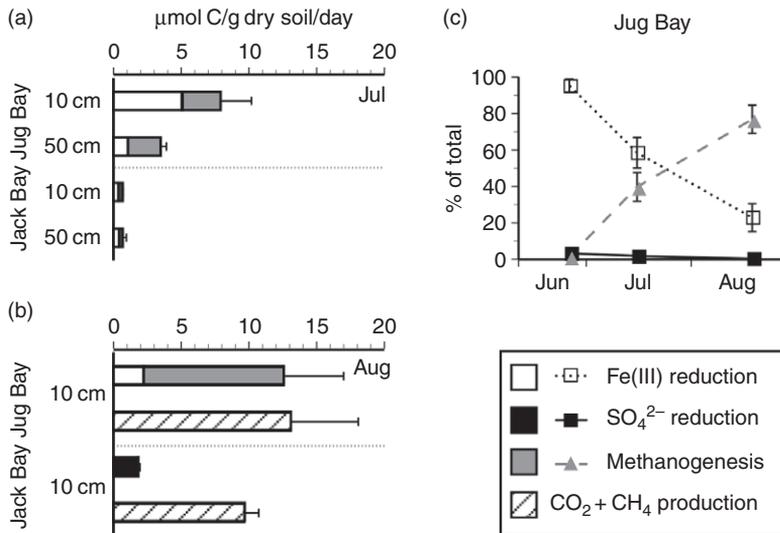
Figure 3 (a) and (b): Soil organic C mineralization rates in a tidal freshwater marsh (Jug Bay) and a brackish marsh (Jack Bay) in July and August 2002. The July data (a) provide a comparison of rates at 10 and 50 cm depth. The August data (b) provide a comparison of the total rate of anaerobic C decomposition as determined by the sum of CO_2 and CH_4 production (striped bars) versus the sum of C mineralization from three possible anaerobic pathways (Fe(III) reduction, SO_4^{2-} reduction, and CH_4 production). (c) Seasonal changes in the relative importance of Fe(III) reduction (open squares), SO_4^{2-} reduction (filled squares), and methanogenesis (filled triangles) to from June to August. Error bars show ±SE, $n = 3–5$ replicate cores. From Neubauer et al. (2005b).

the growing season in parallel to plant activity, again suggesting that plants indirectly regulate this microbial process (Figure 3). In both cases, it is likely that plants influence soil iron cycling through ROL-driven regeneration of Fe(III) oxides in the rhizosphere. Indeed, the rhizosphere is a hot spot of iron cycling because it supports vigorous Fe(II) oxidation and Fe(III) reduction (Weiss et al., 2004, 2005; Neubauer et al., 2007, 2008).

Manganese-respiration has received very little attention because concentrations of Mn(III, IV) are usually far lower than Fe(III) in soils (Neubauer et al., 2005b). In theory, this limitation could be overcome by differences in Fe and Mn chemistry, such as the fact that Mn(III, IV)-reduction is favored thermodynamically over Fe(III) reduction. Indeed, solid-state Au/Hg voltammetric microelectrode profiles in a TFW suggested that Mn(III, IV) reduction is more important than Fe(III) reduction in some locations (Ma et al., 2008).

Humic substances are the most recent class of terminal electron acceptor identified in anaerobic substrates (Nevin and Lovley, 2000). It is difficult to directly measure microbial humic acid reduction. However, it has been observed that the amount of CO_2 and CH_4 produced in root-free, anaerobic soil incubations often far exceeds the summed contributions of denitrification, metal reduction, and sulfate reduction (Neubauer et al., 2005b; Keller and Bridgham, 2007). Microbial

reduction of humic substances may be supporting the unexplained CO_2 respiration measured in these incubations.

Sulfate reduction is not expected to be an important pathway for C mineralization in TFWs because of limitation by low SO_4^{2-} availability at concentrations <1 mM, but it has rarely been measured in TFWs (Figure 3). However, sulfate reduction rates in TFWs will increase as SO_4^{2-} concentrations rise due to sea–level rise and saltwater intrusion into tidal freshwater rivers (Weston et al., 2006). There is evidence that increased rates of sulfate reduction will stimulate organic matter mineralization (Portnoy and Giblin, 1997; Weston et al., 2006; Craft, 2007). However, other studies reported no differences in rates of anaerobic organic matter mineralization in comparisons of brackish versus tidal freshwater marsh soils (Neubauer et al., 2005b, Figure 3) and sediments (Kelley et al., 1990). This is an important question to understand with respect to climate change because of the implications for soil C pools and nutrient turnover in former TFWs (Neubauer and Craft, 2009).

