Connecting Atmosphere and Wetland: Trace Gas Exchange

Peter M. Lafleur*
Trent University

Abstract

This article reviews the exchange of carbon dioxide (CO_2) and methane (CH_4) gases between wetland and atmosphere, with a primary emphasis on ecosystem-scale fluxes and their environmental controls. It is intended to complement a previous review of wetland energy and water exchanges (Lafleur 2008). It is shown that wetland exchanges of these gases are greatly variable in space and time, especially CH_4. Most wetlands appear to be sinks for atmospheric CO_2, while almost all are emitters of CH_4. The strongest environmental control on the CO_2 flux is drought, which often determines whether a wetland will be a net sink or source for atmospheric CO_2. Due to complex biochemistry and transport mechanisms, methane efflux from wetlands often ranges over several orders of magnitude within a single wetland and among wetlands, making it difficult to quantify the environmental controls on this flux. The magnitude of gas fluxes is not strongly related to wetland type, which implies that modelling of these fluxes should consider wetlands a continuum and attempt to address processes as they vary along this continuum instead of as discrete entities. Although more research is required into the magnitude, variation and controls on trace gas fluxes in all wetland types, some wetlands (tropical and temperate marshes) are particularly understudied.

Introduction

Wetlands are ubiquitous across the globe and are important ecological systems that offer a variety of services from providing wildlife habitat and biodiversity to water filtration and runoff control. Their exchanges of energy and mass with the atmosphere are integral to their functioning, but also affect local, regional and global climates. As such, the study of these exchanges is of interest to wetland scientists and managers. In recent years, the specter of climatic change, specifically global warming resulting from an increase of greenhouse gases in the atmosphere, has focused considerable attention on the exchange of trace gases between ecosystems and the atmosphere. Although the list of such greenhouse gases is large, the two most important (and most abundant) are carbon dioxide and methane.[1] Wetlands have been recognized as an important agent in the

global cycling of both these gases in the past and present (Gorham 1991, 1995; Roulet 2000). Consequently, this awareness has spawned considerable interest in the study of wetland–atmosphere exchange of trace gas exchanges, which forms the basis of this review.

This article focuses on the magnitude, seasonal patterns and factors controlling wetland exchange of carbon dioxide and methane gases. It follows from, and is intended to complement, a previous review on wetland energy and water exchanges (Lafleur 2008). Two important ideas carried over from the earlier review are that wetland type plays some role in determining these exchanges and that wetland–atmosphere exchanges are best understood by considering the wetland as an integrated system where vegetation, soil and hydrology are all linked and their coupling serves to mediate interactions with the atmosphere. The review is structured as follows. Initially, a background section, largely abridged from Lafleur (2008), on the nature of wetlands and theory of surface-atmosphere interactions is given. The exchange of carbon dioxide and methane is then dealt with separately and are followed by an examination of the complete wetland carbon budget. A brief discussion of the global significance of wetland trace gas exchanges is then presented. Finally, the article ends with conclusions and suggestions for future research directions.

Background

Wetlands are found on virtually every continent on the globe and occur at all latitudes from 60°S to 80°N. Recent estimates suggest they cover between $8–10 \times 10^6$ km^2, with the largest concentrations occurring in the boreal and subarctic zones of the Northern Hemisphere (Lehner and Döll 2004). Wetlands comprise about 2% of the global surface and 6% of the land area. Despite their small areal coverage, wetlands are disproportionately important in their store of carbon in the soil. The global store of carbon in soils is estimated to be about 1500–2000 Gt; of this amount 202 to 535 Gt is stored in wetlands (Mitra et al. 2005).[2] The large uncertainty in this estimate arises because of non-uniform spatial sampling, differences in wetland definitions and methods of sampling. Based on the works of Gorham (1991) and others, it is likely that the largest portion of the wetland carbon store (> 80%) is contained in the so-called 'northern peatlands', referring to boreal and arctic peat forming ecosystems. Estimates of soil carbon in tropical and other wetlands are perhaps an order of magnitude less than in the northern peatlands, but such estimates are highly uncertain for reasons noted above (Mitra et al. 2005). Given this distribution, it is not surprising then that much of the recent research into wetland trace gas exchange has concentrated on northern peatlands.

Wetlands are highly sophisticated and diverse habitats taking many forms. They can be classified into more or less distinct groups based on chemical, morphological and vegetation criteria (Gore 1983). Yet, the

complexity of these ecosystems makes this a very tricky business and no one classification scheme is perfect. This article adopts the simplified classification used in the earlier review (Lafleur 2008), where wetlands are divided into the following categories. Bogs primarily receive water from precipitation, are peat-forming wetlands, typically have an extensive ground cover of moss (most commonly *Sphagnum* spp.), and may or may not have a significant vascular vegetation canopy. Fens may or may not be peat forming wetlands, may or may not have moss cover, but typically have herbaceous (grass or sedge) vascular plant canopies, water flows laterally through them and the water table is at or above the surface for part of the year. Fens are sometimes subdivided into poor and rich systems, referring to characteristics of their water chemistry, where the rich systems have higher pH and concentrations of mineral nutrients. Marshes are highly mineral rich wetlands typically vegetated with tall reeds and are often found on the edge of water bodies. Swamps are dominated by tall woody or herbaceous vegetation, are usually mineral rich and tend to be located in tropical and sub-tropical regions.

ECOSYSTEM–ATMOSPHERE TRACE GAS INTERACTIONS – THEORETICAL CONSIDERATIONS

The exchange of trace gases between wetland and atmosphere is a combination of biological and physical processes (Figure 1). Carbon dioxide (CO_2) is taken in through the pores (stomata) on leaves of vascular plants, or through cell walls of non-vascular species such as mosses, for photosynthesis (P), the process by which plants use sunlight to convert water and CO_2 into the raw materials for growth. A certain amount of CO_2 is released by plant leaves, bark and roots (plant respiration) primarily as a result of conversion of the raw materials into energy and plant growth materials, but also, to a lesser extent, because of inefficiencies in the photosynthetic process. CO_2 is also released when organic matter decays as microbes consume the dead plant material (microbial decomposition). The sum of these carbon losses from soil and plants is called ecosystem respiration (ER). The sum of P and ER is the net ecosystem CO_2 exchange (NEE) and represents the net amount of CO_2 taken up or released by the ecosystem. Similarly, methane (CH_4) is produced by soil microbes, usually under anoxic conditions below the water table, and then transported to the atmosphere by various pathways. Although there are a great many factors that control trace gas exchange processes, they can be broadly grouped into two categories: biological (e.g. plant species and physiology, nutrients and microbial status) and environmental (e.g. light, moisture and temperature). Researchers who have measured wetland CO_2 and CH_4 exchanges have attempted to explain their findings in terms of such factors. Although a great deal of literature has been produced on all aspects of carbon exchange and storage, biophysical functioning, and chemical processes in relation to
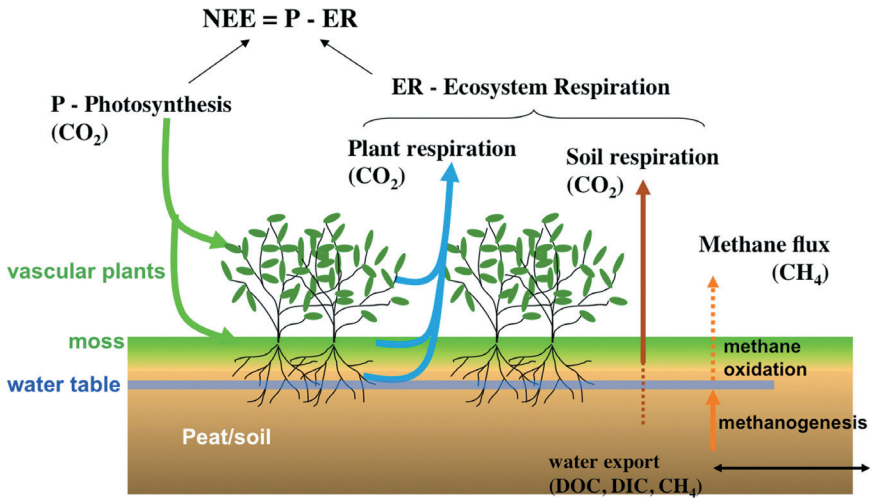
Fig. 1. Schematic of carbon exchanges a wetland. Carbon dioxide (CO_2) fluxes include uptake by photosynthesis (P) and release by ecosystem respiration (ER), the net of these two fluxes is net ecosystem exchange (NEE). ER is composed of plant (autotrophic) respiration and soil microbial (heterotrophic) respiration. Methane (CH_4) is produced below the water table by soil microbes and leaves the wetland 1) directly through ebullition or diffusion and 2) through transport along plant internal structures. The dotted line above the water table represents consumption/oxidation of CH_4 as it passes through the aerobic zone. Dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and CH_4 can also enter or leave the wetland through lateral water transport.

