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THE CARBON BALANCE OF NORTH AMERICAN WETLANDS

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Abstract: We examine the carbon balance of North American wetlands by reviewing and synthesizing the published literature and soil databases. North American wetlands contain about 220 Pg C, most of which is in peat. They are a small to moderate carbon sink of about 49 Tg C yr^{-1}, although the uncertainty around this estimate is greater than 100%, with the largest unknown being the role of carbon sequestration by sedimentation in freshwater mineral-soil wetlands. We estimate that North American wetlands emit 9 Tg methane (CH_4) yr^{-1}; however, the uncertainty of this estimate is also greater than 100%. With the exception of estuarine wetlands, CH_4 emissions from wetlands may largely offset any positive benefits of carbon sequestration in soils and plants in terms of climate forcing. Historically, the destruction of wetlands through land-use changes has had the largest effects on the carbon fluxes and consequent radiative forcing of North American wetlands. The primary effects have been a reduction in their ability to sequester carbon (a small to moderate increase in radiative forcing), oxidation of their soil carbon reserves upon drainage (a small increase in radiative forcing), and reduction in CH_4 emissions (a small to large decrease in radiative forcing). It is uncertain how global changes will affect the carbon pools and fluxes of North American wetlands. We will not be able to predict accurately the role of wetlands as potential positive or negative feedbacks to anthropogenic global change without knowing the integrative effects of changes in temperature, precipitation, atmospheric carbon dioxide concentrations, and atmospheric deposition of nitrogen and sulfur on the carbon balance of North American wetlands.

Key Words: carbon, methane, North America, plants, sedimentation, soil, wetlands

INTRODUCTION

Wetlands are important in global carbon dynamics because of their large soil carbon pools, high methane (CH_4) emissions, and potential for carbon sequestration in peat formation, sediment deposition, and plant biomass. For example, peatlands occupy about 3% of the terrestrial global surface, yet they contain 16–33% of the soil carbon pool (Gorham 1991, Maltby and Immirzi 1993). Because this peat formed over thousands of years, these areas represent a large carbon pool but with relatively slow rates of accumulation. By comparison, estuarine wetlands and some freshwater mineral-soil wetlands rapidly sequester carbon as soil organic matter due to burial in sediments. Large areas of wetlands have been converted to other land uses globally and in North America (Dugan 1993, OECD 1996), which has resulted in a net flux of carbon to the atmosphere (Armentano and Menges 1986, Maltby and Immirzi 1993). Additionally, wetlands emit 92 to 237 Tg CH_4 yr^{-1}, which is a large fraction of the total annual global flux of about 600 Tg CH_4 yr^{-1} (Ehhalt et al. 2001). This is important because CH_4 is a potent greenhouse gas, second only in importance to only carbon dioxide (CO_2) (Ehhalt et al. 2001).

A number of previous studies have examined the role of peatlands in the global carbon budget (reviewed in Mitra et al. 2005), and Roulet (2000) focused on the role of Canadian peatlands in the Kyoto process. Here, we augment previous studies by considering all types of wetlands (not just peatlands) and integrate new data to examine the carbon balance in the wetlands of Canada, the United States, and Mexico. We also briefly compare these values to those from global wetlands. We limit this review to those components of the carbon budget that result in a net gaseous exchange with the atmosphere on an interannual basis and do not consider other internal carbon fluxes. We do not consider dissolved organic carbon (DOC) fluxes from wetlands, although they may be substantial (Moore 1997, Trettin and Jurgensen 2003), because the oxidation of the DOC would be counted as atmospheric fluxes of CO_2 and CH_4 in the receiving ecosystems downstream, and we do not want to double-count fluxes. Portions of this review were originally written as a chapter in the State of the Carbon Cycle Report (SOCCR) for North America, as part of the U.S. Climate Change Program (Bridgham et al. 2007), but this review has been updated and is considerably more extensive in the description of methods, assumptions, and supporting data.

Given that many undisturbed wetlands are a natural sink for CO_2 and a source of CH_4, a note of caution in interpretation of our data is important. Using the Intergovernmental Panel on Climate Change (IPCC) terminology, the term *radiative forcing* denotes "an externally imposed perturbation in the radiative energy budget of the Earth's climate system" (Ramaswamy et al. 2001). Thus, it is the change from a baseline condition in wetland greenhouse gas fluxes that constitutes a radiative forcing that will impact climate change, and carbon fluxes in unperturbed wetlands are important only in establishing a baseline condition. For example, historical steady state rates of CH_4 emissions from wetlands have zero net radiative forcing, but an increase in CH_4 emissions due to climatic warming would constitute a positive radiative forcing. Similarly, steady state rates of soil carbon sequestration in wetlands have zero net radiative forcing, but the lost sequestration capacity and the oxidation of the extant soil carbon pool in drained wetlands are both positive radiative forcings.

METHODS

We provide here an overview of the data sources, assumptions, and methods that were synthesized for this paper. Further detail on how individual estimates were derived can be found in footnotes in the individual tables. While an assessment of uncertainty is essential to evaluate our estimates, quantitative uncertainty estimates were often not possible because either uncertainty estimates were not in the original sources or multiple sources were synthesized to derive a single estimate. Where possible, we have given reported uncertainties and/or ranges of estimates. Furthermore, we have used an overall qualitative ranking system in the tables and figures to give our best professional judgment of the quality of each estimate.

We consider the following categories of wetlands based upon major ecological differences that drive carbon cycling: peatlands ($\geq$ 40 cm of surface organic matter) with and without permafrost, freshwater mineral-soil (FWMS) wetlands ($\leq$ 40 cm of surface organic matter), and estuarine wetlands dominated by herbaceous vegetation (tidal marshes), mangroves, and unvegetated (mud flats)

Current Wetland Area and Rates of Loss

The current and original (i.e., prior to large-scale human disturbance) wetland area and rates of loss are the basis for all further estimates of pools and fluxes in this paper. The ability to estimate soil carbon pools and fluxes in North American wetlands is constrained by the national inventories (or lack thereof) for Canada, the U.S., and Mexico (Davidson et al. 1999). A regular national inventory of Canada's wetlands has not been undertaken, although wetland area has been mapped by ecoregion (National Wetlands Working Group 1988). Extensive recent effort has gone into mapping Canadian peatlands (Tarnocai 1998, Tarnocai et al. 2005). We calculated the current area of Canadian FWMS wetlands as the difference between total freshwater wetland area and peatland area given by the National Wetland Working Group (1988). The original area of FWMS wetlands was obtained from Rubec (1996). Canadian salt marsh estimates were taken from a compilation by Mendelssohn and McKee (2000). The compilation does not include brackish or freshwater tidal marshes, and we were unable to locate other area estimates for these systems. The original area of these marshes was estimated from the National Wetland Working Group (1988), but it is highly uncertain. There are no reliable country-wide estimates of mud flat area for Canada, but a highly uncertain extrapolation was possible based upon the ratio of mudflat to salt marsh area reported by Hanson and Calkins (1996).

The National Wetland Inventory (NWI) program of the U.S. has repeatedly sampled several thousand wetland sites using aerial photographs and more limited field verification. These relatively high quality data are summarized in a series of reports detailing changes in wetland area in the conterminous U.S. for the periods of the mid-1950s to mid-1970s (Frayer et al. 1983), mid-1970s to mid-1980s (Dahl and Johnson 1991), and 1986 to 1997 (Dahl 2000). However, the usefulness of the NWI inventory reports for carbon budgeting is limited by the level of classification used to define wetland categories within the Cowardin et al. (1979) wetland classification system. At the level used in the national status and trend reports, vegetated freshwater wetlands are classified by dominant physiognomic vegetation type, and it is impossible to make the important distinction between peatlands and FWMS wetlands. The data are not at an adequate spatial resolution to combine with USDA Natural Resources Conservation Service (NRCS) soil maps to discriminate between the two types of wetlands (T. Dahl, pers. comm.). Because of these data limitations, we used the NRCS soil inventory of peatlands (i.e., Histosols and Histels, or peatlands without and with permafrost, respectively) to estimate the original area of peatlands (Bridgham et al. 2000) and combined these data with regional estimates of loss (Armentano and Menges 1986) to estimate current peatland area in the conterminous U.S. We calculated the current area of FWMS wetlands in the conterminous U.S. by subtracting peatland area from total wetland area (Dahl 2000). This approach was limited by the Armentano and Menges peatland area data being current only up to the early 1980s, although large losses of peatlands since then are unlikely due to the institution of wetland protection laws.

We used a similar approach for Alaskan peatlands: peatland area was determined by the NRCS soil inventory (Bridgham et al. 2000), and overall wetland inventory was determined by standard NWI methods (Hall et al. 1994). However, our peatland estimate of 132,000 km^2 (Table 1) is just 22% of the often-cited value by Kivinen and Pakarinen (1981) of 596,000 km^2. Kivinen and Pakarinen also used NRCS soils data (Rieger et al. 1979) for their peatland estimates, but they defined a peatland as having a minimum organic layer thickness of 30 cm, whereas the current U.S. and Canadian soil taxonomies require a 40-cm thickness. The original 1979 Alaska soil inventory has been reclassified with current U.S. soil taxonomy (J. Moore, AK State Soil Scientist, pers. comm.). Using the reclassified soil inventory, Alaska has 417,000 km^2 of wetlands with a histic modifier that are not Histosols or Histels, indicating significant carbon accumulation in the surface horizons of FWMS wetlands. Thus, we conclude that Kivinen and Pakarinen's Alaska peatland area estimate is higher because many Alaskan wetlands have a thin organic horizon that is not deep enough to qualify as a peatland under current soil taxonomy. Our smaller peatland area significantly lowers our estimate of carbon pools and fluxes in Alaskan peatlands compared to earlier studies (see RESULTS, Carbon Pools below).

The area of salt marsh in the conterminous U.S., Alaska, and Canada were taken from Mendelssohn and McKee (2000). Because these U.S. estimates include brackish tidal marshes, they cannot be compared directly to the area of Canadian salt marsh. Compilations of tidal freshwater tidal wetland area are difficult to find, but there is approximately 1,640 km^2 on the east coast of the U.S. (Odum et al. 1984) and 470 km^2 on the U.S. Gulf Coast (Field et al. 1991). Although some freshwater tidal wetlands are forested, this total was added to the tidal marsh area for the conterminous U.S. Mangrove area was also taken from Mendelssohn and McKee (2000), and is similar to an estimate by Lugo and Snedaker (1974).

The original area of tidal wetlands in the conterminous U.S. was based on the NWI (Dahl 2000), which we considered to be the most defensible estimate available. However, 'original' here only refers to the 1950s, so it is almost certain that the actual original tidal wetland area in the conterminous U.S. was larger than our estimate based on a 7.7% loss of area (Valiela et al. 2001). By comparison, Valiela et al. (2001) estimated a loss of 31% of mangrove area in the U.S. from 1958 to 1982 based on the difference in two independent estimates. We assumed that the original area of Alaskan tidal wetlands was similar to the current area because there has been relatively little development pressure in Alaska. We arbitrarily used a global loss of 25% for tidal marshes outside North America.

No national wetland inventories have been done for Mexico. Current freshwater wetland estimates for Mexico were taken from Davidson et al. (1999) and Spiers (1999), who used inventories of discrete wetland regions performed by a variety of organizations. Thus, freshwater wetland area estimates for Mexico are highly unreliable and are possibly a large underestimate. For mangrove area in Mexico, we used the estimates compiled by Mendelssohn and McKee (2000), which are similar to estimates reported in Spalding et al. (1997) and Davidson et al. (1999). We could find no estimates of tidal marsh or mud flat area for Mexico. Since

Table 1. Current and historical area of wetlands in North America and the world (10^3 km^2). Historical refers to approximately 1800, unless otherwise specified. Based upon best professional judgment, the uncertainty categories are: ***** = 95% certain that the actual value is within 10% of the estimate reported; **** = 95% certain that the actual value is within 25%; *** = 95% certain that the actual value is within 50%; ** = 95% certain that the actual value is within 100%; * = uncertainty > 100%.

