

Are *Phragmites*-dominated wetlands a net source or net sink of greenhouse gases?

Hans Brix^{a,*}, Brian K. Sorrell^b, Bent Lorenzen^a

^a Department of Plant Ecology, University of Aarhus, Nordlandsvej 68, DK-8240 Risskov, Denmark

^b National Institute of Water and Atmospheric Research, P.O. Box 8602, Riccarton, Christchurch, New Zealand

Abstract

Phragmites australis wetlands act as a sink for greenhouse gases by photosynthetic assimilation of carbon dioxide (CO₂) from the atmosphere and sequestration of the organic matter produced in the wetland soil. The wetlands also act as a source for greenhouse gases by emission of sediment-produced methane (CH₄) to the atmosphere. In *P. australis* wetlands, the dominant mechanism of CH₄ release to the atmosphere is internal gas transport in the plants, primarily by pressurized convective gas flow. The time periods of carbon fixation and CH₄ release therefore vary seasonally and diurnally. The balance between net CO₂-assimilation and CH₄ emission determines if a wetland can be regarded as a net sink or a net source of greenhouse gases, and hence, the function of the wetland in relation to global climate change. On an annual basis up to 15% of the net carbon fixed by the wetlands may be released to the atmosphere as CH₄. Because of the different infrared absorption characteristics and atmospheric longevity of CH₄ and CO₂, the warming effect of CH₄ in the atmosphere is about 21 times higher on a mass basis than CO₂ over a 100-year timescale. Thus, the immediate carbon balance, coupled with the different physical characteristics of the two gases, would suggest that although some wetlands function as a net sink for CO₂, the wetlands still increase the greenhouse effect because of their release of CH₄. However, the short adjustment time for CH₄ in the atmosphere means that, over a longer time scale, the radiative forcing of CH₄ is less relative to CO₂ and the wetlands effectively become a sink for greenhouse gases. Wetlands may therefore be regarded as a source for greenhouse gases and so increase radiative forcing if evaluated on a short time scale (decades), but as a sink for greenhouse gases and thus attenuating radiative forcing if evaluated over longer time scales (>100 years). © 2001 Elsevier Science B.V. All rights reserved.

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* Corresponding author. Tel.: +45-8942-4714; fax: +45-8942-4747.
E-mail address: hans.brix@biology.au.dk (H. Brix).

1. Introduction

The increase in the concentration of 'greenhouse' gases in the troposphere during the last 200 years and its relation to human activities in the biosphere is now well-documented. Long-term studies of atmospheric carbon dioxide (CO₂) and methane (CH₄) concentrations, including analyses of ancient trapped gases in polar ice cores, have provided records that clearly relate the historical increases to fossil fuel burning and land use change by humans (Siegenthaler and Oeschger, 1987; Raynaud et al., 1993; IPCC, 1995).

Carbon fixation via the primary production of autotrophs and its release during decomposition have always been important processes regulating atmospheric CO₂ and CH₄ concentrations, even in prehistoric and pre-industrial times. Photosynthetic carbon uptake by terrestrial autotrophs removes CO₂ from the atmosphere, and although some of this may be rapidly recycled by respiration, much is also incorporated into the organic carbon of the soil, where its re-mineralization by microbial respiration is much slower. This organic carbon accretion in soils has always been the major terrestrial carbon sink; its longevity can vary from <10 years to many millions of years, depending on the lability of the form of organic carbon, the suitability of the soil environment for microbial activity, and the depth of the organic horizon. Most of the long-term terrestrial carbon accretion that could assist in mitigating increases in atmospheric CO₂ and CH₄ concentrations is associated either with forests, which produce large amounts of recalcitrant lignified tissue, or wetlands, where the anaerobic soil environment depresses microbial decomposition rates. Furthermore, the sub-saturation of C3 photosynthesis at modern atmospheric CO₂ levels also suggests that these communities are likely to increase their carbon storage as the atmospheric CO₂ concentration continues to rise, especially as it is now known that even old, mature forest stands have increased their carbon storage due to fertilization by the anthropogenic CO₂ increase (Grace et al., 1995).