wetlands, the present review concentrates on ecosystem-scale studies of the wetland–atmospheric exchange, that is, the whole ecosystem flux of these carbon gases between wetland and atmosphere.

Wetland–atmosphere fluxes of any quantity are determined by turbulence in the atmosphere and the concentration gradient between the surface and atmosphere (Lafleur 2008). In theory, this is a very complex process and beyond the scope of this review. Instead, a brief qualitative description of the basics of CO_2 and CH_4 exchanges is offered. The efficiency with which the atmosphere can move trace gases either toward or away from the surface is a function of turbulence. In general, the windier it is the more atmospheric mixing is enhanced, resulting in larger fluxes. The surface plays a small role in this through its physical stature, referred to as roughness (i.e. the more numerous and taller the obstacles on it that extend up into the air stream the rougher it is). Rougher surfaces promote vertical mixing compared to smooth surfaces. The concentration gradient between surface and atmosphere is best envisioned in terms of the source-sink strength of the respective media (i.e. wetland surface and atmosphere). For example, in terms of CO_2, this gas is generally well-mixed within the atmosphere and its concentration varies little from place to place. The free atmosphere

global average in 2006 was 381 ppmv (Canadell et al. 2007). CO_2 is produced by plant roots and microbes in the soil, thus the concentration in the soil air volume is often many times larger than in the atmosphere, making the soil a source and the atmosphere a sink for this portion of the CO_2 exchange. However, when plants are actively photosynthesizing in the day the CO_2 concentration inside the leaves and at the surface of the leaf is depressed below the atmospheric level and the plant canopy is a sink for the atmospheric source. This process usually dominates over the soil exchange in the day and the resulting flux is from atmosphere to surface. At night, no photosynthesis takes place and the whole ecosystem (plants and soil) is a source of CO_2 and the atmosphere a sink, thus the flux is from surface to atmosphere. For CH_4, the surface is rarely a sink as the processes that generate methane in the soil are responsible for concentrations well above the average level in atmosphere (1.774 ppmv in 2005, IPCC 2007). Thus, for most wetlands the flux of CH_4 is from the surface to atmosphere. The pathways for CH_4 are either direct emission from the soil or water surface or through the plant cellular structure (Figure 1). Therefore, the main environmental factors controlling this efflux are microbial community, substrate physical and chemical properties and vegetation type.

The exchange of any trace gas can be measured in various ways. At the scale of the ecosystem, the most common means is the eddy covariance technique (Baldocchi 2003; Moncrieff et al. 1997). The main requirement is an instrument capable of very fast sampling of the gas concentration (typically ≥ 10 times as second, that is, ≥ 10 Hz). Combined with an anemometer to sample the vertical wind velocity, fluxes can be resolved mathematically. Gas fluxes are typically expressed as a molar flux with units of concentration per unit area per time (e.g. $\mu mol\ m^{-2}\ s^{-1}$). The resulting quantity is called the eddy flux, F_e, and it represents the integrated flux over an up-wind area of the wetland of several 100 to 1000's of square metres. This flux area is called the footprint, the size of which varies with atmospheric conditions and its position with wind direction. The gas concentration in the air layer below the level at which the eddy fluxes are measured also changes with time. These changes in storage must be accounted for as part of the ecosystem exchange, resulting in a storage flux, F_s. The addition of these two fluxes is NEE. Although conventions vary, in this article NEE is given a negative sign when directed toward the surface (i.e. the wetland is a sink) and a positive sign when toward the atmosphere (i.e. the wetland is a net source). The fluxes are usually evaluated over short time periods (20–60 min) and then can be integrated to represent the daily, seasonal or annual exchanges. Field ready infrared gas analysers for fast measurement of CO_2 have been available for several years now and have been widely used for this purpose.

Methane (CH_4) can also be measured with eddy covariance techniques, but is a technologically more costly and complicated business. Only a few such studies have been published to date, but it is expected to become

more common in future. In the past a common approach has been to employ small chambers on the surface and measure the gas concentration change (CH_4 or CO_2) over time from which a flux is computed. Although various types of chambers are used (static, steady-state, closed or open), the static chambers are most common. The chamber approach is advantageous in that it is relatively inexpensive and technically uncomplicated compared to the eddy covariance approach. As well, it can be used to measure spatial variation in gas flux within an ecosystem and can be used in combination with environmental manipulations for hypothesis testing; for example, live vegetation can be removed to measure soil flux only or the chamber can be shrouded to measure 'dark processes'. Regardless of the application, practitioners need to be aware of inherent problems with chamber measurements and their effects on flux interpretations (Hooper et al. 2002). Despite these technical concerns, spatial extrapolation to represent the ecosystem exchange is challenging. Although few comparisons of the two methodologies (eddy covariance versus chambers) exist, such studies often underscore the potential mismatch between scales of measurement (Clement et al. 1995; Zamolodchikov et al. 2003).

Research on Trace Gas Exchanges

PATTERNS OF CARBON DIOXIDE EXCHANGE

In general, it is believed that CO_2 fluxes in wetlands are smaller than for many other upland ecosystems. However, this view is based largely on information from the northern peatlands where cool, wet conditions limit both photosynthesis and decomposition processes. Plant growth, and hence the conditions that enhance or hamper growth, largely govern the exchange of CO_2. For this reason, the exchange of CO_2 (i.e. NEE) is likely to vary between wetland types and between similar wetlands existing in different climatic regions. As a result of the concerns over global warming, recent research on wetland trace gas exchange has often focused on two prominent questions: (1) Are wetlands a sink or source for CO_2? and (2) How will this change under a warmer climate?