	Permafrost peatlands	Non-permafrost peatlands	Freshwater mineral soil	Tidal marsh	Mangrove	Mudflat	**Total**
Canada							
Current	422[a****]	714[a****]	159[b**]	0.44[c***]	0[*****]	6[d*]	1301[****]
Historical	424[e****]	726[f****]	359[g**]	1.3[b***]	0[*****]	7[h***]	1517[****]
Alaska							
Current	89[i****]	43[i****]	556[j****]	1.4[c****]	0[*****]	7[k****]	696[*****]
Historical	89[****]	43[****]	556[****]	1.4[****]	0[*****]	7[****]	696[*****]
Conterminous USA							
Current	0[*****]	93[l****]	312[m*****]	20[c*****]	3[c*****]	2[n*****]	431[*****]
Historical	0[*****]	111[i****]	762[o***]	22[n****]	4[n****]	3[n****]	901[***]
Mexico							
Current	0[*****]	10[p*]	21[p*]	0[*]	5[c*]	ND[q]	36[*]
Historical	0[*****]	---------- 45[p*] ----------		0[*]	8[h*]	ND	53[*]
North America							
Current	511[****]	861[****]	1,047[****]	22[****]	8[*]	15[*]	2,463[****]
Historical	513[****]	894[r****]	1,706[r***]	25[***]	12[*]	17[*]	3,167[***]
Global							
Current	---------- 3,443[s***] ----------		2,315[t***]	22[u*]	181[v*]	ND	5,961[***]
Historical	---------- 4,000[w***] ----------		5,000[x***]	29[y*]	278[z*]	ND	9,307[x***]

[a] Tarnocai et al. (2005).
[b] National Wetlands Working Group (1988).
[c] Brackish and salt marsh areas from Mendelssohn and McKee (2000); freshwater tidal wetlands for the conterminous U.S. only from Odum et al. (1984) and Field et al. (1991).
[d] Estimated from the area of Canadian salt marshes and the ratio of mudflat to salt marsh area reported by Hanson and Calkins (1996).
[e] Accounting for losses due to permafrost melting in western Canada (Vitt et al. 1994). This is an underestimate, as similar, but undocumented, losses have probably also occurred in eastern Canada and Alaska.
[f] 9000 km^2 lost to reservoir flooding (Rubec 1996), 250 km^2 to forestry drainage (Rubec 1996), 124 km^2 to peat harvesting for horticulture (Cleary et al. 2005), and 16 km^2 to oil sands mining (Turetsky et al. 2002). See note e. for permafrost melting estimate.
[g] Rubec (1996).
[h] Estimated loss rate for the Americas from Valiela et al. (2001) for approximately 1980 to 1990.
[i] Historical area from NRCS soil inventory (Bridgham et al. 2000), except Alaska inventory updated by N. Bliss (STATSGO query Feb. 2006). < 1% wetland losses have occurred in Alaska (Dahl 1990).
[j] Total freshwater wetland area in Hall (1994) minus peatland area.
[k] Hall et al. (1994).
[l] Historical area from Bridgham et al. (2000) minus losses in Armentano and Menges (1986).
[m] Overall freshwater wetland area from Dahl (2000) minus peatland area.
[n] Dahl (2000). Historical area estimates are only from the 1950s.
[o] Total historical wetland area from Dahl (1990) minus historical peatland area minus historical estuarine area.
[p] Spiers (1999) and Davidson (1999).
[q] No data.
[r] Assuming that historical proportion of peatlands to total wetlands in Mexico was the same as today.
[s] Bridgham et al. (2000) for USA, Tarnocai et al. (2005) for Canada, Joosten and Clarke for remainder of world. Recent range in literature 2,974,000–3,985,000 km^2 (Matthews and Fung 1987, Aselmann and Crutzen 1989, Maltby and Immirzi 1993, Bridgham et al. 2000, Joosten and Clarke 2002).
[t] Average of 2,289,000 km^2 from Matthews and Fung (1987) and 2,341,000 km^2 Aselmann and Crutzen (1989).
[u] Chmura et al. (2003). Underestimated because no inventories were available for the continents Asia, South America and Australia which are mangrove-dominated but also support salt marsh.
[v] Spalding (1997).
[w] Range from 3,880 to 4,086 in Maltby and Immirzi (1993). For subsequent calculations, used 4,000,000 km^2.
[x] Approximately 50% loss from Moser et al. (1996).
[y] Assumed a 25% loss rate outside N.A. for tidal marshes; a loss rate of 35% was used for mangroves (Valiela et al. 2001).

most vegetated Mexican tidal wetlands are dominated by mangroves (Olmsted 1993, Mendelssohn and McKee 2000), the omission of Mexican tidal marshes should not significantly affect our carbon budget. However, there may be large areas of mud flat that would significantly increase our estimate of carbon pools and sequestration in this country. We used the Valiela et al. (2001) estimate of 38% for mangrove loss in the Americas, which roughly covers the period 1980 to 1990. This is less than the rough worldwide estimate of 50% wetland loss since the 1880s that is often cited (see Zedler and Kercher 2005) and is probably conservative. A global loss rate of 35% was used for mangrove area globally based on the analysis of Valiela et al. (2001).

Carbon Pools

FWMS Wetlands (Gleysols). Gleysols are a soil classification used by the Food and Agriculture Organization of the United Nations (FAO) and many countries that denotes mineral soils formed under waterlogged conditions (FAO-UNESCO 1974). Tarnocai (1998) reported a soil carbon density of 200 Mg C ha^{-1} for Canadian Gleysols, which we used in this paper for Canadian FWMS wetlands, but he did not indicate to what depth this extended. Batjes (1996) determined soil carbon content globally from the *Soil Map of the World* (FAO 1991) and a large database of soil pedons. He gave a very similar average value for soil carbon density of 199 Mg C ha^{-1} (CV = 212, n = 14 pedons) for Gleysols of the world to 2-m depth; to 1-m depth, he reported a soil carbon density of 131 Mg C ha^{-1} (CV = 109, n =142 pedons).

Gleysols are not part of the U.S. soil taxonomy scheme, and mineral soils with attributes reflecting waterlogged conditions are distributed among numerous soil groups. We queried the STATSGO soils database for soil carbon density in 'wet' mineral soils of the conterminous U.S. (all soils that had a surface texture described as peat, muck, or mucky peat, or were listed on the 1993 list of hydric soils but were not classified as Histosols) (N. Bliss, query of NRCS STATSGO database, Dec. 2005). We used the average soil carbon density of 162 Mg C ha^{-1} from this query for FWMS wetlands in the conterminous U.S. and Mexico.

Some caution is necessary in the use of Gleysol or 'wet' mineral soil carbon densities because apparently they include large areas of seasonally wet soils that are not considered wetlands by the more conservative definition of wetlands used by the U.S. and many other countries and organizations. For example, Eswaran et al. (1995) estimated that global wet mineral-soil area was 8,808,000 km^2, which is substantially greater than the commonly accepted mineral-soil wetland area estimated by Matthews and Fung (1987) of 2,289,000 km^2 and Aselmann and Crutzen (1989) of 2,341,000 km^2, even accounting for substantial global wetland loss. In our query of the USDA STATSGO database for the U.S., we found 1,258,000 km^2 of wet soils in the conterminous U.S. versus our estimate of 312,000 km^2 of FWMS wetlands currently and 762,000 km^2 originally (Table 1). We assume that including these wet-but-not-wetland soils will decrease the estimated soil carbon density, but to what degree we do not know. However, just the differences in area will give large differences in the wetland soil carbon pool. For example, Eswaran et al. (1995) estimated that wet mineral soils globally contain 108 Pg C to 1-m depth, whereas our estimate is 46 Pg C to 2-m depth (Table 2).

For Alaska, many soil investigations have been conducted since the STATSGO soil data were coded. We updated STATSGO by calculating soil carbon densities from data obtained from the NRCS on 479 pedons collected in Alaska, and then we used these data for both FWMS wetlands and peatlands. For some of the Histosols, missing bulk densities were calculated using averages of measured bulk densities for the closest matching class in the USDA Soil Taxonomy (NRCS 1999). A matching procedure was developed for relating sets of pedons to sets of STATSGO components. If there were multiple components for each map unit in STATSGO, the percentage of the component was used to scale area and carbon data. We compared matching sets of pedons to sets of components at the four top levels of the U.S. Soil Taxonomy: Orders, Suborders, Great Groups, and Subgroups. For example, the soil carbon for all pedons having the same soil order were averaged, and the carbon content was applied to all of the soil components of the same order (e.g., Histosol pedons are used to characterize Histosol components). At the Order level, all components were matched with pedon data. At the suborder level, pedon data were not available to match approximately 20,000 km^2 (compared to the nearly 1,500,000 km^2 area of soil in the state), but the soil characteristics were more closely associated with the appropriate land areas than at the Order level. At the Great Group and Subgroup levels, pedon data were unavailable for much larger areas, even though the quality of the data when available became better. For this study, we used the Suborder-level matching. The resulting soil carbon density for Alaskan FWMS wetlands was 469 Mg C ha^{-1}, reflecting large areas of wetlands with a histic epipedon as noted above.

Table 2. Soil carbon pools (Pg) and fluxes (Tg yr^{-1}) of wetlands in North America and the world. "Sequestration in current wetlands" refers to carbon sequestration in extant wetlands; "oxidation in former wetlands" refers to emissions from wetlands that have been converted to non-wetland uses or conversion among wetland types due to human influence; "net carbon balance" is the sum of sequestration in current wetlands, oxidation in former wetlands, and plant carbon sequestration (see Table 3); "historical loss in sequestration capacity" refers to the loss in the carbon sequestration function of wetlands that have been converted to non-wetland uses; "change in flux from wetland conversions" is the sum of oxidation in former wetlands and historical loss in sequestration capacity. Positive flux numbers indicate a net flux a net flux into the ecosystem, whereas negative numbers indicate a net flux into the atmosphere. Based upon best professional judgment, the uncertainty categories are: ***** = actual value is within 10% of the estimate reported; **** = actual value is within 25%; *** = actual value is within 50%; ** = the actual value is within 100%; * = uncertainty > 100%.

	Permafrost peatlands	Non-permafrost peatlands	Freshwater mineral soil	Tidal Marsh	Mangrove	Mudflat	**Total**
Canada							
Pool Size in Current Wetlands	44.2[a****]	102.9[a****]	4.6[b**]	0.01[c***]	0[c*****]	0.10[d*]	151.8****
Sequestration in Current Wetlands	5.5[e***]	13.6[e***]	2.7[f*]	0.09[c**]	0[c*****]	1.21[d**]	23.0**
Oxidation in Former Wetlands	----------	-0.2[g**]	----------	0.0[h*]	0.0[i*]	0[*****]	0.0[*]	−0.2**
Net Carbon Balance	----------	18.9[***]	----------	2.7[*]	0.09[*]	0[*****]	1.21[**]	22.9**
Historical Loss in Sequestration Capacity	0.0[e****]	−0.2[e****]	−3.4[f*]	−0.17[*]	0[*****]	−0.33[*]	−4.2*
Change in Flux From Wetland Conversions	----------	−0.4[*****]	----------	−3.4[*]	−0.17[*]	0[*****]	−0.33[*]	−4.3*
Alaska							
Pool Size in Current Wetlands	9.3[j**]	6.2[j**]	26.0[k**]	0.025[***]	0[******]	0.13[***]	41.7**
Sequestration in Current Wetlands	1.2[e**]	0.8[e**]	9.4[f*]	0.29[**]	0[*****]	1.6[**]	13.3*
Oxidation in Former Wetlands	0.0[*****]	0.0[*****]	0.0[*****]	0.0[*****]	0[*****]	0.0[*****]	0.0*****
Net Carbon Balance	1.2[**]	0.8[**]	9.4[*]	0.29[**]	0[*****]	1.6[**]	13.3*
Historical Loss in Sequestration Capacity	0.0[*****]	0.0[*****]	0.0[*****]	−0.003[*****]	0[*****]	0.00[*****]	0.0*****
Change in Flux From Wetland Conversions	0.0[*****]	0.0[*****]	0.0[*****]	−0.003[*****]	0[*****]	0.00[*****]	0.0*****
Conterminous USA							
Pool Size in Current Wetlands	0[*****]	14.0[l***]	5.1[k****]	0.40[****]	0.061[*****]	0.046[******]	19.6***
Sequestration in Current Wetlands	0[*****]	6.6[m***]	5.3[f*]	4.4[**]	0.50[**]	0.51[**]	17.3*
Oxidation in Former Wetlands	0[*****]	−18.0[n**]	0.0[h**]	0.0[*]	0.0[*]	0.0[*]	−18.0**
Net Carbon Balance	0[*****]	−5.7[**]	9.8[*]	4.4[**]	0.50[**]	0.51[**]	9.5*
Historical Loss in Sequestration Capacity	0[*****]	−1.2[m***]	−7.6[f*]	−0.36[*]	−0.042[*]	−0.14[*]	−9.4*
Change in Flux From Wetland Conversions	0[*****]	−19.2[**]	−7.6[*]	−0.36[*]	−0.042[*]	−0.14[*]	−27.4*
Mexico							
Pool Size in Current Wetlands	0[*****]	1.5[l**]	0.3[k*]	0.0[*]	0.13[*]	ND	1.9*
Sequestration in Current Wetlands	0[*****]	1.6[o*]	0.4[f*]	0.0[*]	1.6[*]	ND	3.6*
Oxidation in Former Wetlands	0[*****]	ND	ND	0.0[*]	0.0[*]	0.0[*]	ND
Net Carbon Balance	0[*****]	1.6[*]	0.4[*]	0.0[*]	1.6[*]	0.0[*]	3.6*
Historical Loss in Sequestration Capacity	0[*****]	ND	ND	0.0[*]	−0.97[*]	ND	ND
Change in Flux From Wetland Conversions	0[*****]	ND	ND	0.0[*]	−0.97[*]	ND	ND
North America							
Pool Size in Current Wetlands	53.5[****]	124.6[****]	36.0[****]	0.44[***]	0.19[***]	0.28[***]	215****
Sequestration in Current Wetlands	6.6[***]	22.6[***]	17.7[*]	4.8[**]	2.1[*]	3.3[*]	57.2*

Table 2. Continued.