The role of wetlands in terrestrial carbon cycling is particularly complex, however, as these environments are intimately associated with all aspects of the production and consumption of both CO₂ and CH₄. Most wetlands are net CO₂ sinks, accreting organic matter into soils over time (Bridges, 1978), but the anaerobic decomposition that allows them to accumulate such large sediment carbon deposits is also responsible for favoring methanogenic archaea as the terminal decomposers, and hence, wetlands are generally net CH₄ sources (Bartlett and Harriss, 1993). In pre-industrial times, they were the overwhelmingly predominant source of atmospheric CH₄; currently they account for some 22% of atmospheric CH₄ production as compared with the 66% produced by the anthropogenic sources that are responsible for the increases since 1830 (Cicerone and Oremland, 1988; Bartlett and Harriss, 1993). As CH₄ is generally accepted to have a much greater global warming potential (GWP) than CO₂, wetlands are usually viewed as net contributors to the balance of radiation-absorbing carbon gases in the atmosphere (IPCC, 1995). Further complicating the issue, however, are the multiple gas transport pathways and mechanisms that release CH₄ at varying rates and allow the entry of oxygen in some sites, suppressing methanogenesis and supporting CH₄-oxidizing bacteria (Chanton and Whiting, 1995). Hence, wetlands vary considerably in their carbon cycling and emissions, depending on vegetation type, water table, and climate.

In the present paper, we re-examine the net contribution of wetlands to the atmospheric carbon balance, focusing on common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) wetlands. Primary productivity and carbon cycling have been studied more extensively in this species than in most wetland plants, as it is one of the most widespread and productive plant species in the world (Clevering and Lissner, 1999). The large total area of reed wetlands and their global distribution also makes the understanding of this species' carbon cycling particularly relevant to global issues such as atmospheric carbon changes. In this analysis, we consider first the net carbon exchanges that occur in reed wetlands during growth, and the accretion of organic matter, its decomposition and CH₄ cycling. We then consider the implications of this for atmospheric carbon balances and global warming processes, especially given the different GWP and lifetime of CH₄ relative to CO₂ over different time scales.

2. Carbon cycling in *Phragmites australis* wetlands

The carbon cycling processes in wetlands dominated by *P. australis* have been studied in detail as part of the European Community 'EUREED' programme on the dynamics and stability of *P. australis* dominated wetlands (Brix, 1999). The calculations in this paper are based mainly on data from the Danish study site (Vejlerne Nature Reserve), but also data from other European sites are included to illustrate the dynamic gas-exchange in these wetlands.

2.1. Primary productivity

Reed ecosystems can have very high standing biomass values, and correspondingly high annual primary productivity. The data presented in Table 1 show the maximum seasonal biomass at eight wetland sites distributed throughout Europe. The seasonal growth patterns as well as the primary production of the stands vary considerably between sites, partly as a consequence of different phenotypic responses of the plants to the local environmental conditions and partly because of genetically fixed differences between populations. Central and

Table 1

Maximum seasonal biomass (g dry weight m⁻²; mean ± 1 S.D.) of living shoots and living rhizomes of *Phragmites australis* at sites studied as part of the EUREED II project^a

Site	Shoot biomass (g dry weight m ⁻²)	Rhizome biomass (g dry weight m ⁻²)
Umeå (Sweden)	308 ± 145	5468 ± 1245
Lake Tåkern (Sweden)	338 ± 53	4525 ± 1710
Vejlerne Reserve (Denmark)	562 ± 86	6222 ± 1056
Slotermeer (The Netherlands)	1305 ± 122	3577 ± 538
Rozmberk Fishpond (Czech Republic)	827 ± 47	3401 ± 518
Lake Fertó (Hungary)	1950 ± 792	2803 ± 987
Danube Delta (Romania)	2590 ± 230	4090 ± 757
Comana Lake, Octaploid (Romania)	4165 ± 750	11178 ± 5694

^a The biomass were estimated independently on four 1 m² plots at each site (unpublished data compiled by H. Čížkova).

southern European populations begin growth later than Atlantic populations and the maximum growth rate recorded in the first half of the growth period increases from north to south (H. Čížková, 1999, unpublished results). The maximum seasonal shoot biomass generally increases from north to south, and northern populations have greater rhizome-to-shoot ratio compared to the southern populations. This is partly explained by the limited shoot growth for the northernmost site (Umeå), while all the northern sites keep fairly high rhizome biomass. It is not known whether the high biomass is due to higher rhizome production or to a greater life span of the rhizomes in cold climates.