The vast majority of the past research is seasonal in scope and concentrated in the snow-free or growing period. As a consequence, patterns of seasonal and diurnal cycles of CO_2 exchange are well known. Figure 2a shows a typical seasonal cycle of NEE, from the perspective of a northern boreal location exhibiting distinct seasons. Daily NEE is small immediately after snowmelt, increases rapidly in spring as temperatures and light levels increase, reaches a mid-summer peak and then declines in autumn as plants begin to senesce. It is notable that on some days the ecosystem is a net loss of CO_2 even in mid-summer. Typically, such days are heavily overcast and cool, as there is close correspondence between the amount of radiation received and NEE. However, the general trend is for NEE to become
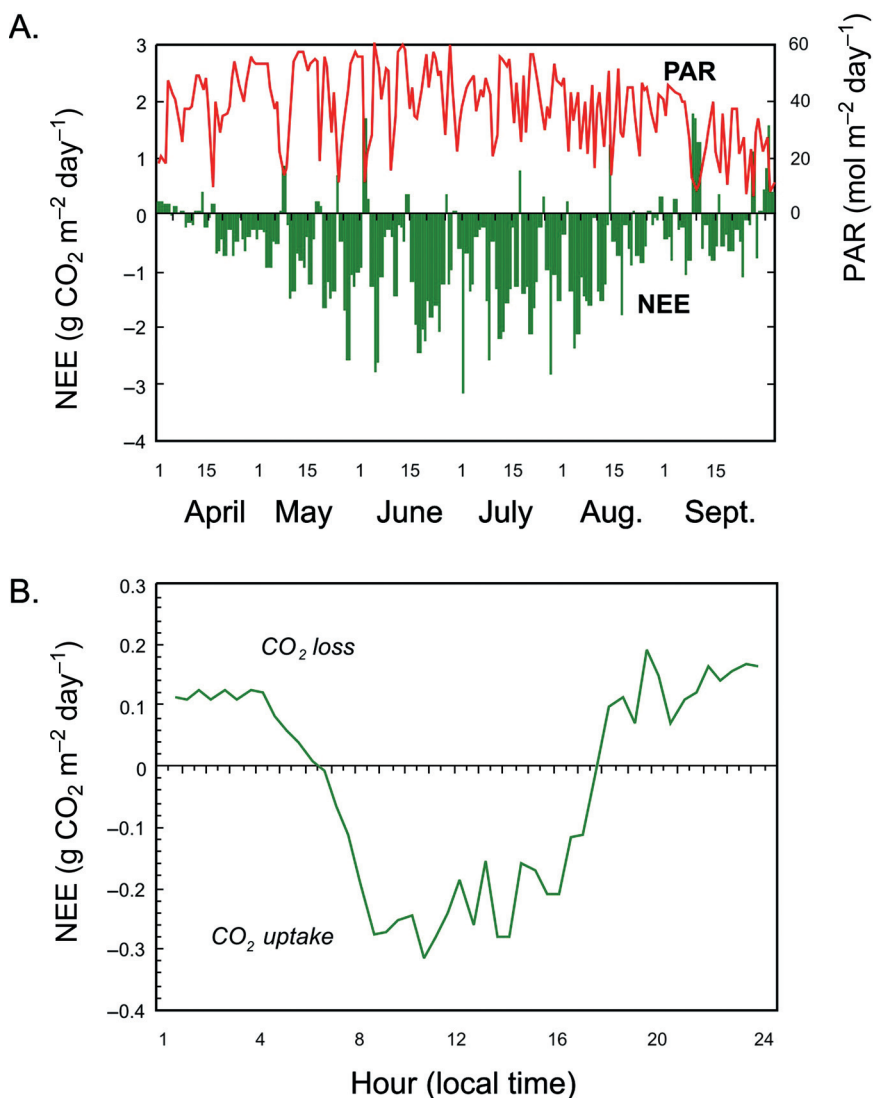
Fig. 2. Examples of trends in net ecosystem CO_2 exchange (NEE). (A) Seasonal trend in NEE from end of snowmelt until fall senescence. Bars show daily NEE, where positive values are a loss of CO_2 to the atmosphere from the wetland and negative values are a gain of CO_2 to the wetland. Solid line is the daily flux of photosynthetically active radiation (PAR). (B) Diurnal cycle of NEE. Data are taken from a bog peatland in Ontario, Canada (see Lafleur et al. 2003).

more negative (show greater up-take by the wetland) as spring evolves into summer. Although both photosynthesis and respiration are increasing throughout this period, the trend suggests that P increases at a faster rate as it is a time when the wetland vegetation is rapidly growing. Several researchers have shown that in temperate and boreal regions the seasonal

trend in daily NEE at a given wetland is often closely related to the development of the vegetation canopy, often expressed in terms of leaf area index (LAI)[3] (Bonneville et al. 2008; Laurila et al. 2001; Rennermalm et al. 2005). Differences in NEE between sites are also strongly related to LAI (Humphreys et al. 2006; Laurila et al. 2001). In tropical regions where distinct wet and dry seasons are common, NEE also displays seasonality. Morison et al. (2000) studied an Amazonian riverine wetland and found that NEE was lower during the dry period compared to the wet season. Interestingly, the productivity was relatively unaffected by the dry conditions and the difference in NEE was almost entirely due to increased respiration during the dry period. Heinsch et al. (2004) found that NEE responded similarly to wet and dry periods at a marsh on the Texas coast. However, in their study productivity was much more affected by wet and dry cycles than ecosystem respiration.

The typical diurnal pattern of NEE is illustrated in Figure 2b. This u-shaped trend results from the interplay between the two flows of CO_2, uptake by photosynthesis and release by respiration (Figure 1). At night, P = 0 and NEE takes on the magnitude and trend of ER, which tends to vary only slowly from hour to hour. Soon after sunrise, NEE becomes dominated by P, which itself is strongly controlled by light, thus it increases in magnitude until near mid-day, then decreases in the afternoon, and approaches zero again at sunset. This strong correspondence between P and light, specifically the narrow part of the solar spectrum used exclusively for photosynthesis, also called the photosynthetically active radiation (PAR),[4] has become a powerful tool in CO_2 exchange studies. Since measurements of NEE are not always continuous due to instrument malfunction and poor weather, such relationships are used to 'gap-fill' the missing data (Falge et al. 2001). They are also a useful means of comparing CO_2 exchange between ecosystems circumventing the complicating effects of differences in weather. In one such study, Frolking et al. (1998) summarized NEE–PAR relationships for a variety of bogs and fens, mainly from North America, and showed that exchange rates differed between these two wetland classes, with bogs having lower CO_2 exchanges. However, the differences were small and may have been a result of the limited data set employed in the study. Later studies, using NEE–PAR analysis, have demonstrated a greater range in CO_2 exchange among wetland types (Humphreys et al. 2006; Laurila et al. 2001). Perhaps more importantly, Frolking et al. (1998) also showed that average wetland NEE was indeed smaller than for other ecosystem types (Figure 3).

Figure 4 represents a survey of mid-growing season daily net CO_2 exchange rates for various wetlands. These data show that under peak growing conditions all sites were sinks, but CO_2 fluxes were quite variable between and within sites. The highest rates were observed in a tropical wetland (Morison et al. 2000). Interestingly, other tropical wetlands did not exhibit such high fluxes. The differences are due to strong control by
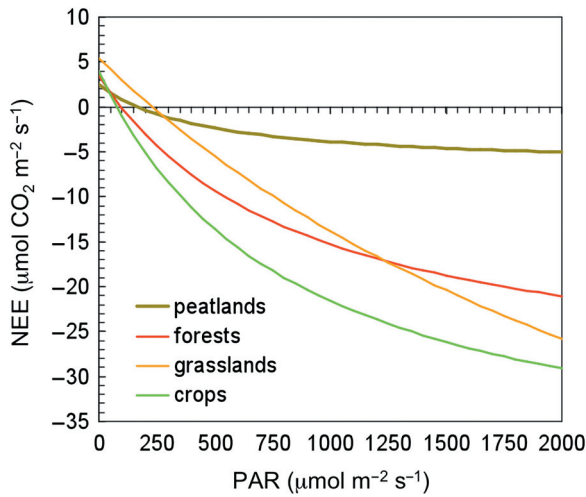
Fig. 3. Relationship between net ecosystem CO_2 exchange (NEE) and photosynthetically active radiation (PAR) for wetlands and other ecosystem types. Wetland curve is from the work of Frolking et al. (1998), other ecosystems from Ruimy et al. (1995). Negative NEE represents an uptake of carbon dioxide.
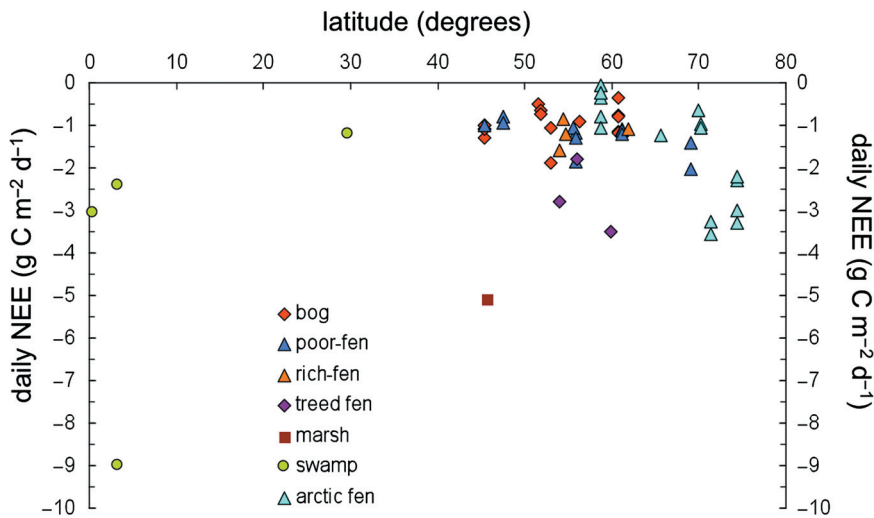