	Permafrost peatlands	Non-permafrost peatlands	Freshwater mineral soil	Tidal Marsh	Mangrove	Mudflat	**Total**
Oxidation in Former Wetlands	----------	−18.2**	0.0**	0.0*	0.0*	0.0*	−18.2**
Net Carbon Balance	----------	16.7**	22.3*	4.8**	2.1*	3.3*	49.2*
Historical Loss in Sequestration Capacity	0*****	−1.4***	−11.0*	−0.53*	−1.0*	−0.48*	−14.5*
Change in Flux From Wetland Conversions	----------	−19.6**	−11.0*	−0.53*	−1.0*	−0.48	−32.7*
Global							
Pool Size in Current Wetlands	----------	462p***	46q***	0.43r*	4.9r*	ND	513***
Sequestration in Current Wetlands	----------	55s***	39f*	4.6r*	38r*	ND	137*
Oxidation in Former Wetlands	----------	−205t***	ND	0*	0*	0*	−205**
Net Carbon Balance	----------	−150**	39*	4.6*	38*	ND	−68*
Historical Loss in Sequestration Capacity	----------	−16t**	−45f*	−0.69u*	−20v*	ND	−82*
Change in Flux From Wetland Conversions	----------	−221t***	> −45*	−0.69*	−20*	ND	−287*

[a] Tarnocai et al. (2005).
[b] Tarnocai (1998).
[c] Rates and pools calculated from Chmura (2003) using country-specific data (sedimentation accumulation rates in Mg C ha^{-1} yr^{-1}: Mexican mangroves = 3.3, conterminous U.S. mangroves = 1.8. conterminous tidal marshes = 2.2, tidal marshes in Canada and Alaska = 2.1); areas from Table 1.
[d] Assumed the same carbon density and accumulation rates as the adjacent vegetated wetland ecosystem (mangrove data for Mexico and salt marsh data elsewhere).
[e] Assumed carbon accumulation rate of 0.13 Mg C ha^{-1} yr^{-1} for permafrost peatlands and 0.19 Mg C ha^{-1} yr^{-1} for non-permafrost peatlands. Reported range of long-term apparent accumulation rates from 0.05–0.35 (Ovenden 1990, Maltby and Immirzi 1993, Trumbore and Harden 1997, Vitt et al. 2000, Turunen et al. 2004).
[f] Rate calculated as the geometric mean sediment accumulation rate of 2.2 Mg sediment ha^{-1} yr^{-1} (range 0–80) from Johnston (1991) and Craft and Casey (2000) times 7.7% C (CV = 109) (Batjes 1996).
[g] Sum of −0.24 Tg C yr^{-1} from horticulture removal of peat (Cleary et al. 2005) and 0.10 Tg C yr^{-1} from increased peat sequestration due to permafrost melting (Turetsky et al. 2002).
[h] Assumed that the net oxidation of 8.6% of the soil carbon pool (Euliss et al. 2006) over 50 yr after conversion to non-wetland use.
[i] Assumed that conversion of tidal systems is caused by fill and results in burial and preservation of SOM rather than oxidation.
[j] Soil carbon densities of 1,441 Mg C ha^{-1} for Histosols and 1,048 Mg C ha^{-1} for Histels (Tarnocai et al. 2005).
[k] Soil carbon density of 162 Mg C ha^{-1} for the conterminous U.S. and Mexico and 468 Mg C ha^{-1} for Alaska based upon NRCS STATSGO database and soil pedon information. See text.
[l] Assumed soil carbon density of 1,500 Mg C ha^{-1}. See text.
[m] Webb and Webb (1988). See text.
[n] Estimated loss rate as of early 1980s (Armentano and Menges 1986). Overall wetlands losses in the U.S. have declined dramatically since then (Dahl 2000) and probably even more so for Histosols, so this number may still be representative.
[o] Using peat accumulation rate of 1.6 Mg C ha^{-1} (range 1.0–2.25) (Maltby and Immirzi 1993).
[p] From Maltby and Immirzi (1993). Range of 234 to 679 Pg C (Gorham 1991, Maltby and Immirzi 1993, Eswaran et al. 1995, Batjes 1996, Lappalainen 1996, Joosten and Clarke 2002).
[q] Soil carbon density of 199 Mg C ha^{-1} (Batjes 1996).
[r] Chmura (2003).
[s] Joosten and Clarke reported range of 40 to 70 Tg C yr^{-1}. Using the peatland estimate in Table 13.1 and a C accumulation rate of 0.19 Mg C ha^{-1} yr^{-1}, we calculate a global flux of 65 Tg C yr^{-1} in peatlands.
[t] Current oxidative flux is the difference between the change in flux and the historical loss in sequestration capacity from this table. The change in flux is from Maltby and Immirzi (1993) (reported range −176 to −266 Tg C yr^{-1}) and the historical loss in sequestration capacity is from this table for N.A., from Armentano and Menges (1986) for other northern peatlands, and from Maltby and Immirzi (1993) for tropical peatlands.
[u] Assumed that global rates approximate the North America rate because most salt marshes inventoried are in NA.
[v] Assumed 25% loss globally since the late 1800s.

Peatland Soil Carbon Pools. The carbon pool of permafrost and non-permafrost peatlands in Canada had been previously estimated by Tarnocai et al. (2005) based upon an extensive database. Good soil carbon density data are unavailable for peatlands in the U.S., as the NRCS soil pedon information typically only goes to a maximum depth from 1.5 to 2 m, and many peatlands are deeper than this. Therefore, we used the carbon density estimates of Tarnocai et al. (2005) of 1,441 Mg C ha^{-1} for Histosols and 1,048 Mg C ha^{-1} for Histels to estimate the soil carbon pool in Alaskan peatlands.

The peatlands of the conterminous U.S. are different in texture (and probably depth) than those in Canada and Alaska, so it is probably inappropriate to use the soil carbon densities for Canadian peatlands for those in the conterminous U.S. For example, we compared the relative percentage of the Histosol suborders (excluding the small area of Folists, as they are predominantly terrestrial soils) for Canada (Tarnocai 1998), Alaska (updated STATSGO data, J. Moore), and the conterminous U.S. (NRCS 1999). The relative percentages of Fibrists, Hemists, and Saprists, respectively, in Canada are 37%, 62%, and 1%, in Alaska are 53%, 27%, and 20%, and in the conterminous U.S. are 1%, 19%, and 80%. Using the STATSGO database (N. Bliss, query of NRCS STATSGO database, Dec. 2005), the average soil carbon density for Histosols in the conterminous U.S. is 1,089 Mg C ha^{-1}, but this is an underestimate, as many peatlands were not sampled to their maximum depth. Armentano and Menges (1986) reported average carbon density of conterminous U.S. peatlands to 1-m depth of 1,147 to 1,125 Mg C ha^{-1}. Malterer (1996) gave soil carbon densities of conterminous U.S. peatlands of 2,902 Mg C ha^{-1} for Fibrist, 1,874 Mg C ha^{-1} for Hemists, and 2,740 Mg C ha^{-1} for Saprists, but it is unclear how he derived these estimates. Eswaran et al. (1995) and Batjes (1996) gave an average soil carbon densities to 1-m depth for global peatlands of 776 and 2,235 Mg C ha^{-1}, respectively. We chose to use an average carbon density of 1,500 Mg C ha^{-1}, which is in the middle of the reported range, for peatlands in the conterminous U.S. and Mexico.

Estuarine Soil Carbon Pools. Tidal wetland soil carbon density was based on a country-specific analysis of data reported in an extensive compilation by Chmura et al. (2003). There were more observations from the U.S. ($n = 75$) than from Canada ($n = 34$) or Mexico ($n = 4$), and consequently, there were more observations of marshes than mangroves. The Canadian salt marsh estimate was used for Alaskan salt marshes and mud flats. In the conterminous U.S. and Mexico, country-specific tidal marsh or mangrove estimates were used for mudflats. Although Chmura et al. (2003) reported some significant correlations between soil carbon density and mean annual temperature, scatter plots suggested that the relationships are weak or driven by a few sites. Thus, we used mean values for scaling and did not separate the data by region or latitude. Chmura et al. (2003) assumed a 50-cm-deep profile for the soil carbon pool, which may be an underestimate.

Plant Carbon Pools. While extensive data on plant biomass in individual wetlands have been published, no systematic inventory of wetland plant biomass has been undertaken in North America. Nationally, the forest carbon biomass pool (including above- and belowground biomass) has been estimated to be 54.9 Mg C ha^{-1} (Birdsey 1992), which we used for forested wetlands in the U.S. and Canada. This approach assumes that wetland forests do not have substantially different biomass carbon densities than terrestrial forests. There is one regional assessment of forested wetlands in the southeastern U.S., which comprise approximately 35% of the total forested wetland area in the conterminous U.S. We used the southeastern U.S. regional inventory to evaluate this assumption; aboveground tree biomass averaged 125.2 m^3 ha^{-1} for softwood stands and 116.1 m^3 ha^{-1} for hardwood stands. Using an average wood density and carbon content, the carbon density for these forests would be 33 Mg C ha^{-1} for softwood stands and 42 Mg C ha^{-1} for hardwood stands. However, these estimates do not include understory vegetation, belowground biomass, or dead trees, which account for 49% of the total forest biomass (Birdsey 1992). Using that factor to make an adjustment for total forest biomass, the range would be 49 to 66 Mg C ha^{-1} for the softwood and hardwood stands, respectively. Accordingly, the assumption of using 54.9 Mg C ha^{-1} seems reasonable for a national-level estimate.

The area of forested wetlands in Canada came from Tarnocai et al. (2005), in Alaska from Hall et al. (1994), and in the conterminous U.S. from Dahl (2000).

Since Tarnocai et al. (2005) divided Canadian peatland area into bog and fen, we used aboveground biomass for each community type from Vitt et al. (2000) and assumed that 50% of biomass is belowground. We used the average bog and fen plant biomass from Vitt et al. (2000) for Alaskan peatlands. For other wetland areas, we used an

average value of 20.0 Mg C ha^{-1} for non-forested wetland biomass carbon density (Gorham 1991).

Tidal marsh root and shoot biomass data were estimated from a compilation in Mitsch and Gosselink (Table 8–7, 1993). There was no clear latitudinal or regional pattern in biomass, so we used mean values for each. Mangrove biomass has been shown to vary with latitude, so we used the empirical relationship from Twilley et al. (1992) for this relationship. We made a simple estimate using a single latitude that visually bisected the distribution of mangroves either in the U.S. (26.9°) or Mexico (23.5°). Total biomass was estimated using a root to shoot ratio of 0.82 and a carbon mass to biomass ratio of 0.45, both from Twilley et al. (1992).

Net Carbon Fluxes

For all subsequent analyses, positive carbon fluxes indicate net fluxes into an ecosystem, whereas negative carbon fluxes indicate net fluxes to the atmosphere.

Peatland Soil Carbon Accumulation Rates. Most studies report the long-term apparent rate of carbon accumulation (LORCA) in peatlands based upon basal peat dates, but this assumes a linear accumulation rate through time. However, due to the slow decay of the accumulated peat, the true rate of carbon accumulation will always be less than the LORCA (Clymo et al. 1998), so most reported rates are inherently biased upwards. Tolonen and Turunen (1996) found that the true rate of peat accumulation was about 67% of the LORCA, but given the uncertain nature of these calculations, we have not incorporated them into our estimates.