The annual net production of aboveground biomass in general correlates very well with the maximum standing crop of aboveground parts (see review by Westlake, 1982). The annual net aboveground production of *P. australis* is reported to be 3–15% higher than the maximum aboveground biomass because of shoot mortality, leaf shedding and grazing during the growth period (Westlake, 1982). Thus, the net annual aboveground production may be up to 5 kg dry matter for the most productive sites (Table 1; octaploid populations at the Danube Delta). The belowground production is much more difficult to estimate because roots and rhizomes grow and die at different rates and times and because materials are translocated to and from shoots (Schierup, 1978). Westlake (1982) reviewed available data and found that the ratio of belowground to aboveground production varied between 0.34 and 1.4 in different studies. He also suggested that as a rule-of-thumb the ratio between belowground and aboveground standing crop (at the time of maximum aboveground biomass) for *P. australis* is ~2.5. However, the data in Table 1 show that this ratio in general is much higher at northern (colder) sites than at southern (warmer) sites, possibly because of differences in the lifetime of the belowground tissues. Hence, from the available data it seems fair to assume that the belowground production of *P. australis* is of a similar magnitude as the aboveground production.

2.2. Sediment carbon cycling and gas release

The proportions of the carbon fixed in photosynthesis that either remain in the sediment as carbon accretion or are decomposed to CO₂ and CH₄ depend on the activity of the suite of fermentative bacteria involved in soil organic matter decomposition. During the growing season, below-ground CO₂ and CH₄ production in healthy reed wetlands is usually limited by the availability of labile, low-molecular weight organic compounds suitable for microbial respiration, and their production during this time appears to be tightly linked to the direct release of low-molecular weight carbon by rhizomes and roots during active growth, rather than the standing biomass that is accumulated (Van der Nat and Middelburg, 2000). At other times of the year, temperature limits decomposition processes, especially methanogenesis (Sorrell et al., 1997), but there is little evidence in reed ecosystems for any large amounts of carbon fixed in one season being emitted as CO₂ or CH₄ in subsequent seasons. Hence, most of the recalcitrant carbon destined for sediment accretion is derived from the standing shoot and rhizome biomass, which in reed is heavily lignified. Water table fluctuations in wetlands also confer significant temporal variation; atmospheric oxygen is drawn into sediments by lower water tables in summer, reducing methanogenesis and stimulating CH₄ oxidation (Sorrell et al., 1997; Grünfeld and Brix, 1999). Healthy reed stands in mid-summer can have very low methanogenesis rates and CH₄ emissions due to low water tables.

CO₂ and CH₄ accumulate rapidly in the interstitial water as a result of these respiratory processes, and can be released to the atmosphere via the water column either by diffusion across the sediment surface, or by the ebullition of sediment gas bubbles. The net direct contribution of below-ground carbon cycling to atmospheric releases can be readily estimated from a combination of in vitro incubations, gas bubble traps and chamber methods (Maston and Harriss, 1995). Approximately 50% of the net annual photosynthetic CO₂ fixation is ultimately respired to CO₂ and CH₄ in the sediment (see Section 2.4), but very little of this is released to the atmosphere by direct diffusive release and ebullition.

2.3. Diffusion and convective gas flow within *P. australis*

The total flux of CO₂ and CH₄ to the atmosphere in a vascular plant-dominated wetland is the sum of three inter-related processes: gas diffusion and ebullition from the sediment (see Section 2.2), and internal plant-mediated transport. In most cases, plant transport is the dominant release mechanism in vegetated wetlands, as the internal airspace system is a rapid gas pathway between sediment and atmosphere (Whiting and Chanton, 1992; Sorrell and Boon, 1994; Chanton and Whiting, 1995; Verville et al., 2000). Indeed, CH₄ release through plants is usually sufficient to strip CH₄ from the sediment gas pool and reduce the diffusive and ebullitive flux in comparison with adjacent unvegetated sediment (Chanton et al., 1989; Sorrell and Boon, 1994). Data presented here on plant-mediated release have been obtained using methods for analyzing internal gas compositions and internal pressures and flows described previously (Brix et al., 1992, 1996).