3.2. Processes regulating methane production, oxidation, and emission

Plants are the largest source of organic C that ultimately supports methanogenesis in soils, so factors that influence plant productivity indirectly regulate CH_4 emissions. Several lines of evidence suggest that CH_4 production is closely coupled to photosynthesis and NPP (Megonigal et al., 2004). In TFWs the evidence includes plant removal experiments (van der Nat and Middelburg, 1998a), a $^{14}CO_2$ tracing experiment (Megonigal et al., 1999), and relationships between CH_4 emissions and photosynthetic rates (Vann and Megonigal, 2003). Nonetheless, plants simultaneously reduce potential CH_4 emissions by releasing O_2 from roots into the soil that regenerates competing terminal electron acceptors such as Fe(III) and supports microbial CH_4 oxidation. The net effect of plants on CH_4 production, oxidation, and transport favors increased CH_4 emissions. Perhaps the most definitive evidence of this are numerous observations of greater CH_4 emissions from planted than plant-free soils (Kelley et al., 1995; van der Nat and Middelburg, 2000) and the strong positive correlation between NPP and CH_4 emissions across North America (Whiting and Chanton, 1993).

Methanogenesis is suppressed when there is an adequate supply of competing electron acceptors. In mineral-rich TFW soils, the dominant competing electron acceptor is Fe(III), which plants regenerate as poorly crystalline Fe(III) oxides in the rhizosphere (Weiss et al., 2004). Suppression of methanogenesis by Fe(III) reduction can range from complete to negligible depending on several factors, including plant activity (van der Nat and Middelburg, 1998a; Neubauer et al., 2005b). Sea-level rise should suppress CH_4 production in TFWs as rising SO_4^{2-} availability increases the activity of sulfate-reducing bacteria that suppress methanogenesis (Neubauer and Craft, 2009).

CH_4-oxidizing bacteria are abundant in microaerobic zones of the wetland plant rhizosphere where they have the potential to respond to variations in plant
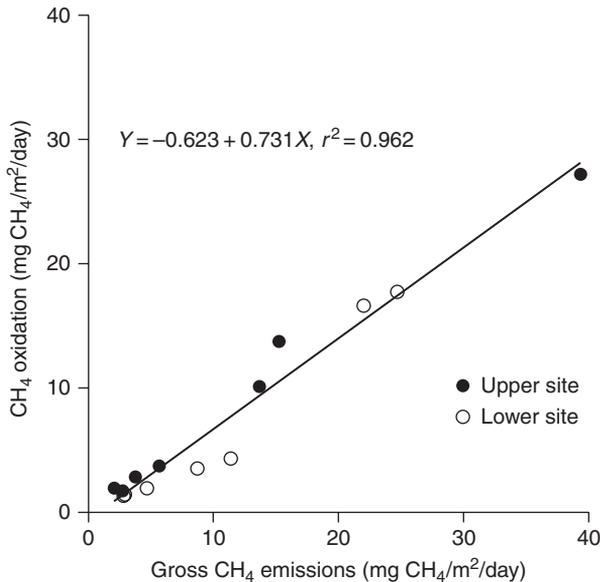
Figure 4 Relationship between rates of gross CH_4 emission and CH_4 oxidation measured over a 13-month period in two tidal freshwater wetlands. From Megonigal and Schlesinger (2002).

physiology and morphology that influence ROL (van der Nat and Middelburg, 1998a,b). CH_4 oxidation activity in TFW soils can be O_2-limited (van der Nat and Middelburg, 1998b) or CH_4-limited (Figure 4; Megonigal and Schlesinger, 2002).

4. Nitrogen Biogeochemistry

Historically, many tidal freshwater marsh nutrient studies have focused on understanding if and how marshes affect estuarine water quality, and were designed to quantify exchanges of dissolved inorganic nitrogen (DIN) between marshes and tidal waters (collectively, "flux studies," e.g., Grant and Patrick, 1970; Heinle and Flemer, 1976; Simpson et al., 1978; Bowden, 1986; Chambers, 1992; Campana, 1998; Ziegler et al., 1999). This type of study provides valuable information, but is also limited by high spatio-temporal variability and difficulties in obtaining accurate hydrologic budgets to scale up the measurements. Flux studies do not provide detailed information on internal transformations that are occurring within marsh soils and sediments. Numerical simulation models (Morris and Bowden, 1986) allow process rates (e.g., organic matter production and mineralization) to be calculated from measurements of soil organic and inorganic nutrients. If robustly designed, these models can be used to explore how the system might respond to future environmental changes (e.g., level of watershed nutrient loading). Recently, isotope tracers have been used to determine both the fate of water column nitrogen

(N) and the processes by which the N is transformed or removed from the water column (Gribsholt et al., 2005, 2006, 2007). This approach provides an elegant means of quantifying N transformations that eliminates many of the issues associated with flux studies and process rate measurements. Isotope tracer studies can be used to quantify fluxes and transformations in the water column (Tobias et al., 2003; Gribsholt et al., 2005, 2006, 2007) and processes occurring throughout the root zone across a range of temporal scales (White and Howes, 1994; Tobias et al., 2001b).