Fig. 4. Comparison of mid-growing season daily CO_2 fluxes from wetland sites. Values are averages for mid-growing season, typically July in the boreal and arctic zone. See Figure 5 for sources.

vegetation type and level of flooding (Jones and Humphries 2002). In the boreal and arctic zones, except for one marsh site, no one wetland type stands out as having greater fluxes than another. The majority of fluxes vary between −0.5 and −4.0 g C m^{-2} day^{-1}, with most near −1.0 g C m^{-2} day^{-1}.

For any one wetland type the variation in flux seen in Figure 4 is the result of differences in climate, moisture, and vegetation composition and phenology.

ENVIRONMENTAL CONTROLS ON CO_2 EXCHANGE

As noted above, PAR is a dominant control on photosynthesis and thus NEE at hourly and daily time scales. This influence must also extend to seasonal time scales. However, few if any studies have demonstrated this point. Apart from light, temperature can have an influence on NEE by affecting both P and ER. For temperate and high latitude wetlands warmer temperatures during the growing season promote plant growth, increasing P. At the same time, ER is a strong function of temperature (Chapman and Thurlow 1996; Silvola et al. 1996). Within a single growing season wetland P and ER are strongly correlated with temperature (Lindroth et al. 2007), which may not be surprising since light, air temperature and plant growth all follow a distinct seasonal cycles that are more or less in phase. The two processes have somewhat offsetting effects on NEE, but most research suggests that changes in P will dominate during a growing season. Evidence from multi-year flux studies shows that temperature had a strong interannual influence on NEE at some wetlands (Groendahl et al. 2007), but not at others (Aurela et al. 2004; Griffis et al. 2000; Lafleur et al. 2003). It may be assumed that where no such trend was present the relationship may have been confounded by other variables. Humidity can also influence wetland CO_2 exchange, through the control of stomatal conductance. Many wetland plants show reduced conductance for water vapour (and CO_2) under high afternoon vapour pressure deficits (Lafleur 2008). Such an effect influences P only and has been observed in a variety of wetland types (Humphreys et al. 2006). Response to low humidity can also contribute to differences in morning and afternoon P response to PAR (Syed et al. 2006). Humidity effects are likely to be most important at hourly and daily time scales, but would be unlikely to explain seasonal differences in P or NEE.

Although the factors noted above can affect the seasonal pattern and magnitude of NEE at a given site from one year to the next, there is a growing consensus that drought is the most important determinant of interannual differences in wetland NEE. Shurpali et al. (1995) and Joiner et al. (1999) both showed that for boreal *Sphagnum* dominated fens NEE was severely reduced in drought years compared to years with high water tables. In both studies, the effect of drought was to switch the seasonal NEE from a net CO_2 sink to a net source. Subsequently, the effects of drought on decreasing NEE have been found at a number of wetland sites (Arneth et al. 2002; Aurela et al. 2007; Bubier et al. 2003; Griffis et al. 2000; Lafleur et al. 2003). Not all of these studies reported a net seasonal loss of CO_2, instead it appears that the impact of the drought on seasonal totals of NEE is dependent upon the extent and timing of the drought

event. While the drought impact on NEE is firmly established, the underlying causes of this effect (changes to ER, P or both) are not so well-understood. While there is no doubt that drought affects both soil respiration and P of wetland plants (Alm et al. 1999; Silvola et al. 1996), there is no consensus on which effect is most important at the whole ecosystem scale. Some studies have suggested that drought impacts P more than ER (Arneth et al. 2002; Griffis et al. 2000; Lafleur et al. 2003; Shurpali et al. 1995), while others have argued that ER was most affected (Alm et al. 1999; Aurela et al. 2007; Bubier et al. 2003). It is likely that wetland type (through differences in plant communities, soil biology and hydrology) may play a role. However, one of the difficulties with these interpretations is that micrometeorological methods do not measure the components P and ER directly; instead, they are derived from the NEE flux, making such findings a little less convincing. Nevertheless, this is one important area of research that requires further study.

SEASONAL NET ECOSYSTEM EXCHANGE

A survey of available data shows that most studies of wetland CO_2 exchange have found that growing seasons NEE totals were a net sink for atmospheric carbon (Figure 5). Although some caution is required in directly comparing such results because the magnitude of the seasonal flux will vary as a result of length of the study period, meteorological conditions and surface type, it seems that growing season NEE varies considerably between wetlands. The majority of sites were modest CO_2 sinks (-50 to -100 g C m^{-2} period^{-1}) and in a three cases large sinks (< -150 g C m^{-2} period^{-1}) were recorded. These latter studies are of interest as they represent distinctly different environments: a boreal tree fen (Syed et al. 2006), a temperate freshwater (cattail) marsh (Bonneville et al. 2008), and a sub-tropical cypress swamp (Clark et al. 1999). Multi-year studies at the same wetland (indicated by the whiskers in Figure 5) reinforce the notion that wetlands are growing season sinks for CO_2 (e.g. Arneth et al. 2002; Aurela et al. 2004; Lafleur et al. 2003). Such studies show that the interannual variability in NEE at the same site is typically of the same magnitude as the variation between sites. In all cases where studies have measured seasonal CO_2 losses, the loss was attributed exclusively to drought conditions during the year of study (e.g. Arneth et al. 2002; Griffis et al. 2000; Shurpali et al. 1995).