Emissions via the internal gas transport of reed can occur either by internal diffusion or pressurized convective gas flow. The two processes are not independent; the diurnal changes in internal gas concentrations achieved by convection modify rates of diffusion. Internal pressurization and flow begin shortly after sunrise and peak in the early afternoon, decreasing rapidly in the late afternoon when there is no direct sunlight incident on the pressurizing influx shoots, and ceasing at night (Fig. 1). The corresponding changes in internal CH₄ concentration (Fig. 2a) reflect the diurnal fluctuations in flow. The CH₄ concentrations in both influx and efflux culms increase during the night, as CH₄ from the sediment continues to enter the plant and accumulate in the stagnant internal gas; once flow begins after sunrise the incoming air flushes the CH₄-rich gas from the influx culms initially, then out of the efflux culms, resulting in peak emission in the early afternoon (Fig. 2b). Flow continues to maintain a higher efflux than influx concentration through the remainder of the day until sunset. The consequence of this flow-driven change in internal concentration is that the diffusive flux of CH₄ from reed beds follows the same diurnal pattern, with equivalent releases from influx and efflux culms at night but much higher releases from efflux culms than influx culms in the day-time.

Previous studies on these two transport mechanisms have shown that convective flow accomplishes much greater rates of gas transport than diffusion (Armstrong and Armstrong, 1990; Sorrell and Boon, 1994). This is also the case for CH₄ release in reed (Fig. 2b). Although diffusive release continues over the 24 h period, the rapid release achieved by convection in the day-time overwhelms the total diffusive release by a factor of >5. Hence, the diurnal pattern of release in summer largely follows the diurnal fluctuation in convection. The total daily release by plant transport is, in turn, much greater than the relatively trivial

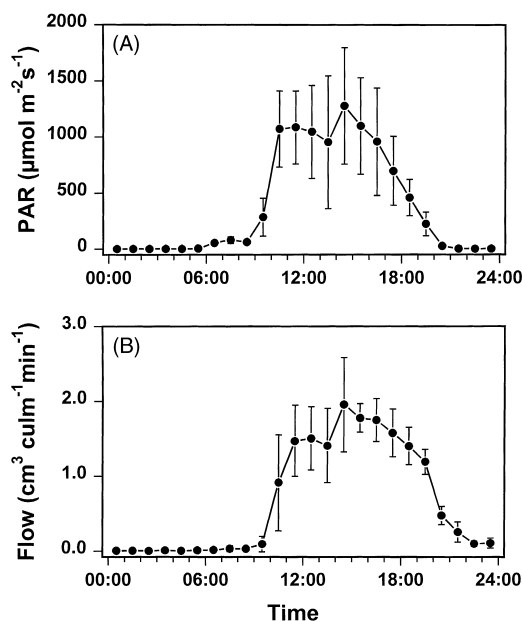


Fig. 1. Diurnal cycles of (A) photosynthetic active radiation (PAR) and (B) the corresponding internal convective gas flow in *Phragmites australis* shoots, as measured continuously in situ by the by-pass technique (Brix et al., 1996). By this technique the internal gas transport pathway is blocked by injection of a fluid into the pith cavity of one basal internode, the gas flow by-passes the blocked internode via tiny tubes, and the flow is measured by a flowmeter. Data are from Lake Opatovický (Czech Republic), July 1996. Hourly mean values \pm 1 standard deviation are shown.

release across the sediment–water interface, and accounts for most (ca. 70%) of the gross methanogenesis in the wetland. The remaining 20% not released can be accounted for by below-ground CH₄ oxidation (see Section 2.2 above) most of which will be associated with root-associated methanotrophy, driven by root O₂-release (King, 1996; Lombardi et al., 1997).

2.4. Seasonal and annual patterns of CH₄ emission and carbon dynamics

Additional variation in CH₄ emission is imposed by seasonal, spatial and geographic differences. Data in Table 2 show that emissions are much lower in winter, when methanogenesis and convective flow are reduced, and are much lower in oligotrophic habitats with sandy sediments, where the sediments are more oxidized and produce less CH₄.

Phragmites-dominated wetlands in temperate latitudes show a dramatic seasonal variation in their net carbon exchange. An example of this seasonality is illustrated in Fig. 3, which shows the seasonal cycle of net CO₂ assimilation and CO₂ and CH₄ emission from a reed-dominated wetland in Denmark. The winter months are a period of a slight net carbon release, as there is no photosynthesis but some microbial activity and gas release continues. Spring and summer are periods of net carbon fixation. The CH₄ emission is highest during