We only know of two comprehensive N models for tidal freshwater marshes that consider exchanges of N between the marsh, estuary, and atmosphere, as well as internal N transformations in soils (Figure 5a,b; Bowden et al., 1991; Neubauer
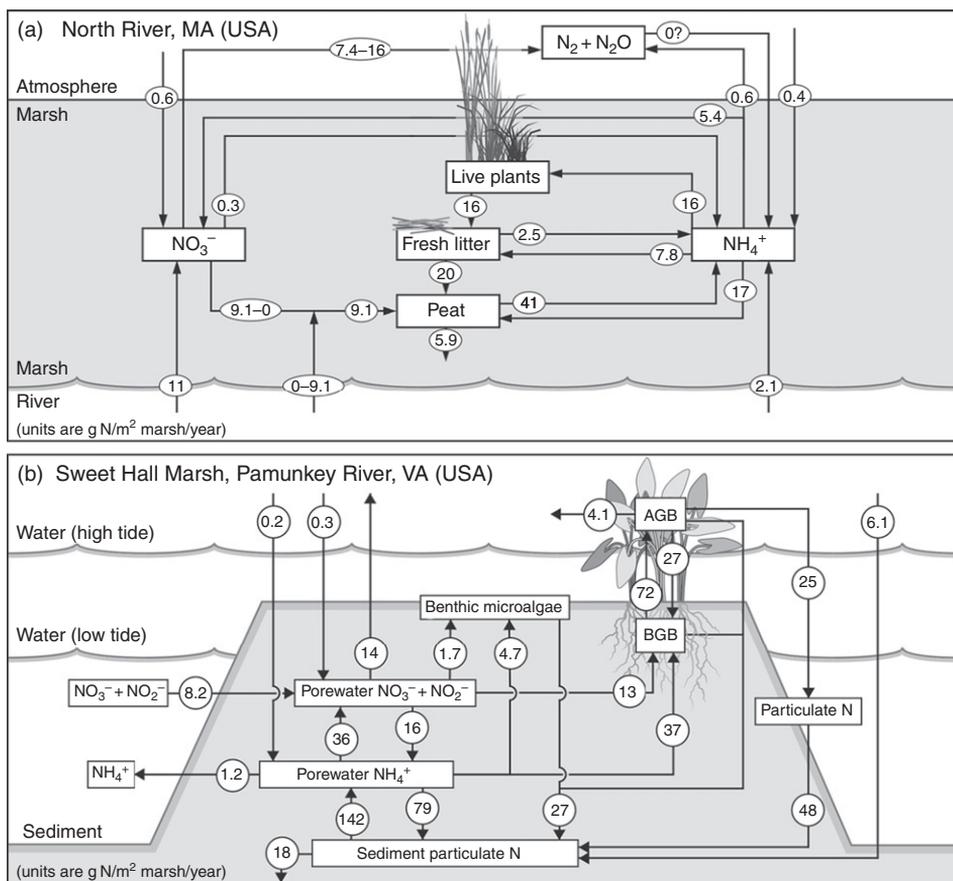
Figure 5 Ecosystem-scale tidal freshwater marsh N models. (a) Process-oriented N budget for a 15.8 ha marsh based on field, laboratory, and modeling efforts. Figure is redrawn from Bowden et al. (1991). (b) Process-based N mass balance model for a 401 ha marsh based on measured field fluxes, with unmeasured fluxes calculated from literature values or to force the model to steady-state conditions. Figure is reproduced, with slight modifications, from Neubauer et al. (2005a). AGB = aboveground biomass; BGB = belowground biomass. Fluxes in each figure are g N/m^2/year.

et al., 2005a). Both models were built with seasonal data from different locations, but neither is seasonally or spatially explicit. The model by Bowden and colleagues (Figure 5a) describes N cycling at a North River, Massachusetts, USA, marsh that had organic-rich soils (40–63% organic matter) and a well-developed, persistent plant litter layer. Neubauer and collaborators (2002) studied Sweet Hall marsh on the Pamunkey River, USA, which had relatively little plant litter and more mineral soils (16–21% organic). Average nutrient concentrations (NH_4^+ and NO_3^-) in the North River were ~4 times greater than those in the Pamunkey River (Neubauer et al., 2005a). Despite the limitations of mass balance modeling and differences between these marshes in plant community type, soil type, marsh elevation, nutrient loading, and climate, several features of the N cycle were similar and may be common to TFWs generally:

1. Exchanges of NH_4^+ and NO_3^- between the TFW and tidal waters were small compared to rates of internal N cycling and transformations in soils. N in sediments deposited on the soil surface can be a significant source of new N to marshes, although the importance of this N source varies with flooding frequency and a suite of factors that influence sediment deposition rates (Darke and Megonigal, 2003).
2. Marsh–estuary exchanges of NO_3^- are generally directed into the marsh (i.e., net uptake by the marsh) and are similar in magnitude to rates of denitrification, suggesting the two processes are coupled.
3. TFWs are efficient at recycling and retaining nutrients within the soil profile. The efficiency of nutrient recycling may be greater in older wetlands with deep soils than in younger wetlands (Morris and Bowden, 1986).
4. The generation of inorganic N via organic matter mineralization can provide more than enough N to support primary production. This suggests that plant production may be largely uncoupled from nutrient loading in the adjacent tidal waters over relatively short periods of time (ca. one to several years). Over longer periods of time, the progressive assimilation and accumulation of water column N by the TFW offsets N losses to denitrification and helps build the soil N pool, which can then be mineralized to support plant demands.