Does CO_2 exchange depend on wetland type? Although some of the dominant factors that affect CO_2 exchange (i.e. water table depth and plant species) tend to vary systematically between wetland types (e.g. bogs tend to be drier and have less dense vegetation than fens), CO_2 exchange is influenced by a large number of competing influences, such that it is almost impossible to attribute difference in NEE solely to wetland class. As well, due to the paucity of data for some wetland types, the full range
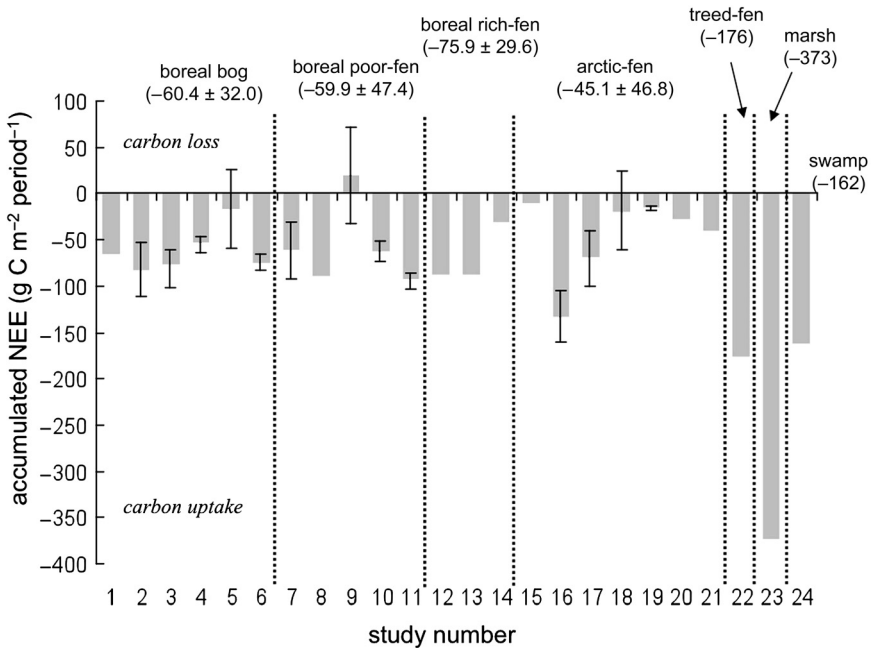
Fig. 5. Survey of growing season CO_2 flux measurements from wetland sites. Where more than one season was measured, bar represent mean values and whiskers represent the range of values. Values at the top represent means and standard deviations for all observations in each wetland category. Data sources with number of days included in the study = *xxxd*: 1. Lund et al. (2007) *183d*, 2. Nieveen et al. (1998) *92d*, 3. Lafleur et al. (2003) *122d*, 4. Arneth et al. (2002) *91d–225d*, 5. Arneth et al. (2002) *124d–242d*, 6. Sottocornola and Kiely (2005) *184d*, 7. Lafleur et al. (1997) *124d* & Joiner et al. (1999) *124d*, 8. Glenn et al. (2006) *104d*, 9. Shurpali et al. (1995) *145d*, 10. Aurela et al. (2001) (2002) *71d*, 11. Sagerfors et al. (2008) *153d*, 12. Suyker et al. (1997) *141d*, 13. Aurela et al. (2007) *214d*, 14. Glenn et al. (2006) *184d*, 15. Zamolodchikov et al. (2003) *85d*, 16. Harazono et al. (2003) *147d*, 17. Soegaard and Nordstroem (1999) *54d* & Nordstroem et al. (2001) *87d* & Rennermalm et al. (2005) *47d*, 18. Griffis et al. (2000) *75d*, 19. Vourlitis and Oechel (1997) *90d*, 20. Vourlitis and Oechel (1997) *77d*, 21. Coyne and Kelley (1975) *60d*, 22. Syed et al. (2006) *184d*, 23. Bonneville et al. (2008) *122d*, 24. Clark et al. (1999) *214d*.

of fluxes is not known. Although these factors will temper the conclusions one can draw about the influence of wetland type on CO_2 exchange, some general points can be made from the data averages presented in Figure 5. It is notable that mean values for the northern peatland groups (bog and fens), the most studied groups, are not dramatically different. They range from −45 to −60 g C m^{-2} period^{-1}. The arctic wetlands are at the low end of this range, which might be expected as they have very shorter growing seasons and usually much cooler average temperatures. The boreal rich fens, which are typically dominated by sedge vegetation and high water tables, are at the high end of the range. The conditions in these wetlands that tend to promote large NEE are the fast growing nature of the dominating sedge plants and the high water tables, which

restrict ecosystem respiration. Trees were present at two of the three wetland types with very high NEE (treed fen and swamp), these wetlands had larger LAIs compared to most non-treed wetlands and they were also both wet systems where ER may have been limited (Clark et al. 1999). The other site, a cattail marsh, also had high LAI (maximum = 3.6). Unfortunately, there are only one or two samples in each of these classes; more studies in these ecosystems are needed before definitive conclusions can be drawn.

ANNUAL CO_2 EXCHANGE

From the perspective of the atmosphere carbon balance, it is the annual exchange of CO_2 that is of prime importance. At middle and northern latitudes, there is a period where the plants are senesced and the upper soils may freeze or be covered with snow. During this period the photosynthesis stops yet ER still continues, albeit at a reduced rate. This non-growing season loss can be an important contributor to the annual NEE. Until recently, annual NEE measurements were not available; yet a few researchers had attempted to estimate annual NEE from modeling or statistical approaches (e.g. Soegaard and Nordstroem 1999). The first complete measured annual time series of daily NEE for a natural wetland was presented by Lafleur et al. (2001) for a bog in southern Canada (Figure 6). The annual trend in NEE indicates a pattern not unlike the typical diurnal
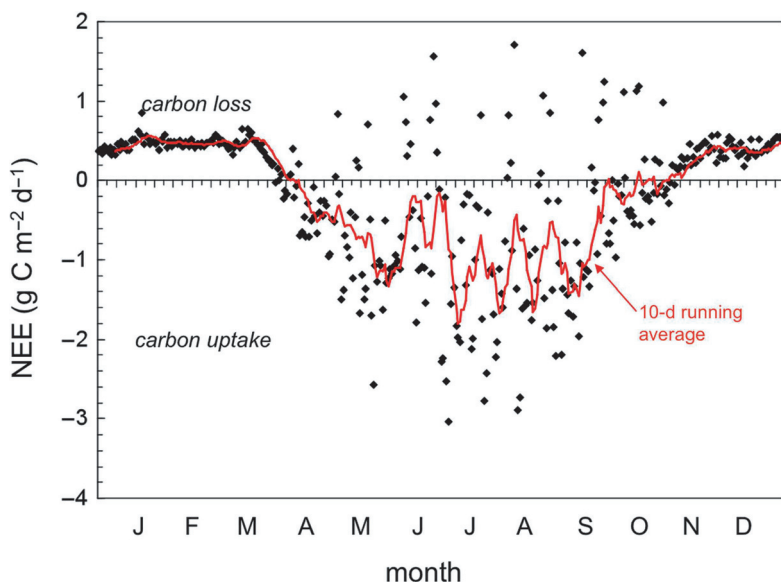

Fig. 6. Annual time series of daily NEE (diamonds) for the Mer Bleue bog in 1999. Red line is a smoothed time series created from 10 day averages. Data after Lafleur et al. (2001).
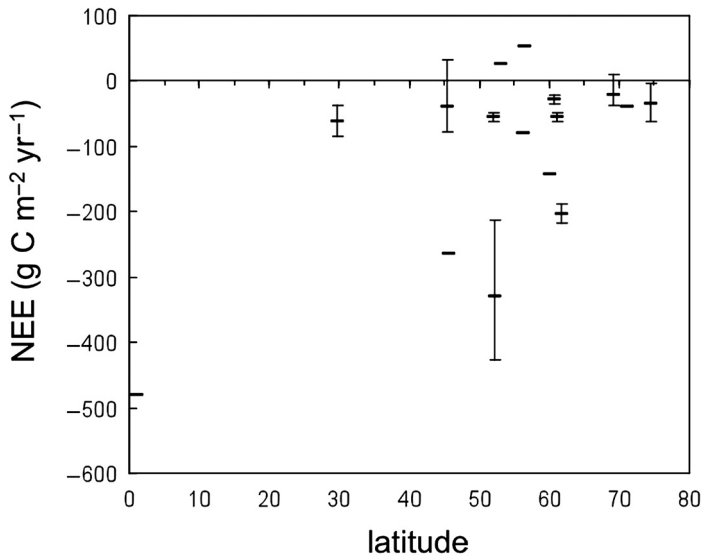
Fig. 7. Survey of annual NEE measured at wetland sites sorted by latitude. Bars are mean values and whiskers represent the range where more than 1 year was studied.

cycle (shown above – Figure 2b). Small, but steady, losses of CO_2 occur in the winter months, NEE slowly shifts to a net uptake situation in spring and reaches a summer peak uptake, then declines throughout the late-summer and autumn becoming a loss again. Most importantly, this research showed that the total sum of the CO_2 losses in winter offset about 25–40% of the growing season NEE gains (Lafleur et al. 2003). In other words, losses during the non-growing period are an important component of annual carbon balance of wetlands. Subsequently, a number of studies have confirmed the importance of winter losses to the annual NEE of various wetlands (Aurela et al. 2002, 2004, 2007), even in non-snowy environments (Sottocornola and Kiely 2005).