For estimates of soil carbon sequestration in conterminous U.S. peatlands, we used the LORCA data from 82 sites and 215 cores throughout eastern North America (Webb and Webb III 1988). They reported a median vertical peat accumulation rate of 0.066 cm yr^{-1} (arithmetic mean = 0.092, sd = 0.085). To convert this value into a carbon accumulation rate, we determined an area-weighted and depth-weighted average bulk density (0.28 g cm^{-3}) and organic matter content (69%) from all Histosol soil map units greater than 202.5 ha (n = 3,8843) in the conterminous U.S. from the National Soil Information System (NASIS) database provided by S. Campbell (USDA NRCS, Portland, OR). As mentioned above, 80% of the peatlands in the conterminous U.S. are classified as Saprists (NRCS 1999), and this is reflected in their high bulk density and low organic matter content. We further assumed that organic matter is composed of 58% carbon (NRCS Soil Survey Laboratory Information Manual, http://soils.usda.gov/survey/nscd/lim/). We calculated an average carbon accumulation rate of 0.71 Mg C ha^{-1} yr^{-1} for peatlands in the conterminous U.S. For comparison, Armentano and Menges (1986) used soil carbon accumulation rates that ranged from 0.48 Mg C ha^{-1} yr^{-1} in northern conterminous U.S. peatlands to 2.25 Mg C ha^{-1} yr^{-1} in Florida peatlands.

Peatlands accumulate less soil carbon at higher latitudes, with especially low accumulation rates in permafrost peatlands (Ovenden 1990, Robinson and Moore 1999). The rates used in this paper reflect this gradient, ranging from 0.13 to 0.19 to 0.71 Mg C ha^{-1} yr^{-1} in permafrost peatlands, non-permafrost Canadian and Alaskan peatlands, and peatlands in the conterminous U.S. and Mexico, respectively (Table 2).

Freshwater Mineral-Soil Wetland Carbon Accumulation Rates. Many studies have estimated sediment deposition rates in FWMS wetlands, with a geometric mean rate of 2.2 Mg sediment ha^{-1} yr^{-1} (n = 26, arithmetic mean = 16.3, range 0 to 80.0) in a compilation by Johnston (1991), along with those reported more recently in Craft and Casey (2000). As can be seen by the difference between the geometric and arithmetic means, this dataset is log-normally distributed with several large outliers. Assuming 7.7% carbon for FWMS wetlands (Batjes 1996), this gives a geometric mean accumulation rate of 0.17 Mg C ha^{-1} yr^{-1}. Johnston (1991) and Craft and Casey (2000) reported more studies with only vertical sediment accumulation rates, with a geometric mean of 0.23 cm yr^{-1} (n = 34, arithmetic mean = 0.63 cm yr^{-1}, range −0.6 to 2.6). If we assume a bulk density of 1.00 g cm^{-3} for FWMS wetlands (Batjes 1996, Smith et al. 2001), this converts into an unrealistically large accumulation rate of 1.85 Mg C ha^{-1} yr^{-1}.

We suggest that caution is necessary in interpretation of these data for a number of reasons. There is large variability in sedimentation rates among studies, and even within a site, sedimentation rates are highly variable depending on the local deposition environment (Johnston et al. 2001). Researchers may have preferentially chosen wetlands with high sedimentation rates to study this process, providing a bias towards greater carbon sequestration. Rates of erosion and resultant deposition have substantially decreased during the last century in the conterminous U.S. (Craft and Casey 2000, Trimble and Crosson 2000). More fundamentally, it is important to distinguish between autochthonous carbon

(derived from on-site plant production) and allochthonous carbon (imported from outside the wetland) in soil carbon storage. The soil carbon stored in peatlands is of autochthonous origin and represents sequestration of atmospheric CO_2 at the landscape scale. In contrast, a unknown portion of the soil carbon that is stored in FWMS wetlands is of allochthonous origin. However, conterminous U.S. soils average between 0.9 and 1.3% soil carbon, which is much less than the average carbon content of FWMS wetlands (7.7%) (Batjes 1996), suggesting a substantial autochthonous input to FWMS wetlands.

At a landscape scale, redistribution of sediments from uplands to wetlands represents net carbon sequestration only to the extent that the soil carbon is replaced in the terrestrial source area and/or decomposition rates are substantially lower in the receiving wetland (Stallard 1998, Harden et al. 1999). Agricultural lands are a major source of erosion (Meade et al. 1990, as cited in Stallard 1998), but it appears that, after large initial losses, soil carbon is relatively stable (Stallard 1998, Smith et al. 2001) or even increases (Harden et al. 1999) under modern agricultural techniques. It is also generally assumed that sediment carbon deposited in anaerobic environments, such as occur in many wetlands, is relatively recalcitrant (Stallard 1998, Smith et al. 2001). For example, in a variety of Minnesota wetland soils, carbon mineralization was approximately six times slower anaerobically than aerobically (Bridgham et al. 1998). However, time since initial deposition and organic quality of sediments appears to be an important constraint on its relative reactivity. Kristensen et al. (1995) found that relatively fresh, labile organic matter had similar decomposition rates aerobically and anaerobically, whereas 'aged,' recalcitrant organic matter decomposed ten times slower anaerobically. Gunnison et al. (1983) found that freshly flooded soils had twice as rapid carbon mineralization rates as sediments. In newly constructed reservoirs, sediments maintained these rapid mineralization rates even 6–10 years after initial flooding. Overall, these latter two studies suggest that there may be substantial carbon mineralization in freshly deposited allochthonous sediments in wetlands, but we feel that the data are not adequate to account for this effect quantitatively.

We use a landscape-level sediment sequestration rate of 0.17 Mg C ha^{-1} yr^{-1} for FWMS wetlands in North America, while acknowledging that the low level of confidence in this estimate. Johnston (1991) and Craft and Casey (2000) only gave sedimentation rates in FWMS wetlands in the conterminous U.S. Since most FWMS wetlands in Canada are in more developed and agricultural regions, we felt that it was reasonable to use the sedimentation estimates from these studies. However, most Alaskan FWMS wetlands are relatively pristine, with little anthropogenic sediment input, but as described above, most have an extensive histic epipedon, so at least historically, they have actively accumulated soil carbon. Given that our soil carbon accumulation rate for Alaskan peatlands is 0.19 Mg C ha^{-1} yr^{-1}, our sediment sequestration rate of 0.17 Mg C ha^{-1} yr^{-1} for Alaskan FWMS wetlands does not seem unreasonable.

Estuarine Soil Carbon Accumulation Rates. An important difference between soil carbon sequestration in tidal and non-tidal systems is that sequestration in tidal wetlands occurs primarily through burial driven by sea-level rise (Chmura et al. 2003, Hussein et al. 2004). For this reason, carbon accumulation rates can be estimated well with data on changes in soil surface elevation and carbon density. Rates of soil carbon accumulation were calculated using data from Chmura et al. (2003) separated by country as described above for the soil carbon pool (rates in Mg C ha^{-1} yr^{-1} are 3.3 for Mexican mangroves; 1.8 and 2.2 for mangroves and tidal marshes, respectively, in the conterminous U.S.; 2.1 for tidal marshes in Canada and Alaska). These estimates were based on a variety of methods including ^{137}Cs dating, ^{210}Pb dating, and accumulation above a marker horizon, which integrate vertical soil accumulation rates over periods of time ranging from 1–100 years. The soil carbon sequestered in estuarine wetland sediments is likely to be a mixture of both allochthonous and autochthonous sources. However, without better information, we assumed that *in situ* rates of soil carbon sequestration in estuarine wetlands is representative of the true landscape-level rate.

Plant Biomass Accumulation Rates. For ecosystems at approximately steady state, plant biomass should be reasonably constant on average because plant production is roughly balanced by mortality and subsequent decomposition. We assumed insignificant plant biomass accumulation in freshwater and estuarine marshes because they are dominated by herbaceous plants that do not accumulate carbon in wood. Sequestration in plants in relatively undisturbed forested wetlands in Alaska and many parts of Canada is probably small, although there may be substantial logging of Canadian forested wetlands for which we do not have data. Similarly, no data were available to evaluate the effect on carbon

fluxes of harvesting of woody biomass in Mexican mangroves.

Tree biomass carbon sequestration averages 1.40 Mg C ha^{-1} yr^{-1} in U.S. forests across all forest types (Birdsey 1992). Using the tree growth estimates from the southeastern U.S. regional assessment of wetland forests (Brown et al. 2001) yields a lower estimate of sequestration in aboveground tree biomass ($\sim$ 0.50 Mg C ha^{-1} yr^{-1}). We have used this lower value and area estimates from Dahl (2000) to estimate for carbon sequestration in the forested wetlands of the conterminous U.S.

Methane and Nitrous Oxide Fluxes

Moore and Roulet (1995) reported a range of fluxes from 0 to 130 g CH_4 m^{-2} yr^{-1} from 120 peatland sites in Canada, with the majority emitting $<$ 10 g CH_4 m^{-2} yr^{-1}. They estimated a low average flux rate of 2 to 3 g CH_4 m^{-2} yr^{-1}, which extrapolated to an emission of 2–3 Tg CH_4 yr^{-1} from Canadian peatlands. We used an estimate of 2.5 g CH_4 m^{-2} yr^{-1} for Canadian peatlands and Alaskan freshwater wetlands. However, lack of adequate sampling of CH_4 emitted from permafrost thaw lakes may have substantially underestimated CH_4 emissions from arctic wetlands (Walter et al. 2006).

To our knowledge, the last synthesis of field measurements of CH_4 emissions from North American wetlands was done by Bartlett and Harriss (1993). We supplemented their analysis with all other published field studies (using chamber or eddy covariance techniques) we could find that reported annual or average daily CH_4 fluxes in the conterminous U.S. (Figure 1, Appendix 1). We excluded a few studies that used cores or estimated diffusive fluxes. In cases where multiple years from the same site were presented, we took the average of those years. Similarly, when multiple sites of the same type were presented in the same paper, we took the average. Studies were separated into freshwater and estuarine wetlands.

In cases where papers presented both an annual flux and a mean daily flux, we calculated a conversion factor (annual flux / average daily flux) to quantify the relationship between those two numbers (Appendix 1). When we looked at all studies (n = 30), this conversion factor was 0.36, suggesting that there is a 360-day emission season. There was surprisingly little variation in this ratio, and it was similar in freshwater (0.36) and estuarine (0.34) wetlands. In contrast, previous syntheses used a 150-day emission season for temperate wetlands (Matthews and Fung 1987, Bartlett and Harriss 1993). While substantial winter CH_4 emissions have been found in some studies, it is likely that flux data from most studies have a non-normal distribution, with occasional periods of high flux rates that are better captured with annual measurements.

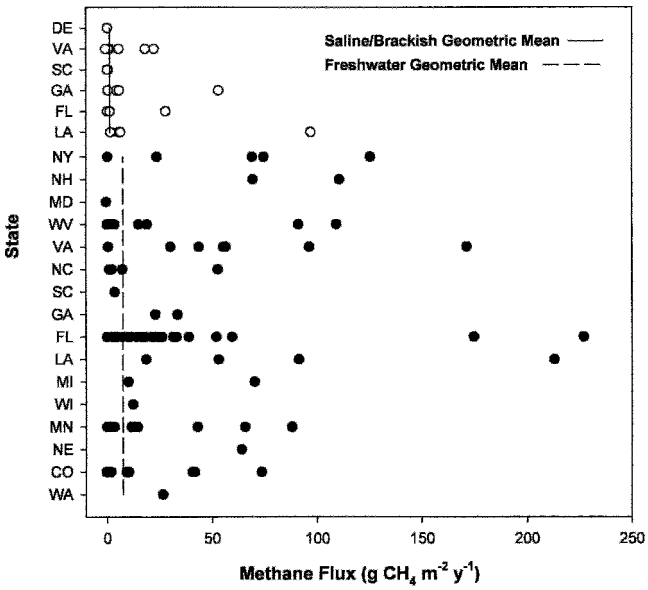

Figure 1. Methane fluxes from wetlands in the conterminous U.S. sorted by state and freshwater (FW, closed circles) and saline/brackish (SW, open circles). References are in Appendix 1.

Using the conversion factors for freshwater and estuarine wetlands, we estimated average annual emissions from the average daily fluxes. The data were highly log-normally distributed, so we used geometric means. For freshwater wetlands, the geometric mean estimated annual flux rate was 7.1 g CH_4 m^{-2} yr^{-1} (n = 74, 1 SE = 2.2, arithmetic mean = 38.6), which is very similar to the geometric mean measured rate of 8.1 g CH_4 m^{-2} yr^{-1} (n = 32, arithmetic mean = 32.1). For estuarine wetlands, the geometric mean estimated annual flux rate was 1.3 g CH_4 m^{-2} yr^{-1} (n = 25, 1 SE = 3.3, arithmetic mean = 9.8), which is smaller than the geometric mean measured rate of 5.0 g CH_4 m^{-2} yr^{-1} (n = 13, arithmetic mean = 16.9).

Finally, we combined both approaches. In cases where a paper presented an annual measured value, we used that number. In cases where only an average daily number was presented, we used that value corrected with the appropriate conversion factor. For conterminous U.S. wetlands, FWMS Canadian wetlands, and Mexican wetlands, we used a geometric mean flux of 7.6 g CH_4 m^{-2} yr^{-1}, and for estuarine wetlands, we used a geometric mean flux of 1.3 g CH_4 m^{-2} yr^{-1} (Figure 1).