4.1. Nitrogen exchanges

Exchanges of NH_4^+ between TFWs and floodwaters are controlled by the diffusive gradient between soil pore waters and tidal waters, which is influenced strongly by microbial NH_4^+ assimilation. Thus, TFWs with an extensive litter layer often show net NH_4^+ uptake from the water column (Heinle and Flemer, 1976; Bowden, 1986) despite high pore water concentrations because the litter layer is acting as a sink for both pore water and water column NH_4^+. Other wetlands are sources of NH_4^+ to tidal waters (Campana, 1998; Ziegler et al., 1999; Neubauer et al., 2005a). Although wetland–estuary exchanges of NH_4^+ (and other N forms) may be significant on a whole-estuary basis, the magnitude of these fluxes is generally small relative to N transformations occurring within soils (e.g., Figure 5a,b). In a pair of elegant $^{15}NH_4^+$ labeling experiments conducted in May (early growing season with

active plant growth) and September (late growing season with senescent/flowering plants), the fate of water column NH_4^+ was tracked over ~15 days in a N–rich tidal freshwater marsh in Belgium, EU (Gribsholt et al., 2005, 2006, 2007). Despite the temporal separation between the experiments, the fates of NH_4^+ were remarkably similar between the months. In each experiment, the majority of the water column NH_4^+ was exported from the system without being transformed by the marsh (Figure 6). Approximately 4% of the NH_4^+ was sequestered by the marsh and ended up in plant biomass, litter, or the marsh soil (either via physical sorption or microbial assimilation). Overall, microbial pathways of N uptake were more important than the direct assimilation of tidal water NH_4^+ by plants (Gribsholt et al., 2006). However, plants are likely to play indirect roles in modifying water column N loads by providing both O_2 and labile organic C to soil microbes. The ^{15}N label also was found in other N pools within the water column, indicating that active N transformations were occurring within the water column and/or in flooded marsh soils. Of these N transformations, nitrification accounted for the largest fraction of the added NH_4^+, with smaller amounts in the suspended parti-culate N, N_2, and N_2O pools. The marsh soils appeared to be a significant site for nitrification in May (Gribsholt et al., 2005), whereas soil denitrification rates were highest in September (Gribsholt et al., 2006).

TFWs are often significant sinks for water column particulate N deposited on the soil during tidal flooding. The N content of accumulated sediments ranged from 4 to 16 mg N/g sediment in several tidal freshwater marshes in Virginia (Morse et al., 2004; Neubauer et al., 2005a) and is significantly correlated with the soil N content (Morse et al., 2004). The sediment-associated N is presumably a combination of detrital material, microbial biomass, and NH_4^+ sorbed to mineral surfaces. On an annual
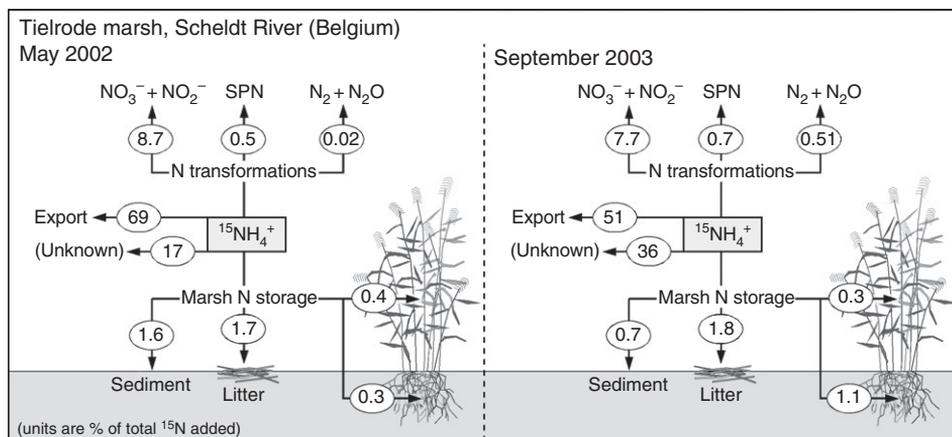
Figure 6 Transformations and uptake of NH_4^+, as inferred by whole-ecosystem $^{15}NH_4^+$ labeling of a 3,477 m^2 marsh area (Gribsholt et al., 2006). Fluxes indicate the percent of the added $^{15}NH_4^+$ label that was recovered in each N pool after label addition. The total input of ^{15}N was 1.97 and 1.41 mol ^{15}N-NH_4^+ in May and September, respectively; the label addition increased the total tidal water NH_4^+ concentration by 14% (May) to 73% (September). SPN, suspended particulate N.

basis, inputs of allochthonous particulate N can be large with respect to the marsh N budget, contributing up to 20 g N/m^2/year (Bowden et al., 1991; Morse et al., 2004; Neubauer et al., 2005a). There is significant spatial variation in deposition rates driven by marsh elevation and flooding frequency (Morse et al., 2004). Over decadal scales, the burial of N sequesters significant amounts of N in tidal freshwater marsh soils, on the order of 10–30 g N/m^2/year (Table 1 and references therein). Deposition and burial rates are much higher in Sweet Hall marsh than the North River marsh (cf. Figure 5a,b), a difference reflected in the lower organic content of Sweet Hall versus North River marsh soils. Indeed, regional patterns of sedimentation may explain why soil accretion rates in TFWs of the Northeast United States are correlated only with organic accumulation, while those in the southeastern United States are correlated with both mineral and organic accumulation (Neubauer, 2008).