In spite of winter losses, where the winter may comprise up to 8 or more months of the year, most measured estimates of annual NEE for wetlands indicate small to modest sinks for atmospheric CO_2 (Figure 7). There is considerable variation in annual NEE between sites. The largest CO_2 sink in this data set was recorded at a tropical papyrus swamp (Saunders et al. 2007). As noted above, CO_2 exchange rates can be very large for tropical wetlands. Although no other measurements of annual NEE for tropical wetlands are available at this time, modelling studies suggest that in some tropical systems annual NEE may be 2 to 3 times larger than this measured flux (Jones and Humphries 2002). Two other large CO_2 sinks appear in Figure 7. One was at a temperate marsh (Bonneville et al. 2008) and the other was at a disturbed peatland meadow, which had been used previously for agriculture (Hendriks et al. 2007). In the disturbed case, the

large sink was attributed to a recent elevation of the water table, which limited ER, the cessation of the agricultural management, and residual fertilization from previous agriculture, which enhanced photosynthesis. In contrast, the temperate cattail marsh was a relatively pristine site, indicating that certain natural wetlands may be capable of sequestering large amounts of atmospheric CO_2. More studies on this type of wetland are needed to confirm this finding.

The annual sink for most wetlands was between −20 and −100 g C m^{-2} year^{-1} (Figure 7). Only two studies showed a net annual loss. One was at a disturbed bog in the Netherlands (Nieveen et al. 1998) and the other was at a Russian bog during a drought year (Arneth et al. 2002). Overall, the average annual CO_2 uptake from this survey of wetlands was −85 ± 142 (standard deviation) g C m^{-2} year^{-1}. Extrapolating this value over the global wetland area gives an annual uptake of ∼0.75 Gt C year^{-1}. This is somewhat higher, but of the same order of magnitude, as given for other estimates of the global wetland sequestration of CO_2 (Mitra et al. 2005). For comparison, the net annual uptake for the globe's forest biomes is estimated at 1.5–2.0 Gt C year^{-1} (Houghton 2005).

METHANE EXCHANGE

Despite its very low concentration in the atmosphere, CH_4 is a highly reactive gas with a capacity to absorb infrared radiation many times greater than that of CO_2. The atmospheric concentration of CH_4 has risen dramatically in recent decades, mostly through human activities. Although there is considerable uncertainly about the global methane budget, wetlands are believed to be the largest natural source of atmospheric CH_4. They account for about one quarter of all emissions, with an estimated annual global emission of 109 to 145 Tg C (Bartlett and Harris 1993; Lelieveld et al. 1998[5]). Thus, an understanding of wetland CH_4 fluxes is crucial for global climate studies. Two previous high quality reviews of the subject have been provided by Bartlett and Harris (1993) and Whalen (2005). The following brief summary draws heavily from these works.

Methane is both produced and consumed in wetland soils through the work of soil microbes, such that the flux to the atmosphere is the net effect of these two processes (Figure 1). The CH_4 producers (methanogens) exist in anaerobic environments where oxygen is limited, thus are found mostly below the water table in the wetland. Ecologically, these micro-organisms feed off of the by-products of other microbes that carry out the decomposition of organic material. The CH_4 consumers (methanotrophs) exist in the aerobic, unsaturated environment above the water table. In both cases, there is no single bacterial species involved; instead these two groups represent a host of species, some performing their tasks in different ways, which adds to the great complexity of the processes. A detailed discussion of the microbiology of CH_4 is beyond the scope of this review,

interested readers are directed to the two reviews noted above and references within.

It is clear that the net CH_4 flux in wetlands must be strongly related to the hydrology, specifically the position of the water table. In general, where the water table is close to or above the soil surface CH_4 flux is larger, because there is little opportunity for methane consumption. As the water table falls below the surface the rate of consumption (i.e. oxidation) increases and the net flux to the atmosphere decreases. Unfortunately, this simple explanation cannot account for all spatial and temporal variation in observed CH_4 fluxes. The constraints on CH_4 production and the mechanisms by which it is transported to the wetland surface can vary greatly. There are three main mechanisms by which CH_4 is transported in the wetland: diffusion, ebullition and conduction along vascular pathways. Diffusion represents the slow, homogeneous transport of CH_4 molecules along a concentration gradient. As CH_4 concentrations are many times higher in the zone of production, smaller in the unsaturated soil and smallest in the atmosphere, this gradient directs CH_4 upward from high concentration to low concentration following Fick's Law of Diffusion. The rate of diffusion is determined by the size of the gradient and characteristics of the soil. It is the least efficient of the three mechanisms.

Ebullition is transport of gas within bubbles. CH_4 produced below the water table is mostly in a dissolved form, however, where diffusion is restricted the dissolved concentration can quickly become supersaturated and gas bubbles form. These bubbles can then be released and the gas escapes in an episodic event, where it is rapidly transported to the surface with little exposure to oxidation. Soil structure, water table depth, and atmospheric pressure all influence ebullition, making it an effective but highly unpredictable process (Baird et al. 2004). Some researchers have been successful in relating the CH_4 flux to changes in atmospheric pressure, under the notion that sharp decreases in pressure initiate the release of trapped CH_4 bubbles in the peat soil matrix (Shurpali et al. 1993; Tokida et al. 2005). The contribution of ebullition to the total methane flux can range from near zero to upwards of 80% (Whalen 2005).

CH_4 is transported through the vascular systems of certain wetland plants, such as sedges, grasses and reeds. This is believed to be the reason that many researchers find a close relationship between CO_2 uptake and CH_4 emissions. Although it is a complex mechanism, of which many aspects are still uncertain, most research agrees that (i) plant-mediated transport is an important pathway for CH_4 emission in some environments, (ii) its effectiveness is likely species related, and (iii) although plant roots can enhance or suppress the production of CH_4, production seems to be greater in plots with plant roots present compared to those without roots (Joabsson et al. 1999).

Given this very complex set of circumstances controlling production and transport of CH_4, it is not surprising that it is difficult to formulate

generalizations about the flux and its controls. CH_4 fluxes typically vary over several orders of magnitude in space and in time. From the discussion above, water table depth (WTD) is a likely factor to explain variations in CH_4 fluxes. Indeed, laboratory studies on peat columns often show CH_4 flux strongly related to WTD (Moore and Dalva 1993). However, few researchers find strong relationships between CH_4 efflux at a given wetland site. Instead, a number of researchers have shown that CH_4 flux is only related to WTD when sites with a wetland are averaged over a season (Bubier et al. 1993, 2005; Waddington and Roulet 1996) or averages from a range of wetland sites are used (Moore and Roulet 1993; Roulet et al. 1992). Typically, the logarithm (base 10) of CH_4 flux varies linearly with WTD. Interestingly, the slopes of these relationships tend to be similar, but the regression constants are dissimilar. This finding would suggest that many wetlands have similar sensitivity to WTD changes, perhaps because this variable is the dominant physical control over methane oxidation. Differences in CH_4 production and transport mechanisms are responsible for variations in base CH_4 emission rates reflected in the regression constants.