When we multiplied the very low published estimates of nitrous oxide emissions from natural and

disturbed wetlands (Joosten and Clarke 2002) by North American wetland area, the flux was insignificant (data not shown). However, nitrous oxide emissions have been measured in few wetlands, particularly in FWMS wetlands and wetlands with high nitrogen inputs (e.g., from agricultural run-off), where emissions might be expected to be higher.

RESULTS AND DISCUSSION

Current Wetland Area and Rates of Loss

The conterminous U.S. has 312,000 km^2 of FWMS wetlands, 93,000 km^2 of peatlands, and 25,000 km^2 of estuarine wetlands, which encompass 5.5% of the land area (Table 1). This represents just 48% of the original wetland area in the conterminous U.S. However, wetland losses in the U.S. decreased from 1,855 $km^2\ yr^{-1}$ in the 1950s to 1970s, to 1,175 $km^2\ yr^{-1}$ in the 1970s and 1980s, to 237 $km^2\ yr^{-1}$ in the 1980s and 1990s (Dahl 2000). Such data mask large differences in loss rates among wetland classes and conversion of wetlands to other classes (Dahl 2000), with potentially large effects on carbon stocks and fluxes. For example, the majority of wetland losses in the U.S. have occurred in FWMS wetlands. As of the early 1980s, 84% of U.S. peatlands were unaltered (Armentano and Menges 1986, Maltby and Immirzi 1993), and given the current regulatory environment in the U.S., recent rates of loss are likely small.

The areas of peatlands (132,000 km^2) and FWMS wetlands (556,000 km^2) in Alaska exceed those in the conterminous U.S. by 42% and 78%, respectively (Table 1). The area of estuarine wetland in Alaska is about three-times less than the conterminous U.S., and about 80% of the Alaskan area is mud flat versus less than 10% in the conterminous U.S.

Canada has 1,301,000 km^2 of wetlands, covering 14% of the land area, of which 87% are peatlands (Table 1). Although the area of mud flat in Canada is highly uncertain, it appears that, as in Alaska, Canadian estuarine wetlands are dominated by mud flats. Canada has lost about 14% of its wetlands, mainly due to agricultural development of FWMS wetlands (Rubec 1996), although the ability to estimate wetland losses in Canada is limited by the lack of a regular wetland inventory.

We estimate that Mexico has 36,000 km^2 of wetlands, with an estimated historical loss of 16,000 km^2 (Table 1). However, given the lack of a nationwide wetland inventory and a general paucity of data, this number is highly uncertain.

Problems with inadequate wetland inventories are even more prevalent in lesser developed countries (Finlayson et al. 1999). We estimate a global wetland area of 6.0×10^6 km^2 (Table 1); thus, North America currently has about 43% of global wetland area. It has been estimated that about 50% of the world's original wetlands have been converted to other uses (Moser et al. 1996).

Carbon Pools

We estimate that North American wetlands have a current soil and plant carbon pool of 220 Pg, which is a substantial proportion of the global wetland carbon pool of 529 Pg C (Tables 2 and 3). Approximately 98% of the carbon in North American wetlands resides in the soil. Peatlands contain 83% of this soil carbon, with by far the largest amount in Canadian peatlands (147 Pg C). The importance of our using a smaller area of Alaskan peatlands than previous estimates becomes obvious here. Using the larger area from Kivinen and Pakarinen (1981), Halsey et al. (2000) estimated that Alaskan peatlands have a soil carbon pool of 71.5 Pg, almost five-fold higher than our estimate of 15.5 Pg (Table 2). However, some of the difference in soil carbon between the two estimates can be accounted for by the 26 Pg C that we calculated resides in Alaskan FWMS wetlands (Table 2). This represents 72% of the soil carbon in North American FWMS wetlands, and this substantial soil carbon pool had not been identified in previous studies. Despite high soil carbon concentrations, estuarine wetlands contain a relatively small soil carbon pool of about 1 Pg because of their small area (Table 2).

The data were inadequate to distinguish between plant carbon pools in peatlands and FWMS wetlands, but most plant biomass probably resides in forested wetlands.

Carbon Fluxes

Peatlands. Intact North American peatlands currently sequester 29 Tg C yr^{-1} (Table 2), with the large area of Canadian peatlands dominating this estimate even after considering the relatively high peat accumulation rates of lower latitude peatlands. However, this carbon sink is partially offset by a net oxidative flux of -18 Tg C yr^{-1} as of the early 1980s in peatlands in the conterminous U.S. that have been drained for agriculture and forestry (Armentano and Menges 1986). Despite a substantial reduction in the rate of wetland loss since the 1980s (Dahl 2000), drained organic soils continue to lose carbon over many decades, so the actual flux to the atmosphere is probably close to the 1980s estimate. There

Table 3. Plant carbon pools (Pg) and fluxes (Tg yr^{-1}) of wetlands in North America and the world. Positive flux numbers indicate a net flux a net flux into the ecosystem, whereas negative numbers indicate a net flux into the atmosphere. Based upon best professional judgment, the uncertainty categories are: ***** = 95% certain that the actual value is within 10% of the estimate reported; **** = 95% certain that the actual value is within 25%; *** = 95% certain that the actual value is within 50%; ** = 95% certain that the actual value is within 100%; * = uncertainty > 100%.

	Permafrost peatlands	Non-permafrost peatlands	Freshwater mineral soil	Tidal marsh	Mangrove	**Total**
Canada						
Pool Size in Current Wetlands	----------	1.4[a]** ----------	0.3[b]**	0.001[c]***	0.0*****	1.7**
Sequestration in Current Wetlands	0.0***	---------- ND ----------		0.0***	0.0*****	0.0***
Alaska						
Pool Size in Current Wetlands	----------	0.4[a]** ----------	1.1[d]**	0.002***	0.0*****	1.5**
Sequestration in Current Wetlands	0.0***	0.0***	0.0***	0.0***	0.0*****	0.0***
Conterminous USA						
Pool Size in Current Wetlands	0.0*****	---------- 1.5[d]*** ----------		0.034***	0.024***	1.5***
Sequestration in Current Wetlands	0.0*****	---------- 10.3[e]** ----------		0.0***	0.0***	10.3**
Mexico						
Pool Size in Current Wetlands	0.0*****	0.0[b]*	0.0[b]*	0.0*	0.051*	0.1*
Sequestration in Current Wetlands	0.0*****	ND	ND	0.0*	ND	0.0*
North America						
Pool Size in Current Wetlands	----------	4.8** ----------		0.037***	0.074*	4.9**
Sequestration in Current Wetlands	0.0***	---------- 10.3** ----------		0.0***	ND	10.3**
Global						
Pool Size in Current Wetlands	----------	6.9[b]** ----------	4.6[b]*	0.007[f]**	4.0[g]**	15.5**
Sequestration in Current Wetlands	0.0***	ND	ND	0.0*	ND	ND

[a] Biomass for non-forested peatlands from Vitt et al. (2000), assuming 50% of biomass is belowground. Forest biomass density from Birdsey (1992), and forested area from Tarnocai et al. (2005) for Canada and from Hall et al. (1994) for Alaska.
[b] Assumed 2000 g C m^{-2} in above- and belowground plant biomass (Gorham 1991).
[c] Biomass data from Mitsch and Gosselink (1993).
[d] Biomass for non-forested wetlands from Gorham. Forest biomass density from Birdsey (1992), and forested area from Hall et al. (1994) for Alaska and Dahl (2000) for the conterminous U.S.
[e] 50 g C m^{-2} yr^{-1} sequestration from forest growth from a southeastern U.S. regional assessment of wetland forest growth (Brown et al. 2001).
[f] Assumed that global pools approximate those from North America because most salt marshes inventoried are in NA.
[g] Twilley et al. (1992).

has also been a loss in sequestration capacity in drained peatlands in the conterminous U.S. of −1.2 Tg C yr^{-1} (Table 2), so the overall soil carbon sink of conterminous U.S. peatlands is about 19 Tg C yr^{-1} smaller than it would have been in the absence of disturbance. This is partially offset by the sequestration of 10 Tg C yr^{-1} in forested wetlands in the conterminous U.S. due to regeneration after logging (Table 3).

Limited peatland areas have been lost in Alaska and Canada. However, we considered extractive uses of peat in both Canada and the U.S., which have been incorporated into the oxidation estimates in Table 2. Use of peat for energy production is, and always has been, negligible in North America, as opposed to other parts of the world (WEC 2001). However, Canada produces a greater volume of horticultural and agricultural peat than any other country in the world (WEC 2001). Currently, 124 km^2 of Canadian peatlands have been under extraction now or in the past, and as of 1990, Canada emitted 0.24 Tg yr^{-1} of CO_2-C equivalents through peat extraction (Cleary et al. 2005). The U.S. production of horticultural peat is about 19% of Canada's (Joosten and Clarke 2002), which assuming a similar life-cycle as for Canada, suggests that the U.S. produces 0.05 Tg yr^{-1} of CO_2-C equivalents through peat extraction.

Freshwater Mineral-Soil Wetlands. Very little attention has been given to the role of FWMS wetlands in North American or global carbon balance estimates, with the exception of CH_4 emissions. Carbon sequestration associated with sediment deposition is a potentially large, but poorly quantified, flux in wetlands (Stallard 1998, Smith et al. 2001). We estimate that North American FWMS wetlands sequester 18 Tg C yr^{-1} in sedimentation (Table 2).

However, as discussed in the Methods, wetland sedimentation rates are extremely variable. Moreover, almost no studies have placed sediment carbon sequestration in FWMS wetlands in a landscape context, considering allochthonous- versus autochthonous-derived carbon, replacement of carbon in terrestrial source areas, and differences in decomposition rates between sink and source areas (Stallard 1998, Harden et al. 1999, Smith et al. 2001). However, it is clear that sedimentation in FWMS wetlands is a potentially substantial carbon sink and an important unknown in carbon budgets. For example, agriculture typically increases sedimentation rates by 10- to 100-fold, and 90% of sediments are stored within the watershed, amounting to about 40 Tg C yr^{-1} in the conterminous U.S. (Stallard 1998, Smith et al. 2001). Our estimate of sediment carbon sequestration in FWMS wetlands seems quite reasonable in comparison to within-watershed sediment storage in North America. Moreover, Stallard (1998) and Smith et al. (2001) estimated a global sediment sink on the order of 1 Pg C yr^{-1}.

Decomposition of soil carbon in FWMS wetlands that have been converted to other land uses appears to be responsible for only a negligible loss of soil carbon currently (Table 2). However, due to the historical loss of FWMS wetland area, we estimate that they currently sequester 11 Tg C yr^{-1} less than they did prior to disturbance (Table 2). This estimate has the same unknowns associated with our estimate of soil carbon sequestration via sedimentation in extant FWMS wetlands.

Estuarine Wetlands. We estimate that North American estuarine wetlands currently sequester 10.2 Tg C yr^{-1}, with a historical reduction in sequestration capacity of 2.0 Tg C yr^{-1} due to loss of area (Table 2). However, the reduction is almost certainly greater because our 'original' area is only from the 1950s. Estuarine wetlands sequester carbon at a rate about 10-folder higher on an area basis than other wetland ecosystems due to high sedimentation rates, high soil carbon content, and constant burial due to sea level rise. Estimates of sediment deposition rates in estuarine wetlands are reasonably robust, but the same 'landscape' issues of allochthonous versus autochthonous inputs of carbon, replenishment of carbon in source area soils, and differences in decomposition rates between sink and source areas exist as for FWMS wetlands. Another large uncertainty in the estuarine carbon budget is the area and carbon content of mud flats, particularly in Canada and Mexico.

Carbon Flux Summary. Overall, North American wetland soils appear to be a moderate carbon sink of 49 Tg C yr^{-1} (Table 2). However, the uncertainty in this estimate is greater than 100%, largely because of the uncertainly in carbon sequestration in sedimentation. We estimate that North American peatlands currently have a net carbon balance of about 17 Tg C yr^{-1} (Table 2). Although there is large uncertainty in this estimate, the sequestration of carbon in the soils of intact peatlands and the oxidation of carbon from drained peatlands is a robust generalization. Despite the relatively small area of estuarine wetlands, they currently contribute about 31% of the net wetland carbon sequestration in the conterminous U.S. and about 21% of the North American total.

The large-scale conversion of wetlands to terrestrial uses has led to a reduction in the wetland soil carbon sink strength of 15 Tg C yr^{-1} from the estimated original rate (Table 2), but this estimate is driven by large losses of FWMS wetlands with their highly uncertain sedimentation carbon sequestration rate. Adding in the current net oxidative flux from drained conterminous U.S. peatlands (-18 Tg C yr^{-1}), we estimate that North American wetlands currently sequester 33 Tg C yr^{-1} less than they did originally (Table 2). Furthermore, we estimate that North American peatlands and FWMS wetlands have lost 2.6 Pg and 0.8 Pg of soil carbon, respectively, and collectively, they have lost 2.4 Pg of plant carbon. Very little data exist to estimate carbon fluxes for freshwater Mexican wetlands, but because of their small area, they will not likely have a large impact on the overall North American estimates.