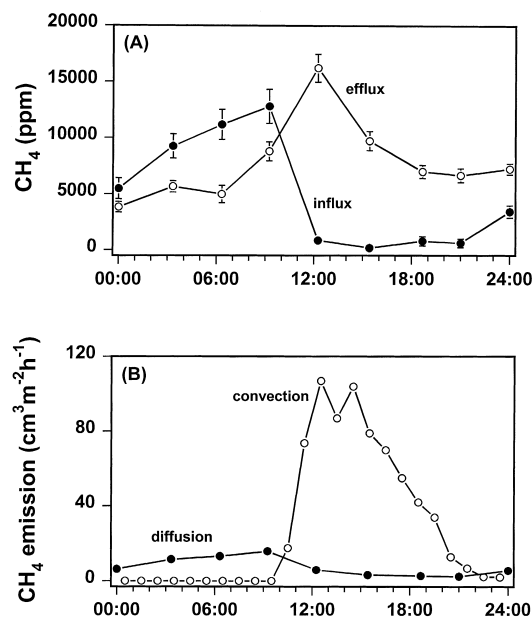


Fig. 2. (A) Diurnal changes in internal CH₄ concentrations (mean ± 1 standard error, $n = 15$) in the influx and efflux culms of *Phragmites australis*, and (B) plant-mediated emission of CH₄ by internal diffusion through the influx and efflux culms and convective gas flow through the culms at Lake Opatovický, Czech Republic, July 1996.

spring and early summer because of high water tables and high availability of labile organic compounds. During summer CH₄ emissions are very low because of a low water table at this site. The total annual carbon exchange resulting from the seasonal variation is shown in Fig. 4. These data reveal that for this particular reed wetland, on an annual molar basis, 17 of the 98 mol m⁻² year⁻¹ fixed in photosynthesis is respired to CH₄ by methanogenesis,

Table 2

Comparison of rates of CH₄ emission from *Phragmites australis* wetlands of different trophic states and in different seasons

Site	Characteristics	CH ₄ emission (cm ³ m ⁻² day ⁻¹)
Lake Øje (Denmark)	Sandy, ice-covered, winter	10
	Summer	160
Lake Brabrand (Denmark)	Organic, ice-covered	64
Kalø Reed Bed (Denmark)	Constructed wetland, April	160
Vejlerne Reserve (Denmark)	July — low water table	13
	September — high water table	37
	Dying back stand, September	170
	Dead stand, organic sediment	600
Lake Fertó (Hungary)	Healthy stand, organic, July	270
Lake Opatovický (Czech Republic)	Eutrophic lake, July	1070

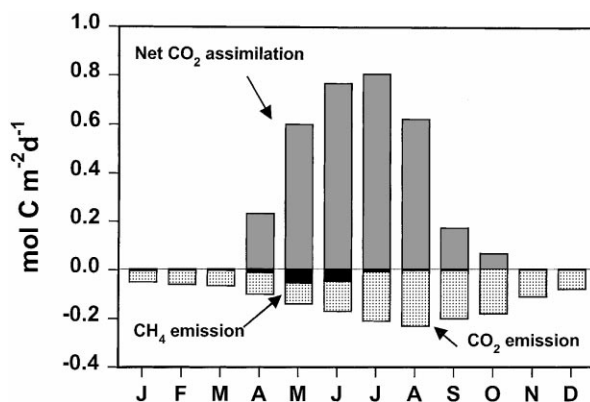


Fig. 3. Estimated seasonal cycle of net CO₂ assimilation and CO₂ and CH₄ emission from a *Phragmites australis* wetland at Vejlerne Nature Reserve, Denmark. Net CO₂ assimilation rates are estimated based on harvest techniques and measurements of growth in permanent plots throughout three seasons. The CH₄- and CO₂-emission rates are largely based on studies performed by gas-exchange chambers (the head space technique) on 10 occasions over 2 years.

but 76% of this CH₄ (13 mol m⁻² year⁻¹) is re-oxidized to CO₂ by CH₄-oxidizing bacteria in the rhizosphere, roots and rhizomes. The annual release of CH₄ is therefore just 24% of methanogenesis, or 4% of net annual CO₂ assimilation. Note also that the fate of the remaining carbon is either direct or indirect respiration back to CO₂ (49% of assimilation), which is emission-neutral, or long-term organic carbon accretion (47% of assimilation). It must be noted that this budget is prepared assuming that there is no net import or export of organic matter to or from the system.