Temperature is also likely to exert a strong control over CH_4 flux. While it has only minor influences on the mechanisms for CH_4 transport, temperature directly influences CH_4 production, and to a lesser extent consumption, because the metabolic processes are strongly temperature related. Temperature coefficients for wetland soil that describe the sensitivity of CH_4 production to a ten degree change in temperature (Q_{10}) range dramatically, between 1 and 35 (Whalen 2005). This wide range of Q_{10} values is attributed to experimental factors (temperature range used, length of study), soil factors (moisture, pH and nitrogen content), and variation in the microbial populations. Again, with such a complicated process, it is not surprising that field studies at individual sites have difficulty relating CH_4 emissions to temperature. As with water table, the best relationships are found when data are averaged across sites and in time (Moore and Roulet 1993; Moore et al. 1990; Pelletier et al. 2007). Such relationships also share similar characteristics as the WTD relationship: they tend to be logarithmic in nature, have similar slope coefficients between sites, but differ in the regression constant. This suggests that sensitivity to temperature may be similar across wetlands, but base rates of CH_4 emission vary between wetland types (Bartlett and Harris 1993). Although not as well-studied, the consumption of CH_4 seems to be less sensitive to changes in temperature than production, both the range and median of Q_{10} are smaller (Whalen 2005). This difference in temperature sensitivity raises the intriguing possibility that the wetland CH_4 flux may increase with climatic warming.

Various authors have produced summaries of measured wetland CH_4 fluxes (Bartlett and Harris 1993; Crill et al. 1992; Matthews and Fung 1987). It is clear from these works that the foremost characteristic of wetland CH_4 emissions is the large spatial and temporal variation, often over three orders of magnitude even at the same wetland. When available
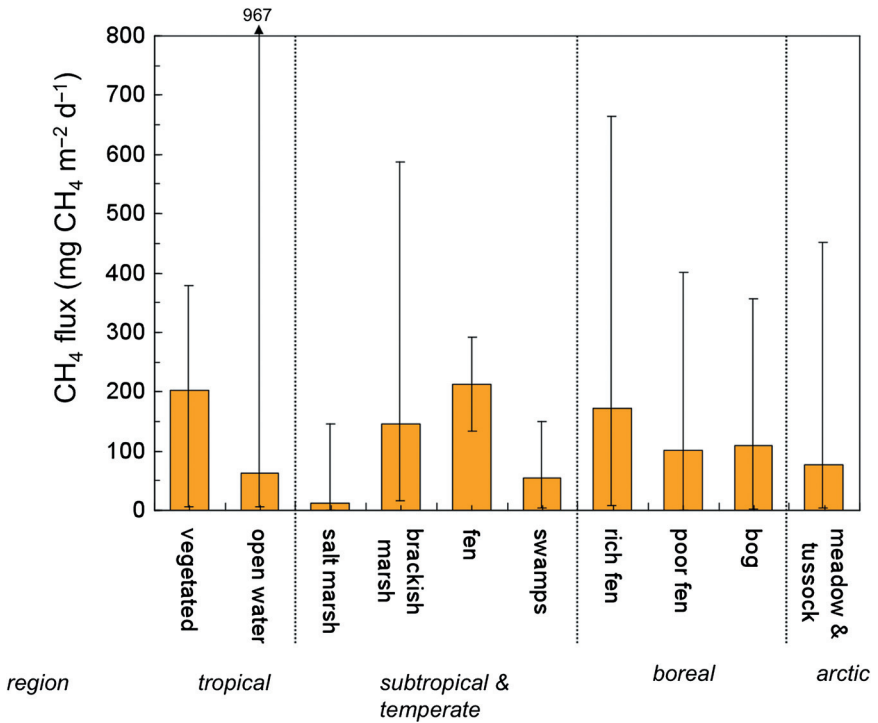
Fig. 8. A survey of methane measurements from wetlands. Bar represent mean daily flux and whiskers represent the range of values. Data are derived from mean fluxes reported by various authors given in Bartlett and Harris (1993).

data are summarized by region and wetland type (Figure 8) it gives the impression that there may be important differences in CH_4 flux among wetland types. However, the variation within any one group is larger than its mean value. In addition, because such comparisons are constructed from average values for each study, the individual flux measurements vary by at least an order of magnitude more than what is shown here. Thus, even though it is very difficult to characterize fluxes by wetland type, such data sets are essential for deriving estimates of regional and global emissions and for parameterizing and validating models of gas flux.

The data comprised in Figure 8 were collected almost exclusively via small chambers that isolate a small (typically < 1 m²) portion of the wetland. This technique is widely used, because it is inexpensive and is very useful for determining the flux from different wetland vegetation communities. However, the results are discontinuous in time and space and must be scaled to the whole wetland to be of use for carbon budgeting. Flux measurements using the eddy covariance technique, which provide an integrated flux from a considerable portion of the wetland and are continuous in time, have been made at only a few wetlands (e.g. Kim et al.

1998; Shurpali et al. 1993; Suyker et al. 1996). Eddy covariance measurements generally support the findings from chamber studies and have provided new insights into the diurnal and seasonal evolution of wetland CH_4 emissions and their relationship with environmental factors. Recently, the first annual time series of CH_4 flux from a wetland was completed at a fen in southern Finland (Rinne et al. 2007). These authors found that emissions occurred throughout the year following a distinct annual cycle where fluxes were low in winter, proceeded by a spring pulse immediately after snowmelt, after which emissions gradually increased to a mid-summer peak and gradually declined into the fall. The annual flux was 9.4 g C m^{-2} year^{-1}, which was a significant component of the total carbon budget of this wetland, equivalent to 22% of the net annual carbon dioxide uptake.

NET ECOSYSTEM CARBON BALANCE

The complete carbon exchange at any wetland involves more than the atmospheric exchanges of CO_2 and CH_4. Chapin et al. (2006) refer to the accounting of all inflows and outflows of carbon to an ecosystem as the net ecosystem carbon balance (NECB). NECB includes atmospheric fluxes and water-borne carbon fluxes associated with dissolved and particulate forms of carbon coming into and leaving the wetland (Figure 1). As yet, few studies have examined all components of the wetland carbon budget. One example, taken from Roulet et al. (2007), illustrates the relative magnitude and year-to-year variations of NECB fluxes at a raised bog (Figure 9). This study clearly showed that there can be considerable
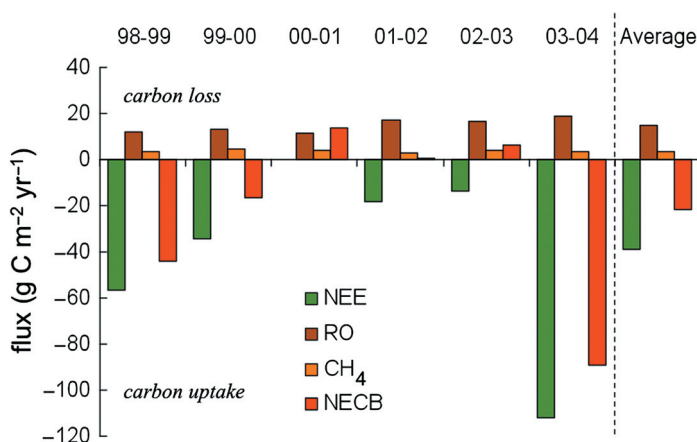

Fig. 9. Components of the complete carbon balance measured at an ombrotrophic bog in southern Ontario, Canada, over 6 years (after Roulet et al. 2007). NEE is the net ecosystem exchange of CO_2, CH_4 is the methane exchange, RO is the dissolved carbon in water runoff, and NECB is the net ecosystem carbon balance. Positive values are carbon losses and negative are carbon gains by the wetland.

Table 1. Summary of wetland carbon balance studies. Positive fluxes are carbon inputs to the wetland, negative fluxes are carbon losses. NEE is net ecosystem exchange of carbon dioxide, CH_4 is net exchange of methane, RO is waterborne net advection of dissolved carbon and methane gas into and out of the wetland, and Pr is carbon inputs from precipitation. All fluxes in units of g C m^{-2} $year^{-1}$.