The global wetland soil carbon balance has only been examined previously in peatlands (Table 2). They currently sequester 40 to 70 Tg C yr^{-1} in intact peatlands (Joosten and Clarke 2002) but have an oxidative flux of -160 to -250 Tg C yr^{-1}, due primarily to peatlands drained for agriculture and forestry and secondarily due to peat combustion for fuel (Armentano and Menges 1986, Maltby and Immirzi 1993). Thus, globally, peatlands may be a moderate atmospheric source of carbon of about -150 Tg yr^{-1} (Table 2). If one considers the historical loss of sequestration capacity, we estimate that human disturbance of global peatlands has caused an increased flux to the atmosphere of -176 to -266 Tg C yr^{-1} (Table 2). The cumulative historical loss in soil carbon stocks has been estimated to be 5.5 to 7.1 Pg C (Maltby and Immirzi 1993).

Although we are aware of no previous evaluation of the carbon balance of global FWMS and estuarine wetlands, using the assumption noted above, we estimate that they are a sink of approximately 39 Tg C yr^{-1}.

Table 4. Methane fluxes (Tg CH_4 yr^{-1}) from wetlands in North America and the world. Based upon best professional judgment, the uncertainty categories are: ***** = 95% certain that the actual value is within 10% of the estimate reported; **** = 95% certain that the actual value is within 25%; *** = 95% certain that the actual value is within 50%; ** = 95% certain that the actual value is within 100%; * = uncertainty > 100%.

	Permafrost peatlands	Non-permafrost peatlands	Freshwater mineral soil	Tidal marsh	Mangrove	Mudflat	**Total**
Canada							
CH_4 Flux from Current Wetlands	1.1[a]***	2.1[b]***	1.2*	0.000***	0.0*****	0.008[c]*	4.4*
Historical change in CH_4 Flux	0.0****	0.3**	−1.5*	−0.001**	0.0*****	0.001**	−1.2*
Alaska							
CH_4 Flux from Current Wetlands	0.2**	0.1**	1.4*	0.002***	0.0*****	0.009**	1.7*
Historical change in CH_4 Flux	0.0****	0.0****	0.0****	0.000****	0.0*****	0.000****	0.0****
Conterminous USA							
CH_4 Flux from Current Wetlands	0.0*****	0.7**	2.4**	0.026***	0.004***	0.003**	3.1**
Historical change in CH_4 Flux	0.0*****	−0.1*	−3.4*	−0.002***	−0.001***	0.022**	−3.5*
Mexico							
CH_4 Flux from Current Wetlands	0.0*****	0.1*	0.2*	0.0*	0.007*	ND	0.2*
Historical change in CH_4 Flux	0.0*****	---------- −0.1* ----------		0.0*	−0.003*	ND	−0.1*
North America							
CH_4 Flux from Current Wetlands	1.3***	3.0**	5.1**	0.028***	0.011***	0.020**	9.4**
Historical change in CH_4 Flux	0.0****	---------- −4.9* ----------		−0.003***	−0.004*	−0.002**	−4.9*
Global							
CH_4 Flux from Current Wetlands	14.1**	22.5[d]**	68.0[d]**	0.028[e]***	0.20*	ND	105[f]***
Historical change in CH_4 Flux	----------	−3.6[g]** ----------	−79[g]*	−0.009[e]*	−0.13*	ND	−83*

[a] Used CH_4 flux of 2.5 g m^{-2} yr^{-1} (range 0 to 130, likely mean 2 to 3) (Moore and Roulet 1995) for Canadian peatlands and all Alaskan freshwater wetlands. Used CH_4 flux of 7.6 g m^{-2} yr^{-1} for Canadian freshwater mineral-soil wetlands and all U.S. and Mexican freshwater wetlands and 1.3 g m^{-2} yr^{-1} for estuarine wetlands–from synthesis of published CH_4 fluxes for the U.S., see Appendix.
[b] Includes a 17-fold increase in CH_4 flux (Kelly et al. 1997) in the 9000 km^2 of reservoirs that have been formed on peatlands (Rubec 1996). and an estimated CH_4 flux of 15 g m^{-2} yr^{-1} (Moore et al. 1998) from 2,630 km^2 of melted permafrost peatlands (Vitt et al. 1994).
[c] Assumed trace gas fluxes from unvegetated estuarine wetlands (i.e. mudflats) was the same as adjacent wetlands.
[d] Bartlett and Harriss (1993).
[e] Assumed that global rates approximate the North America rate because most salt marshes area is in NA.
[f] Ehhalt et al. (2001) gave range of 92 to 237 Tg yr^{-1}.
[g] Using rates from Bartlett and Harriss (1993) and historical loss of area in Table 1.

Methane Emissions

We estimate that North American wetlands emit 9.4 Tg CH_4 yr^{-1} (Table 4). For comparison, a mechanistic CH_4 model yielded emissions of 3.8 and 7.1 Tg CH_4 yr^{-1} for Alaska and Canada (Zhuang et al. 2004), respectively. A regional inverse atmospheric modeling approach estimated total CH_4 emissions (i.e., from all sources) of 16 and 54 Tg CH_4 yr^{-1} for boreal and temperate North America, respectively (Fletcher et al. 2004b).

Methane emissions are currently about 5 Tg CH_4 yr^{-1} less than they were originally in North American wetlands (Table 4) because of the loss of wetland area. We do not consider the effects of conversion of wetlands from one type to another (Dahl 2000), which may have a significant impact on CH_4 emissions. Similarly, we estimate that global CH_4 emissions from natural wetlands are only about half of what they were originally due to loss of area (Table 4). However, this may be an overestimate because wetland losses have been higher in more developed countries than less-developed countries (Moser et al. 1996), and wetlands at lower latitudes have higher emissions on average (Bartlett and Harriss 1993, Fletcher et al. 2004a).

Net Global Warming Potentials

We use global warming potentials (GWPs) as a convenient way to compare the relative contributions of CO_2 and CH_4 fluxes in North American wetlands to the Earth's radiative balance. Many authors have used GWPs as a convenient means to compare the effects of different greenhouse gases on the Earth's radiative balance. The GWP is the radiative effect of a pulse of a substance into the atmosphere relative to CO_2 over a particular time horizon (Ramaswamy et al. 2001). However, it is important to distinguish between *radiative balance*,

which refers to the static radiative effect of a substance, and *radiative forcing*, which refers to an externally imposed perturbation on the Earth's radiative energy budget (Ramaswamy et al. 2001). Thus, changes in radiative balance lead to a radiative forcing, which subsequently leads to a change in the Earth's surface temperature. For example, wetlands have a large effect on the Earth's radiative balance through high CH_4 emissions, but it is only to the extent that emissions change through time that they represent a positive or negative radiative forcing and impact climate change.

We converted the GWPs provided by Ramaswamy et al. (2001) into CO_2-C equivalents so that the net carbon balance (Table 2) and CH_4 flux (Table 4) could be compared directly by multiplying CH_4 fluxes by the GWPs. The result was GWPs for CH_4 of 1.9, 6.3, and 16.9 CO_2-C equivalents on a mass basis across 500-year, 100-year, and 20-year time frames, respectively. Given a 100-year time frame, we estimate that North American peatlands, FWMS wetlands, and estuarine wetlands have *net radiative balances* of -10, -10, and $+10$ Tg CO_2-C yr^{-1}, respectively (for a N.A. total of -10 Tg CO_2-C yr^{-1}), which given the errors in our estimates is probably not significantly different than zero (note that we discuss *net radiative forcing* in the next section). The exception is estuarine wetlands, which are likely a net sink for CO_2-C equivalents because they support both rapid rates of carbon sequestration and low CH_4 emissions. Caution should be exercised in using GWPs because they are based upon a pulse of a gas into the atmosphere, whereas carbon sequestration is more or less continuous. For example, if one considers continuous CH_4 emissions and carbon sequestration in peat over time, most peatlands are a net sink for CO_2-C equivalents because of the long life-time of CO_2 sequestered as peat (Frolking et al. 2006).

Trends and Drivers of Wetland Carbon Fluxes

While extensive research has been done on carbon cycling and pools in North American wetlands, to our knowledge, this is the first attempt at an overall carbon balance for all of the wetlands of North America, although others have examined the carbon balance for North American peatlands as part of global assessments (Armentano and Menges 1986, Maltby and Immirzi 1993). Historically, the destruction of North American wetlands through land-use change has had the largest effect on carbon fluxes and, consequently, the radiative forcing of North American wetlands. The primary effects have been a reduction in their ability to sequester carbon (a small to moderate increase in radiative forcing depending on carbon sequestration by sedimentation in FWMS and estuarine wetlands), oxidation of their soil carbon reserves upon drainage (a small increase in radiative forcing), and a reduction in CH_4 emissions (a small to large decrease in radiative forcing depending on actual CH_4 emissions). Using the change in fluxes from wetland conversions in Tables 2–4 and a 100-year time frame for the CH_4 GWP, the overall effect in North America has been a reduction in *net radiative forcing*, or net cooling, of 8.5 Tg CO_2-C equivalents yr^{-1} (loss in sequestration capacity = -14.5, oxidation flux = -18.2, change in plant flux = 10.3, decrease in CH_4 flux = 30.9). However, given the large errors in some of the estimates, the net radiative forcing is probably not significantly different than zero. Moreover, any decrease in radiative forcing due to lower CH_4 emissions arising from wetland loss must be weighed against the loss of the many critical ecosystem services these systems provide such as havens for biodiversity, recharge of ground water, reduction in flooding, fish nurseries, etc. (Zedler and Kercher 2005).

A majority of the effort in examining future global change impacts on wetlands has focused on northern peatlands because of their large soil carbon reserves, although under current climate conditions, they have modest CH_4 emissions (Moore and Roulet 1995, Roulet 2000, Joosten and Clarke 2002, and references therein). The effects of global change on carbon sequestration in peatlands are probably of minor importance because of the relatively low rate of peat accumulation. However, losses of soil carbon stocks in peatlands drained for agriculture and forestry (Table 2) attest to the possibility of large losses from the massive soil carbon deposits in northern peatlands if they become substantially drier in a future climate. Furthermore, Turetsky et al. (2004) estimated that up to 5.9 Tg C yr^{-1} are released from western Canadian peatlands by fire and predicted that increases in fire frequency may cause these systems to become net atmospheric carbon sources.

Our compilation shows that attention needs to be directed toward understanding climate change impacts to FWMS wetlands, which collectively emit $\sim$ 70% more CH_4 than North American peatlands and potentially sequester an equivalent amount of carbon. The effects of changing water-table depths are somewhat more tractable in FWMS wetlands than peatlands because FWMS wetlands have less potential for oxidation of soil organic matter. In forested FWMS wetlands, increased precipitation and runoff may increase radiative forcing by

simultaneously decreasing wood production and increasing methanogenesis (Megonigal et al. 2005). The influence of changes in hydrology on CH_4 emissions, plant productivity, soil carbon preservation, and sedimentation will need to be addressed to fully anticipate climate change impacts on radiative forcing in these systems.

The effects of global change on estuarine wetlands are of concern because sequestration rates are rapid, and sequestration can be expected to increase in proportion to the rate of sea-level rise provided estuarine wetland area does not decline. Because CH_4 emissions from estuarine wetlands are low, this increase in sequestration capacity could represent a net decrease in radiative forcing, depending on how much of the sequestered carbon is autochthonous. Changes in tidal wetland area with sea-level rise will depend on rates of inland migration, erosion at the wetland-estuary boundary, and wetland elevation change. The rate of loss of tidal wetland area has decreased in past decades due to regulations on draining and filling activities (Dahl 2000). On the other hand, rapid conversion to open water is occurring in some areas of coastal Louisiana (Bourne 2000) and Maryland (Kearney and Stevenson 1991), suggesting that marsh area may decrease with increased rates of sea-level rise (Kearney et al. 2002). A multitude of human and climate factors are contributing to the current losses (Turner 1997, Day Jr. et al. 2000, 2001), and it is uncertain how these factors will interact with sea- level rise (Najjar et al. 2000). A proper assessment of potential changes in the estuarine carbon sink will require an analysis of how these factors interact across different hydrogeomorphic settings.