Over each tidal cycle, a large volume of water floods and ebbs from the surface of TFWs. Because of the high rate of surface water exchange, wetland uptake of DIN from flood waters is inefficient (Hopkinson, 1992) and can meet only a small fraction of plant N demand. This leads to the "requirement" that existing nutrients are retained within the wetland. Indeed, only ~1% of the total N supplied to the NH_4^+ pool from external and internal sources is lost; the remainder is recycled to other N reservoirs in the marsh (Figure 5a,b). It is likely that the slow turnover of marsh pore water (67 to >800 days to 30 cm at Sweet Hall marsh) drives this efficient N retention. Microbial immobilization of NH_4^+ into particulate matter is a primary mechanism by which N is retained in the marsh; this mechanism can retain $\geq$ 50% of mineralized N in both tidal freshwater (Bowden et al., 1991; Neubauer et al., 2005a) and salt marshes (Anderson et al., 1997). In contrast to the pore water NH_4^+ pool, plant biomass N in TFWs is directly exposed to the tides and less efficiently retained, with ~50% exported as dissolved or particulate organic matter (Hopkinson, 1992; Neubauer et al., 2005a). In support of the link between water turnover and system closure, there was little evidence of N export from a "periodically flooded" high marsh (Bowden et al., 1991).

4.2. Nitrogen transformations

In addition to burial, tidal freshwater marshes can also permanently remove DIN from riverine and estuarine waters via denitrification. Sources of NO_3^- for denitrification include nitrification within the marsh and the uptake of external (water column) NO_3^-. Mass balance calculations indicate high rates of N removal in upper estuaries (Howarth et al., 1996) and many characteristics of TFWs appear to favor denitrification (e.g., high active surface area, shallow depth to anaerobic zone, high organic matter availability). However, few studies have directly measured denitrification in TFWs (Groszkowski, 1995; Merrill, 1999; Merrill and Cornwell, 2000). Greene (2005) reported that median denitrification rates for a tidal freshwater marsh (~120 μmol N/m^2/h) were slightly larger than the median rate for a wide range of intertidal and aquatic systems (~75 μmol N/m^2/h). There is considerable spatial variability between and within TFWs (Merrill, 1999; Greene, 2005). The environmental controls on denitrification have been extensively reviewed by several authors (Seitzinger, 1988; Cornwell et al., 1999; Wallenstein et al., 2006) and

will not be covered in great detail here. In tidal freshwater marshes, denitrification rates were correlated with benthic sediment O_2 demand in a New York marsh, but not in a TFW in Maryland, USA (Merrill, 1999). Based on laboratory manipulations, denitrification rates increase with increases in water column NO_3^- (Merrill, 1999; Greene, 2005). Similarly, the N models of Bowden et al. (1991) and Neubauer et al. (2005a) suggest that denitrification is supported primarily by water column NO_3^-. Because ROL and diffusion of O_2 across the soil surface can support oxidation in tidal freshwater marsh soils (Neubauer et al., 2005b), denitrification is likely to be coupled to both in situ nitrification and water column NO_3^- uptake. Gribsholt et al. (2005, 2006, 2007) presented evidence for coupled nitrification–denitrification in TFWs; following the addition of a $^{15}NH_4^+$ label to tidal flood waters, some of the ^{15}N label appeared in the dissolved N_2 and N_2O pools (Figure 6). Much of this nitrification takes place in marsh soils (possibly associated with plant roots) rather than in the water column (Gribsholt et al., 2005) although the importance of the soil as a site for nitrification can vary seasonally (Neubauer et al., 2005a; Gribsholt et al., 2006).

When integrated over the entire network of TFWs within an estuary, nutrient removal may be substantial since small contributions by individual marshes can have a large cumulative impact on water quality. This is especially true in systems with large areas of tidal marsh (relative to open water). For example, in the Patuxent and Choptank rivers, USA, slightly more than 30% of the total N inputs at the fall line are permanently removed by low-salinity tidal marshes via burial and denitrification (Merrill, 1999; Malone et al., 2003). In contrast, N removal by tidal freshwater marshes in larger systems such as the Hudson and Delaware rivers, USA, is less efficient, with only ∼2–5% of the N sequestered or denitrified (Academy, 1998; Merrill, 1999).