Study	NEE	CH_4	RO	P_r	Total
Worrall et al. (2003)	55	−7	−37	4	14
Roulet et al. (2007)	40	−4	−16	1	21
Hendriks et al. (2007)[1]	360	−32	−17	n/a	311
Nilsson et al. (2008)[2]	51	−10	−18	1	24

[1]Data for 2005.
[2]Data averaged for 2004 and 2005.

interannual variation in the carbon budget components, particularly the NEE flux. Although NEE (typically a carbon gain) is usually the largest flux, in some years the loss of dissolved carbon by water borne flux (RO) is of similar magnitude. CH_4 efflux was quite small at this site because of the dry nature of the bog, and the inputs of carbon by rain were a very small addition (< 2 g m^{-2} $year^{-1}$) to the wetland. On average, for the six study years at this bog the atmospheric exchange of CO_2 was the largest component of the wetland carbon exchange, followed by the waterborne export (mostly dissolved organic carbon in this case), then the CH_4 efflux and finally the rain addition. These relative magnitudes in components of the wetland carbon balance are consistent with other studies of shorter duration (Hendriks et al. 2007; Nilsson et al. 2008; Worrall et al. 2003) (Table 1). Wetland type plays an important role here, as both the RO and CH_4 fluxes are largely dependent upon the hydrology of the wetland. Where water fluxes are large, as in the case of fens, fluxes of dissolved carbon also tend to be larger (Nilsson et al. 2008). CH_4 losses are greatest at the wetter sites. An important point to make here is that although CH_4 flux is one of the smallest components of this balance (in mass terms), its overall climate impact must be determined in terms of global warming potential. When considered in this way, it is often as significant as the CO_2 global warming potential (Hendriks et al. 2007).

GLOBAL IMPORTANCE OF WETLANDS GAS EXCHANGES

Despite their relatively small land area, wetlands have the ability to impact global climate through their exchange of CO_2 and CH_4, both of which are greenhouse gases that affect the radiative balance of the atmosphere. It is the net exchange of these gases that affect their atmospheric concentrations, and thus climate. The northern peatlands are believed to be the

most important wetlands for carbon storage, estimated to contain between 250 and 400 Pg of soil carbon.[6] This huge store has accumulated slowly over the past several millennia. At the same time, peatlands and other wetlands have been emitting CH_4 to the atmosphere. How these exchanges may have impacted the radiative balance of the atmosphere, and thus climate, is an important concern, especially with respect to global warming and its potential to alter these exchanges.

Based on current CO_2 and CH_4 exchange rates and a simplified set of assumptions, researchers have shown that on short time scales (20–50 years) wetlands have a net warming impact on climate and on long-time scales (500 years) they have a net a cooling impact (Friborg et al. 2003; Roulet 2000; Whiting and Chanton 2001). Furthermore, Whiting and Chanton's (2001) analysis suggested that wetland type and location were important. At intermediate time scales (~100 years) boreal wetlands were a net source, while temperate and tropical wetlands were a net sink. Later, Frolking et al. (2006) extended these analyses to include a time element by considering sustained (but constant) emissions, instead of a pulse release. They found that the present-day impact of wetlands on climate (in terms of radiative forcing) is a function of past behaviour and is likely negative, meaning that they tend to cool the planet. Recently, Frolking and Roulet (2007) produced a more realistic scenario of northern peatland impacts on the global radiation balance that included estimated changes in exchange rates of CH_4 and CO_2 and estimates of the rate of peatland development since last deglaciation (~15,000 YBP). Their model showed that early in their development peatlands were a net source of greenhouse gases to the atmosphere and the net peatland radiative forcing was to warm the planet. However, over the past 11,000 to 8000 years, they have acted to cool the planet through their net sink of greenhouse gases. Although such analyses contain considerable uncertainty, the main conclusion from these studies is that wetlands are and have been important players in global climate. In the current era of climate warming, wetlands, if left undisturbed, act to partially offset the negative impacts of human activity on our climate.

Conclusions and Future Scope

A considerable amount of research has gone into quantifying CO_2 and CH_4 fluxes from wetlands, especially the northern peatlands. However, more study is needed. The existing body of research has helped to constrain the range of expected fluxes and to identify diurnal, seasonal and annual patterns of these fluxes. In addition, the gross environmental controls on these fluxes have been investigated and significant drivers of seasonal and annual flux rates, such as drought, have been identified. A key feature of wetland trace gas flux is variability, in time and space, especially so for CH_4. Given the complexity and vast array of wetland ecosystems, such a finding is not surprising. However, it does mean that a simple ranking of

expected flux magnitudes cannot be done on the basis of wetland classifications. Some wetlands, such as temperate marshes and treed fens, may have larger exchange rates (for CO_2) than other wetland types such as non-treed fens and bogs. However, there have not been enough ecosystem-scale flux studies on these wetlands to confirm this. Some tropical wetlands have shown very large daily uptake of CO_2, but others do not. The net flux appears to be highly sensitive to the level of flooding in these ecosystems. Again, there are few studies available to draw more extensive conclusions. Few multiyear studies of trace gas exchange rates are available for wetlands, and most of these are of less than five years in duration. Longer terms studies are needed in order to investigate how shifting climate patterns might influence trace gas exchange from wetlands. Overall, there is little doubt that wetland trace gas exchanges are important in the current search to understand the global carbon cycle and our understanding of climatic change. Continued research will also improve our understanding of the functioning of these valuable ecosystems, such that they can be better managed and preserved in a changing world.

Short Biography

Dr. Lafleur received his PhD from McMaster University in Hamilton, Ontario, Canada, in 1988, where he completed a dissertation on atmosphere–wetland interactions of the James Bay coastal wetland complex. That same year he joined the Department of Geography at Trent University, where he now resides as a full professor. His research interests lay in several fields of climatology, where he specializes in research dealing with the interaction and exchanges of energy and mass between terrestrial ecosystems and the atmosphere. Since 1982, he has conducted research and published extensively on the climate aspects of arctic and boreal forest regions of Canada. He has been a member of the science steering committee of the Canadian Carbon Program (formerly Fluxnet Canada Research Network) since 1994.

Notes

* Correspondence address: Peter M. Lafleur, Geography Department, Trent University, 1600 Westbank Drive, Peterborough, Ontario K9J 7B8, Canada. E-mail: plafleur@trentu.ca.

[1] Greenhouse gases are those constituents of the atmosphere that interact with infrared radiation, absorbing and re-emitting this energy. In reality, water vapour is the most prevalent greenhouse

gas in the atmosphere and provides a strong greenhouse feeback to the surface climate. However, popular climate change discussion tends to focus on the gases that are increasing in concentration, at least in part, due to human activity, such as carbon dioxide and methane.

[2] Gt means gigatons, or billions (10^9) of tons, where 1 ton is the metric unit of 1000 kg. Some authors prefer the unit Pg or petagrams, in which peta is the prefix for 10^{15}. Since peta is 10^6 times larger than giga and there are 10^6 g in a ton, 1 Gt = 1 Pg.

[3] LAI is usually quantified as the amount of green leaf area per unit area of ground surface.

[4] PAR is solar energy in the wavelengths from 0.4 to 0.7 μm in size. The PAR flux is usually expressed in units of micromoles per unit area per unit time, that is, $\mu mol\ m^{-2}\ s^{-1}$.

[5] Tg is a teragram, 10^9 g. It is noteworthy that quantity is 10^6 g smaller than the Gt reported above for global CO_2 exchange.

[6] This value, 250–400 Pg, is equivalent to 25–50% of the current atmospheric carbon content. Northern peatlands refers broadly to boreal and subarctic peat accumulating ecosystems. The two most abundant wetland types included here are fens and bogs. However, the definition includes a number of other ecosystem types that may or may not be classified as wetlands in some classifications, such as various tundra types and treed peatlands.

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