One of the greatest concerns is how climate change will affect future CH_4 emissions from wetlands because of their large GWP. Wetlands emit 92 to 237 $\times$ 10^{12} g CH_4 yr^{-1} (Table 4), or 15 to 40% of the global total. Increases in atmospheric CH_4 concentrations over the past century have had the second largest radiative forcing (after CO_2) in human-induced climate change (Ehhalt et al. 2001). Moreover, CH_4 fluxes from wetlands have provided an important radiative feedback on climate over the geologic past (Chappellaz et al. 1993, Blunier et al. 1995, Petit et al. 1999). The large global warming observed since the 1990s may have resulted in increased CH_4 emissions from wetlands (Fletcher et al. 2004a, Wang et al. 2004, Zhuang et al. 2004).

Data (Bartlett and Harriss 1993, Moore et al. 1998, Updegraff et al. 2001) and modeling (Gedney et al. 2004, Zhuang et al. 2004) strongly support the contention that water-table position and temperature are the primary environmental controls over CH_4 emissions. How this generalization plays out with future climate change is, however, more complex. For example, most climate models predicted that much of Canada will be warmer and drier in the future. Based upon this prediction, Moore et al. (1998) proposed that different types of Canadian peatlands would experience a variety of carbon flux responses to climate change. For example, CH_4 emissions may increase in collapsed former-permafrost bogs (which are predicted to be warmer and wetter) but decrease in fens and other types of bogs (warmer and drier). A CH_4-process model predicted that modest warming will increase global wetland emissions, but larger increases in temperature will decrease emissions because of drier conditions (Cao et al. 1998).

One of the greatest unknowns is how increasing atmospheric CO_2 concentrations will affect carbon cycling in wetland ecosystems, which has received far less attention than terrestrial ecosystems. Field studies have been done in tussock tundra (Tissue and Oechel 1987, Oechel et al. 1994), bog-type peatlands (Hoosbeek et al. 2001), rice paddies (Kim et al. 2001), and a salt marsh (Rasse et al. 2005); a somewhat wider variety of wetlands have been studied in small-scale glasshouse systems. Temperate and tropical wetland ecosystems consistently respond to elevated CO_2 with an increase in photosynthesis and/or biomass (Vann and Megonigal 2003). By comparison, the response of northern peatland plant communities has been inconsistent. A hypothesis that remains untested is that the elevated CO_2 response of northern peatlands will be limited by nitrogen availability. In an *in situ* study of tussock tundra, complete photosynthetic acclimation occurred when CO_2 was elevated, but acclimation was far less severe with both elevated CO_2 and a 4°C increase in air temperature (Oechel et al. 1994). It was hypothesized that soil warming relieved a severe nutrient limitation on photosynthesis by increasing nitrogen mineralization.

A consistent response to elevated CO_2-enhanced photosynthesis in wetlands is an increase in CH_4 emissions ranging from 50 to 350% (Vann and Megonigal 2003). It is generally assumed that the increased supply of plant photosynthate stimulates anaerobic microbial carbon metabolism, of which CH_4 is a primary end product. A doubling of CH_4 emissions from wetlands due to elevated CO_2 constitutes a positive feedback on radiative forcing because CO_2 is rapidly converted to a more effective greenhouse gas (CH_4).

An elevated CO_2-induced increase in CH_4 emissions may be offset by an increase in carbon

sequestration in soil organic matter or wood. Although there are very few data to evaluate this hypothesis, a study on seedlings of a wetland-adapted tree species reported that elevated CO_2 stimulated photosynthesis and CH_4 emissions, but not growth, under flooded conditions (Megonigal et al. 2005). It is possible that elevated CO_2 will stimulate soil carbon sequestration, particularly in tidal wetlands experiencing sea-level rise, but a net loss of soil carbon is also possible due to priming effects (i.e., enhancement of decomposition of native soil organic matter by inputs of labile carbon) (Hoosbeek et al. 2004, Lichter et al. 2005). Elevated CO_2 has the potential to influence the carbon budgets of adjacent aquatic ecosystems by increasing export of dissolved organic carbon (Freeman et al. 2004) and dissolved inorganic carbon (Marsh et al. 2005).

Other important anthropogenic forcing factors that will affect future CH_4 emissions include atmospheric sulfate deposition (Vile et al. 2003, Gauci et al. 2004) and nutrient additions (Keller et al. 2005, 2006). These external forcing factors, in turn, will interact with internal ecosystem constraints such as pH and carbon quality (Moore and Roulet 1995, Bridgham et al. 1998), anaerobic carbon flow (Hines and Duddleston 2001), and net ecosystem productivity and plant community composition (Whiting and Chanton 1993, Updegraff et al. 2001, Strack et al. 2004) to determine the actual response.

Options and Measures

Wetland policies in the U.S. and Canada are driven by a variety of federal, state or provincial, and local laws and regulations in recognition of the many wetland ecosystem services and large historical loss rates (Lynch-Stewart et al. 1999, National Research Council 2001, Zedler and Kercher 2005). Thus, any actions to enhance the ability of wetlands to sequester carbon, or reduce their CH_4 emissions, must be implemented within the context of the existing regulatory framework. The most important option in the U.S. has already been largely achieved, and that is to reduce the historical rate of peatland losses with their accompanying large oxidative losses of the stored soil carbon. Decreases in the rates of loss of all wetlands have helped to maintain their soil carbon sequestration potential.

There has been strong interest expressed in using carbon sequestration as a rationale for wetland restoration and creation in the U.S., Canada, and elsewhere (Wylynko 1999, Watson et al. 2000, Euliss et al. 2006). However, large CH_4 emissions from conterminous U.S. wetlands suggest that creating and restoring wetlands may increase net radiative forcing, although adequate data do not exist to fully evaluate this possibility. Roulet (2000) came to a similar conclusion concerning the restoration of Canadian wetlands. Net radiative forcing from restoration will likely vary among different kinds of wetlands and the specifics of their carbon budgets. The possibility of increasing radiative forcing by creating or restoring wetlands is not likely to apply to estuarine wetlands, which emit relatively little CH_4 compared to the carbon they sequester. Restoration of drained peatlands may stop the rapid loss of their soil carbon, which could compensate for increased CH_4 emissions. Canadian peatlands restored from peat extraction operations increased their net emissions of carbon because of straw addition during the restoration process, although it was assumed that they would eventually become a net sink (Cleary et al. 2005).

Regardless of their internal carbon balance, the area of restored wetlands is currently too small to form a significant carbon sink at the continental scale. For example, based upon the U.S. National Wetland Inventory, between 1986 and 1997 only 4,157 km^2 of terrestrial lands were converted into wetlands in the conterminous U.S. (Dahl 2000). Using the soil carbon sequestration rate of 3.05 Mg C $ha^{-2}\,yr^{-1}$ found by Euliss et al. (2006) for restored prairie pothole wetlands, we estimate that wetland restoration in the U.S. would have sequestered 1.3 Tg C over this 11-year period. [Euliss et al. (2006) regressed surface soil carbon stores in 27 restored semi-permanent prairie pothole wetlands against years since restoration to derive their sequestration rate ($r^2 = 0.31$, $P = 0.002$); there was no significant relationship in seasonal prairie pothole wetlands ($r^2 = 0.04$, $P = 0.241$)]. However, larger areas of wetland restoration may have a significant impact on carbon sequestration. A simulation model of planting 20,000 km^2 into bottomland hardwood trees as part of the Wetland Reserve Program in the U.S. showed a sequestration of 4 Tg C yr^{-1} through 2045 (Barker et al. 1996). Euliss et al. (2006) estimated that, if all cropland on former prairie pothole wetlands in the U.S. and Canada (162,244 km^2) were restored, 378 Tg C would be sequestered over 10 years in soils and plants. However, neither study accounted for the GWP of increased CH_4 emissions.

Potentially more significant is the conversion of wetlands from one type to another (e.g., 8.7% (37,200 km^2) of the wetlands in the conterminous U.S. in 1997 were in a previous wetland category in 1986) (Dahl 2000). The net effect of these conversions on wetland carbon fluxes are unknown.

Similarly, Roulet (2000) argued that too many uncertainties exist to include Canadian wetlands in the Kyoto Protocol.

CONCLUSIONS

North American wetlands form a very large carbon pool, primarily because of storage as peat, and are a small to moderate carbon sink (excluding CH_4 effects). The largest unknowns in wetland carbon budgets are the amount and significance of sedimentation in FWMS and estuarine wetlands and CH_4 emissions in freshwater wetlands. With the exception of estuarine wetlands, CH_4 emissions from wetlands may largely offset any positive benefits of carbon sequestration in soils and plants. Given these conclusions, it is probably unwarranted to use carbon sequestration as a rationale for the protection and restoration of FWMS wetlands, although the many other ecosystem services that they provide justify these actions. However, protecting and restoring peatlands will stop the loss of their soil carbon (at least over the long term), and maintaining or increasing estuarine wetlands is likely to contribute to net carbon sequestration even after accounting for CH_4 emissions.

The most important areas for further scientific research in terms of current carbon fluxes in the U.S. are to establish an unbiased (i.e., stratified-random) landscape-level sampling scheme to determine sediment carbon sequestration in FWMS and estuarine wetlands and additional measurements of annual CH_4 emissions to constrain these important fluxes better. It would also be beneficial if the approximately decadal National Wetland Inventory (NWI) status and trends data were collected in sufficient detail with respect to the Cowardin et al. (1979) classification scheme to determine changes among mineral-soil wetlands and peatlands.

Canada lacks any regular inventory of its wetlands, and thus, it is difficult to quantify land-use impacts upon their carbon fluxes and pools. While excellent scientific data exist on most aspects of carbon cycling in Canadian peatlands, Canadian FWMS and estuarine wetlands have been relatively poorly studied, despite having suffered large proportional losses to land-use change. Wetland data for Mexico are almost entirely lacking. Thus, anything that can be done to improve upon this would be helpful. All wetland inventories should quantify the area of estuarine mud flats, which have the potential to sequester considerable amounts of carbon and are poorly understood with respect to carbon sequestration.

The greatest unknown is how global change will affect the carbon pools and fluxes of North American wetlands. We will not be able to predict accurately the role of North American wetlands as potential positive or negative feedbacks to anthropogenic climate change without knowing the integrative effects of changes in temperature, precipitation, atmospheric CO_2 concentrations, and atmospheric deposition of nitrogen and sulfur within the context of internal ecosystem drivers of wetlands. To our knowledge, no manipulative experiment has simultaneously measured more than two of these perturbations in any North American wetland, and few have been done at any site. Modeling expertise of the carbon dynamics of wetlands has rapidly improved in the last few years (Frolking et al. 2002, Zhuang et al. 2004, and references therein), but this needs even further development in the future, including for FWMS and estuarine wetlands.

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Appendix 1. Methane fluxes measured in the conterminous U.S. The conversion factor is the ratio of the measured annual flux to the daily average flux. The estimated annual flux was determined based upon the average conversion factor for freshwater (FW) and saltwater (SW) wetlands. The measured annual flux was used if that was available, otherwise the estimated annual flux was used.