Dissimilatory NO_3^- reduction to NH_4^+ (DNRA) is a mechanism by which NO_3^- can be retained in the marsh rather than lost to the atmosphere via denitrification. There is very little evidence from TFWs about the relative importance of DNRA and denitrification as fates for soil NO_3^-. Bowden (1986) determined that DNRA rates were 5% of NO_3^- supply (i.e., nitrification) rates. In contrast, Neubauer et al. (2005a) calculated that DNRA was about 40% of nitrification. Based on work in other systems, the availability of labile C relative to NO_3^- (i.e., electron donor:electron acceptor ratio) is important in determining the fate of NO_3^-, with DNRA dominating with high organic C availability (Fazzolari et al., 1998; Christensen et al., 2000) and denitrification increasing in importance at higher NO_3^- concentrations (Nijburg et al., 1997; Tobias et al., 2001a,b). Thus, lower NO_3^- in the Pamunkey River (Neubauer et al., 2005a) may explain the higher importance of DNRA in that system. Across the estuarine gradient, DNRA is generally more important (relative to denitrification) in estuarine and marine systems whereas denitrification increases in importance in freshwater systems (Tobias et al., 2001b), a pattern that may be related to sulfide inhibition of denitrification (Brunet and Garcia-Gil, 1996; An and Gardner, 2002).

4.3. Nutrient regulation of plant production

There is evidence to suggest that rates of plant production in tidal freshwater marshes are largely uncoupled from allochthonous nutrient inputs. First, rates of

N mineralization in TFWs are considerably greater than plant N demand and rates of diffusive DIN uptake from tidal waters (e.g., Figures 5a and 5b; Bowden et al., 1991; Neubauer et al., 2005a). In these studies, gross N mineralization provided almost 3 times more NH_4^+ than was needed to support annual plant N requirements. Second, $^{15}NH_4^+$ label tracing showed that less than 2% of the applied ^{15}N was incorporated into plant leaves and roots after ~15 days (Figure 6), suggesting that the plants were not dependent on water column N over short timescales (Gribsholt et al., 2005, 2006, 2007).

Third, there are many examples in which direct fertilization of TFWs with N, P, or N + P generally did not increase in either aboveground biomass or biomass nutrient content (Whigham and Simpson, 1978; Walker, 1981; Booth, 1989; Chambers and Fourqurean, 1991; Morse et al., 2004). However, in other cases fertilization did increase plant growth (DeLaune et al., 1986; Booth, 1989; Frost et al., 2009), so it has proven difficult to unambiguously determine the nature (or existence) of nutrient limitations in TFWs (Chambers and Fourqurean, 1991).

Phosphorus (P) is a limiting nutrient in many freshwater ecosystems because inorganic P precipitates with Fe, Al, Ca, and Mg minerals, and organic P is generally unavailable to plants. In contrast, marine systems are often N limited. This generality has not been adequately tested in TFWs, but P additions did not affect primary productivity in TFWs in Virginia and Georgia, USA (Morse et al., 2004; Frost et al., 2009).

5. PHOSPHORUS BIOGEOCHEMISTRY

Because TFWs are located in upper estuaries where watershed–derived inputs of P are concentrated, these intertidal systems may be key sites in landscapes for P sequestration and transformation. In a pair of tidal freshwater marshes, sediments deposited on the soil surface contained 0.3–1.7 mg P/g sediment and contributed inputs of 0.6–2.3 g P/m^2/year (Morse et al., 2004). Uptake of inorganic P by organisms results in a relative enrichment of organic P in surface soils (Morse et al., 2004). In a South Carolina TFW, much of the soil organic P was bound to humic acids whereas the inorganic P was primarily associated with Fe or Al (Paludan and Morris, 1999).

Phosphatase (the enzyme that liberates organic-bound P) is secreted by plants, algae, and bacteria under conditions of PO_4^{3-} limitation. Phosphatase activity is expected to be greatest where the biological demand for inorganic P is high, most soil P is in organic forms, and soil sorption limits pore water PO_4^{3-} concentrations. The activities of three phosphatase enzymes were highly correlated with aboveground plant biomass and soil organic content in a successional sequence of TFWs (Huang and Morris, 2003). Similar positive correlations between phosphatase activity, soil organic matter, and soil organic P were observed along a salinity gradient, with the highest activity in TFWs (Huang and Morris, 2005). Furthermore, organic P made up a greater fraction of total P in the late (intertidal marsh) versus early (open water) successional stages. The interactions between P

availability and demand may lead to a positive feedback that drives ecosystem succession, whereby high demand for inorganic P reduces available PO_4^{3-} concentrations, leading to an increase in phosphatase activity and increased organic P mineralization, further increasing plant growth (Huang and Morris, 2003). Over years to decades, P mineralization results in a significant decrease in organic P concentrations with increasing soil depth (Paludan and Morris, 1999). Despite high phosphatase enzyme activities in TFW soils, concentrations of dissolved PO_4^{3-} are often low due to the combined effects of biological demand and chemical sorption processes that remove free PO_4^{3-} from marsh pore waters. Sundareshwar and Morris (1999) showed that P sorption is higher in more freshwater systems because sediments tend to have higher surface areas and a lower content of Fe and Al minerals. The lack of significant accumulation of inorganic P in deeper soils (Paludan and Morris, 1999) implies that organic P is not simply mineralized to inorganic P but is instead removed from the soil via plant uptake or hydrological export.