Habitat	State	Method[a]	Salt/ Fresh	Daily Average Flux (mg CH_4 m^{-2} d^{-1})	Measured Annual Flux (g CH_4 m^{-2} yr^{-1})	Conversion Factor	Estimated Annual Flux (g CH_4 m^{-2} yr^{-1})	Used Annual Flux (g CH_4 m^{-2} yr^{-1})	Reference
Fens	CO	C	FW		40.7			40.7	Chimner and Cooper (2003)
Wet Alpine Meadow	CO	C	FW	0.1			0.0	0.0	Neff et al. (1994)
Lake - Average	CO	C	FW	25.4			9.2	9.2	Smith and Lewis (1992)
Wetland - Average	CO	C	FW	28.3			10.3	10.3	Smith and Lewis (1992)
Nuphar Bed	CO	C	FW	202.1			73.6	73.6	Smith and Lewis (1992)
Tundra - Carex Meadow	CO	C	FW	2.8			1.0	1.0	West et al. (1999)
Tundra - Acomastylis Meadow	CO	C	FW	−0.5			−0.2	−0.2	West et al. (1999)
Tundra - Kobresia Meadow	CO	C	FW	−0.8			−0.3	−0.3	West et al. (1999)
Moist Grassy	CO	C	FW	6.1	1.9	0.32	2.2	1.9	Wickland et al. (1999)
Moist Mossy	CO	C	FW	1.5	0.5	0.33	0.5	0.5	Wickland et al. (1999)
Wetland	CO	C	FW		41.7			41.7	Wickland et al. (1999)
Hardwood Hammock	FL	C	FW	0.0			0.0	0.0	Bartlett et al. (1989)
Dwarf Cypress / Sawgrass	FL	C	FW	7.5			2.7	2.7	Bartlett et al. (1989)
Spikerush	FL	C	FW	29.4			10.7	10.7	Bartlett et al. (1989)
Sawgrass < 1 m	FL	C	FW	38.8			14.1	14.1	Bartlett et al. (1989)
Sawgrass/Spkerush/Periphyton	FL	C	FW	45.1			16.4	16.4	Bartlett et al. (1989)
Swamp Forest	FL	C	FW	68.9			25.1	25.1	Bartlett et al. (1989)
Sawgrass > 1 m	FL	C	FW	71.9			26.2	26.2	Bartlett et al. (1989)
Sawgrass	FL	C	FW	107.0			38.9	38.9	Burke et al. (1988)
Pond Open Water	FL	C	FW	624.0			227.1	227.1	Burke et al. (1988)
Everglades - Cladium	FL	C	FW	45.4			16.5	16.5	Chanton et al. (1993)
Everglades - Typha	FL	C	FW	142.9			52.0	52.0	Chanton et al. (1993)
Wet Prairie (Marl)	FL	C	FW	87.0			31.6	31.6	Happell et al. (1993)
Wet Prairie (Marl)	FL	C	FW	27.4			10.0	10.0	Happell et al. (1993)
Marsh (Marl)	FL	C	FW	30.0			10.9	10.9	Happell et al. (1993)
Marsh (Marl)	FL	C	FW	49.6			18.0	18.0	Happell et al. (1993)
Marsh (Peat)	FL	C	FW	45.4			16.5	16.5	Happell et al. (1993)
Marsh (Peat)	FL	C	FW	13.0			4.7	4.7	Happell et al. (1993)
Marsh (Peat)	FL	C	FW	163.6			59.6	59.6	Happell et al. (1993)
Marsh (Peat)	FL	C	FW	20.4			7.4	7.4	Happell et al. (1993)
Wet Prairie / Sawgrass	FL	C	FW	61.0			22.2	22.2	Harriss et al. (1988)
Wetland Forest	FL	C	FW	59.0			21.5	21.5	Harriss et al. (1988)
Cypress Swamp - Flowing Water	FL	C	FW	67.0			24.4	24.4	Harriss and Sebacher (1981)
Open Water Swamp	FL	C	FW	480.0			174.7	174.7	Schipper and Reddy (1994)
Waterlily Slough	FL	C	FW	91.0			33.1	33.1	Schipper and Reddy (1994)
Cypress Swamp - Deep Water	GA	C	FW	92.3			33.6	33.6	Harriss and Sebacher (1981)

Appendix 1. Continued.

Habitat	State	Method[a]	Salt/ Fresh	Daily Average Flux (mg CH_4 m^{-2} d^{-1})	Measured Annual Flux (g CH_4 m^{-2} yr^{-1})	Conversion Factor	Estimated Annual Flux (g CH_4 m^{-2} yr^{-1})	Used Annual Flux (g CH_4 m^{-2} yr^{-1})	Reference
Bottomland Hardwoods/ Swamps	GA	C	FW		23.0			23.0	Pulliam (1993)
Swamp Forest	LA	C	FW	146.0			53.1	53.1	Alford et al. (1997)
Freshwater Marsh	LA	C	FW	251.0			91.4	91.4	Alford et al. (1997)
Fresh	LA	C	FW	587.0	213.0	0.36	213.6	213.0	DeLaune et al. (1983)
Fresh	LA	C	FW	49.0	18.7	0.38	17.8	18.7	DeLaune et al. (1983)
Sphagnum Bog	MD	C	FW	−1.1			−0.4	−0.4	Yavitt et al. (1990)
Bog	MI	C	FW	193.0			70.2	70.2	Shannon and White (1994)
Bog	MI	C	FW	28.0			10.2	10.2	Shannon and White (1994)
Beaver Meadow	MN	C	FW		2.3			2.3	Bridgham et al. (1995)
Open Bogs	MN	C	FW		0.0			0.0	Bridgham et al. (1995)
Bog (Forested Hummock)	MN	C	FW	10.0	3.5	0.35	3.6	3.5	Dise (1993)
Bog (Forested Hollow)	MN	C	FW	38.0	13.8	0.36	13.8	13.8	Dise (1993)
Fen Lagg	MN	C	FW	35.0	12.6	0.36	12.7	12.6	Dise (1993)
Bog (Open Bog)	MN	C	FW	118.0	43.1	0.37	42.9	43.1	Dise (1993)
Fen (Open Poor Fen)	MN	C	FW	180.0	65.7	0.37	65.5	65.7	Dise (1993)
Poor Fen	MN	C	FW	242.0			88.1	88.1	Dise and Verry (2001)
Sedge Meadow	MN	C	FW		11.7			11.7	Naiman et al. (1991)
Submergent	MN	C	FW		14.4			14.4	Naiman et al. (1991)
Deep Water	MN	C	FW		0.5			0.5	Naiman et al. (1991)
Poor Fen	MN	T	FW		14.6			14.6	Shurpali and Verma (1998)
Submerged Tidal	NC	C, E	FW	144.8			52.7	52.7	Kelley et al. (1995)
Banks Tidal	NC	C, E	FW	20.1			7.3	7.3	Kelley et al. (1995)
Tidal Marsh	NC	C	FW	3.0	1.0	0.34	1.1	1.0	Megonigal and Schlesinger (2002)
Tidal Marsh	NC	C	FW	3.5	2.3	0.65	1.3	2.3	Megonigal and Schlesinger (2002)
Prairie Marsh	NE	T	FW		64.0			64.0	Kim et al. (1998)
Poor Fen	NH	C	FW	503.3	110.6	0.22	183.2	110.6	Carroll and Crill (1997)
Poor Fen	NH	C	FW		69.3			69.3	Frolking and Crill (1994)
Forested Peatland	NY	C	FW	0.6	0.2	0.37	0.2	0.2	Coles and Yavitt (2004)
Pools Forested Swamp	NY	C	FW	224.6	69.0	0.31	81.7	69.0	Miller et al. (1999)
Typha Marsh - Mineral Soils	NY	C	FW	344.4			125.3	125.3	Yavitt (1997)
Typha Marsh - Peat Soils	NY	C	FW	65.1			23.7	23.7	Yavitt (1997)
Typha Marsh - All soils	NY	C	FW	204.8			74.5	74.5	Yavitt (1997)
Cypress Swamp - Floodplain	SC	C	FW	9.9			3.6	3.6	Harriss and Sebacher (1981)
Swamp	VA	C	FW	470.3			171.2	171.2	Chanton et al. (1992)
Maple/gum Forested Swamp	VA	C	FW		0.5			0.5	Harriss et al. (1982)
Emergent Tidal Freshwater Marsh	VA	C	FW		96.2			96.2	Neubauer et al. (2000)

Appendix 1. Continued.

Habitat	State	Method[a]	Salt/ Fresh	Daily Average Flux (mg CH_4 m^{-2} d^{-1})	Measured Annual Flux (g CH_4 m^{-2} yr^{-1})	Conversion Factor	Estimated Annual Flux (g CH_4 m^{-2} yr^{-1})	Used Annual Flux (g CH_4 m^{-2} yr^{-1})	Reference
Oak Swamp (Bank Site)	VA	C	FW	117.0	43.7	0.37	42.6	43.7	Wilson et al. (1989)
Emergent Macrophytes (Peltandra)	VA	C	FW	155.0			56.4	56.4	Wilson et al. (1989)
Emergent Macrophytes (Smartweed)	VA	C	FW	83.0			30.2	30.2	Wilson et al. (1989)
Ash Tree Swamp	VA	C	FW	152.0			55.3	55.3	Wilson et al. (1989)
Bog	WA	C	FW	73.0			26.6	26.6	Lansdown et al. (1992)
Lowland Shrub and Forested Wetland	WI	T	FW		12.4			12.4	Werner et al. (2003)
Sphagnum Eriophorum (Poor Fen)	WV	C	FW	6.6			2.4	2.4	Yavitt et al. (1990)
Sphagnum Shrub (Fen)	WV	C	FW	0.1			0.0	0.0	Yavitt et al. (1990)
Polytrichum Shrub (Fen)	WV	C	FW	−0.1			0.0	0.0	Yavitt et al. (1990)
Sphagnum Forest	WV	C	FW	9.6			3.5	3.5	Yavitt et al. (1990)
Sedge Meadow	WV	C	FW	1.5			0.5	0.5	Yavitt et al. (1990)
Beaver Pond	WV	C	FW	250.0			91.0	91.0	Yavitt et al. (1990)
Low Gradient Headwater Stream	WV	C	FW	300.0			109.2	109.2	Yavitt et al. (1990)
Sphagnum-Eriophorum	WV	C	FW	52.1	19.0	0.37	18.9	19.0	Yavitt et al. (1993)
Polytrichum	WV	C	FW	41.1	15.0	0.37	15.0	15.0	Yavitt et al. (1993)
Sphagnum-Shrub	WV	C	FW	4.4	1.6	0.37	1.6	1.6	Yavitt et al. (1993)
Salt Marsh	DE	C	SW	0.5			0.2	0.2	Bartlett et al. (1985)
Red Mangroves	FL	C	SW	4.2			1.4	1.4	Bartlett et al. (1989)
Dwarf Red Mangrove	FL	C	SW	81.9			27.9	27.9	Bartlett et al. (1989)
High Marsh	FL	C	SW	3.9			1.3	1.3	Bartlett et al. (1985)
Salt Marsh	FL	C	SW	0.6			0.2	0.2	Bartlett et al. (1985)
Salt Water Mangroves	FL	C	SW	4.0			1.4	1.4	Harriss et al. (1988)
Salt Marsh	GA	C	SW	13.4			4.6	4.6	Bartlett et al. (1985)
Short Spartina Marsh - High Marsh	GA	C	SW	145.2	53.1	0.37	49.5	53.1	King and Wiebe (1978)
Mid Marsh	GA	C	SW	15.8	5.8	0.37	5.4	5.8	King and Wiebe (1978)
Tall Spartina Marsh - Low Marsh	GA	C	SW	1.2	0.4	0.34	0.4	0.4	King and Wiebe (1978)
Intermediate Marsh	LA	C	SW	**912**[b]					Alford et al.(1997)
Salt Marsh	LA	C	SW	15.7	5.7	0.36	5.4	5.7	DeLaune et al. (1983)
Brackish	LA	C	SW	267.0	97.0		91.1	97.0	DeLaune et al. (1983)
Salt Marsh	LA	C	SW	4.8	1.7	0.35	1.6	1.7	DeLaune et al. (1983)

Appendix 1. Continued.

Habitat	State	Method[a]	Salt/ Fresh	Daily Average Flux (mg CH_4 m^{-2} d^{-1})	Measured Annual Flux (g CH_4 m^{-2} yr^{-1})	Conversion Factor	Estimated Annual Flux (g CH_4 m^{-2} yr^{-1})	Used Annual Flux (g CH_4 m^{-2} yr^{-1})	Reference
Brackish	LA	C	SW	17.0	6.4	0.38	5.8	6.4	DeLaune et al. (1983)
Cypress Swamp - Floodplain	SC	C	SW	1.5			0.5	0.5	Bartlett et al. (1985)
Salt Marsh	SC	C	SW	0.4			0.1	0.1	Bartlett et al. (1985)
Salt Marsh	VA	C	SW	3.0	1.3	0.43	1.0	1.3	Bartlett et al. (1985)
Salt Marsh	VA	C	SW	5.0	1.2	0.24	1.7	1.2	Bartlett et al. (1985)
Salt Meadow	VA	C	SW	2.0	0.4	0.22	0.7	0.4	Bartlett et al. (1985)
Salt Marsh	VA	C	SW	−0.8			−0.3	−0.3	Bartlett et al. (1985)
Salt Marsh	VA	C	SW	1.5			0.5	0.5	Bartlett et al. (1985)
Salt Meadow	VA	C	SW	−1.9			−0.6	−0.6	Bartlett et al. (1985)
Tidal Salt Marsh	VA	C	SW	16.0	5.6	0.35	5.5	5.6	Bartlett et al. (1987)
Tidal Brackish Marsh	VA	C	SW	64.6	22.4	0.35	22.0	22.4	Bartlett et al. (1987)
Tidal Brackish/Fresh Marsh	VA	C	SW	53.5	18.2	0.34	18.2	18.2	Bartlett et al. (1987)
Freshwater									
n					32	18	74	88	
Arithmatic Mean					32.1	0.36	38.6	36.0	
Arithmatic Standard Error					7.9	0.02	6.0	5.0	
Geometric Mean					8.1		7.1	7.6	
Geometric Standard Error					2.1		0.82	2.2	
Saltwater									
n					13	12	25	25	
Arithmatic Mean					16.9	0.34	9.8	10.3	
Arithmatic Standard Error					7.8	0.02	4.1	4.4	
Geometric Mean					5.0		1.3	1.3	
Geometric Standard Error					2.0		0.2	3.3	

[a] C = chamber. T = tower, eddy covariance, E = ebullition measured separately.
[b] Outlier that was removed from further analysis.