Although TFWs are sinks for sediment-associated particulate P, PO_4^{3-} fluxes are highly variable and there can be net PO_4^{3-} uptake (Simpson et al., 1978; Gilbert, 1990), seasonal variability (Simpson et al., 1983; Campana, 1998), or negligible PO_4^{3-} fluxes (Anderson et al., 1998) between TFWs and tidal waters. One factor that may affect spatial and temporal variations in marsh–estuary tidal fluxes of PO_4^{3-} is the interplay between P, Fe, and O_2 dynamics. In soils that are regularly exposed to O_2 during low tides (e.g., the marsh surface and creek bank edges), Fe(II) can oxidize to Fe(III) and lead to the formation of an "iron curtain" of iron oxyhydroxide minerals that efficiently sorb PO_4^{3-}, causing P retention in the marsh (Chambers and Odum, 1990). In combination with diagenetic effects (discussed above), this mechanism may contribute to decreases in total soil P content with increasing depth that have been observed in some TFWs (Bowden, 1984; Chambers and Odum, 1990; Merrill, 1999; Paludan and Morris, 1999), although not in others (Simpson et al., 1983; Greiner and Hershner, 1998). The mineral (i.e., Fe) content of the soils is likely to play a role in the efficiency of such an iron curtain. The ecological implications of the iron curtain on ecosystem P dynamics are unclear because it retains a potentially limiting nutrient within the marsh, but not necessarily in a bioavailable form. Another implication is that high marshes, which are flooded less frequently and therefore exposed to air for longer periods of time, may have an extensive iron curtain that allows for more efficient P retention and recycling than low marshes, leading to increased P accumulation in high versus low marsh habitats (Khan and Brush, 1994).

The storage (burial) of P in marsh soils is an important mechanism by which P can be removed and sequestered from estuarine waters. Over time scales ranging from decades to centuries, TFWs sequester significant amounts of P, with burial rates ranging from <0.5 to >4 g P/m^2/year (Table 1 and references therein). These burial rates are roughly comparable to rates of sediment-associated P deposition onto the marsh surface (Morse et al., 2004). Extrapolating marsh P burial rates to a landscape scale shows that low salinity tidal marshes can effectively sequester a significant fraction (>60%) of watershed derived P in relatively small, marsh-dominated estuarine systems (e.g., Patuxent and Choptank Rivers, MD, Merrill,

1999; Malone et al., 2003). In contrast, about 12% of the combined sewage and riverine-derived P to the upper Hudson River, USA, is buried in freshwater tidal and nontidal marshes (inputs from Limburg et al., 1986; Phillips and Hanchar, 1996; burial rate from Merrill, 1999). Based on average literature values for marsh P burial, only ~7% of the P entering the upper Delaware River estuary, USA, is permanently buried in tidal marshes (Academy, 1998). Thus, TFWs can be long-term sinks for significant amounts of watershed-derived P, but the extent of wetlands within the estuary (relative to the size of the estuary or watershed) appears to be important in determining how efficiently TFWs perform this function.

6. SILICON BIOGEOCHEMISTRY

The weathering of terrestrial silicate (Si) minerals ultimately leads to inputs of dissolved silica (DSi) to estuaries and the coastal ocean where diatom production can be limited by low DSi availability. Recent evidence suggests that silica transformations in TFWs play a key role in transforming silica from biogenic (BSi) to DSi forms. For example, under low discharge conditions (i.e., summer) in the Scheldt Estuary, EU, the input of DSi from fluvial sources was as low as 10,000 kg/month, an amount that can be exported from the 450 ha of TFWs in the system in six tidal cycles (Struyf et al., 2006). Because rates of DSi export increased with decreasing concentrations of DSi in estuarine waters, marsh-mediated recycling of Si may be especially important when low ambient DSi concentrations otherwise limit aquatic primary productivity (Struyf et al., 2006). Understanding the factors that regulate DSi export from TFWs requires additional research on biogeochemical transformations in TFW soils (Struyf et al., 2005a,b, 2007).

7. BIOGEOCHEMICAL EFFECTS OF SEA-LEVEL RISE

The increase in global ocean levels has the potential to affect TFWs by modifying their hydroperiod and by pushing the salt front up-estuary so that these systems are exposed to more saline waters. In general, the biogeochemical effects of changes in flooding frequency will be mediated by changes in plant productivity (Odum et al., 1995; Morris et al., 2002), decomposition (Odum and Heywood, 1978; Chambers and Odum, 1990), and deposition of allochthonous minerals and nutrients via sedimentation (Khan and Brush, 1994; Pasternack and Brush, 1998; Darke and Megonigal, 2003). Future changes in salinity in a given TFW will depend on the wetland's position on the current salinity gradient, rates of sea-level rise, and changes in river discharge. Both sea-level rise and river discharge are influenced by global warming (Burkett et al., 2001).

Changes in salinity can affect a number of nutrient cycling processes including N and P sorption, denitrification, and nitrification (Howarth et al., 1988; Caraco et al., 1989; Rysgaard et al., 1999). The intrusion of salt water and associated SO_4^{2-} can lead to the breakdown of the "iron curtain" of Chambers and Odum (1990).

As Fe oxides are reduced either biologically (by Fe(III)-reducing bacteria) or chemically (via H_2S), sediment-bound P is released and the Fe(II) can be sequestered in Fe–S compounds (e.g., pyrite) (Caraco et al., 1989; Lamers et al., 2001). Elevated salinity can also lead to decreased sorption of NH_4^+ to soil particles as NH_4^+ is displaced by positively charged cations such as Na^+ and Mg^{2+}. Increased NH_4^+ concentrations may suppress N_2 fixation because nitrogenase is inhibited by free NH_4^+ (Howarth et al., 1988). The physiological effects of salinity on nitrifying and denitrifying microbes reduce the activity of these organisms (MacFarlane and Hebert, 1984; Furumai et al., 1988; Stehr et al., 1995, Rysgaard et al., 1999). If increased SO_4^{2-} concentrations accelerate soil organic matter decomposition (see Section 3.1), rates of nutrient mineralization would also increase.

Salt water intrusion will affect greenhouse gas emissions. Thermodynamics dictate that microbial SO_4^{2-} reducers will outcompete methanogens for substrates such as organic C (Megonigal et al., 2004). As a result, salt water intrusion should increase SO_4^{2-} reduction at the expense of CH_4 production. Salt water intrusion could also affect the production of N_2O if high H_2S concentrations inhibit both nitrification and denitrification, as has been shown for unvegetated sediments (Joye and Hollibaugh, 1995; Brunet and Garcia-Gil, 1996; An and Gardner, 2002).

Much of the research on the effects of rising salinity on soil and sediment biogeochemistry has focused on transient effects. Over longer time periods, salt-sensitive plants, animals, and microbes will likely be replaced by salt-tolerant species (Magalhães et al., 2005). There is relatively little known from direct manipulations of salinity about the direction of these longer term effects.

8. Concluding Comments

It is perhaps appropriate that TFW biogeochemistry has not been well studied given the fact TFWs occupy less area than many other wetland ecosystems. However, TFWs are grossly underrepresented even in the tidal wetland literature. A Web of Science search (1980–2008) shows that <5% of all tidal wetland literature concerns TFWs, whereas TFWs can represent ~20% of the total tidal wetland area in a region (Stevenson et al., 1988; Dahl, 1999). There are reasons why TFWs deserve increased attention. They are species–rich ecosystems that support waterfowl, fish, and terrestrial wildlife. They influence the chemistry of adjacent estuarine waters through exchange and transformation of organic C and nutrients. Because of their location at the head of estuaries, TFWs are important sites for the deposition of nutrient-laden sediments, and they can rapidly sequester C, N, and P through burial. In short, TFWs are important features of the landscapes in which they occur.

TFWs are sentinel ecosystems for monitoring the influence of global climate change on coastal ecosystems. Poised at the interface of nontidal rivers and saline estuarine waters, they are influenced by river discharge and sea-level rise. River discharge is sensitive to precipitation and evapotranspiration, which are in turn sensitive to global warming (Palmer et al., 2008). Increasingly frequent incursions

of saline water into TFW ecosystems can be expected as sea levels rise and droughts become more common. It is uncertain what the long-term effects of such episodic events will have on element cycling and plant community composition in TFWs, but based on current distributions of plant species, even small increases in salinity will elicit dramatic changes in plant and microbial community composition, and fundamentally alter the characteristics of TFW biogeochemical cycles (Neubauer and Craft, 2009). At present, there are many hypotheses about the response of TFWs to these perturbations. For example, we could expect TFWs to be less sensitive to sea-level rise than tidal saline wetlands because they are located at the head of estuaries near riverine sediment sources. However, their location also presents barriers for TFW transgression inland due to steep upland slopes. We do not understand TFWs well enough to predict how they will respond to climate and land use change.

Tidal freshwater wetlands have not received the level of biogeochemical scrutiny that has been directed toward nontidal freshwater and tidal saline wetlands. In the absence of more complete knowledge, we often assume that TFW processes adhere to generalizations drawn from better-studied ecosystems. This approach has proved fruitful, but limited. For example, there is now doubt about the assumption that TFW plants are more rapidly decomposed than saline tidal wetland plants (Craft, 2007). Based on hydrology, it seems reasonable to assume that TFWs have relatively open nutrient cycles, but that was not the case in two TFW systems that have been fully studied. Clearly, understanding biogeochemical processes in TFWs will require more direct observations of TFWs in relation to their tidal saline and nontidal analogs.

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