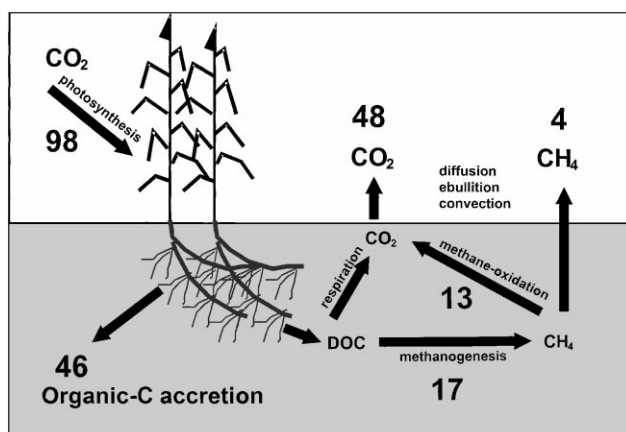


Fig. 4. Summary of estimated rates of carbon cycling in the *Phragmites australis* wetland at Vejlerne Nature Reserve, Denmark. Figures denote the estimated annual rates of the processes indicated (unit: mol C m⁻² year⁻¹). Emissions of CO₂ and CH₄ to the atmosphere occur mainly through the air-space tissue of the plants by diffusion and convection.

3. Net contribution of *P. australis* wetlands to radiative forcing

In common with most other wetlands, reed ecosystems are net molar sinks for carbon but are net emitters of CH₄. The significance of this for atmospheric carbon balances and for radiative forcing issues is complex, depending on the relative infrared absorbance of CO₂ and CH₄, the atmospheric chemistry of the two gases, and the proportion of the net carbon fixation in the ecosystem that is emitted as CH₄.

In order to compare the radiative forcing of CH₄ with CO₂, CH₄ emissions are converted to equivalent CO₂ emissions using GWP as a conversion factor. Rodhe (1990) initially proposed a GWP of 70 for CH₄ on a kg per kg basis, based on the instantaneous difference in the heat absorption characteristics of the two gases, and the so-called 'direct' effects of CH₄ emission on atmospheric chemistry. Subsequent revision of the GWP has taken into account estimates of the 'indirect' effects of CH₄ (i.e. production of tropospheric ozone in the contemporary atmosphere and stratospheric water vapor) and the relative longevity of the two gases (IPCC, 1995). The latter has also been modified, taking into account not only the simple CH₄ lifetime based on a budget of burden divided by global source strength, but also the chemical feedbacks of CH₄ on its own lifetime; the 'adjustment time' for CH₄ in the atmosphere is now calculated as 12.3 ± 3 years. Current GWP values therefore include a timescale consideration, so that the kg per kg GWP for CH₄ is 56, 21 and 6.5 for time horizons of 20, 100 and 500 years, respectively (IPCC, 1995). These adjustment times recognize the exponential decay of CH₄ in the atmosphere, as opposed to the more prolonged decay of CO₂ with a lifetime of ca. 120 years.

The short adjustment time for CH₄ relative to the lifetime of CO₂ in the atmosphere is highly significant as this is the context for the extent to which CH₄ emissions from wetlands contribute to radiative forcing effects. The contribution of wetlands to radiative forcing is therefore dependent on the ratio of CH₄ released to annual net carbon fixed, which in general for wetlands varies between 0.05 and 0.13 on a molar basis (Whiting and Chanton, 1997), and the GWP over a particular timescale as expressed in molar units (GWP of CH₄ = 20, 7.6 or 2.4 mol mol⁻¹ for time horizons of 20, 100 and 500 years, respectively). Hence, whether or not a wetland is a net contributor or net sink for the global warming effect depends on the time period their carbon cycling is considered over. Fig. 5 shows how the net global warming effect of a wetland approaches unity over time, beyond which wetlands are net greenhouse sinks in spite of the CH₄ they produce, and that the lower the molar ratio, the sooner this point is reached. Our data provide a molar ratio of 0.09 for the Danish *P. australis* wetland (Fig. 5), indicating that this wetland can only be considered as a global warming source over timescales <60 years. This calculation recognizes that the decomposition of CH₄ produced from wetlands results in a CO₂ molecule that is emission-neutral in the context of the overall wetland gas exchange. Uncertainties that could affect this estimate include the accuracy of current GWP figures (IPCC, 1995), and the prevailing conditions during plant growth. Changes in productivity and carbon cycling as the atmospheric CO₂ and temperature increase can result in different rates and proportions of aerobic:anaerobic decomposition (Bowes, 1993), and the longevity of the sediment carbon sink. Also, production and emission of other greenhouse gases such as N₂O, which has been ignored in this paper, must be evaluated.

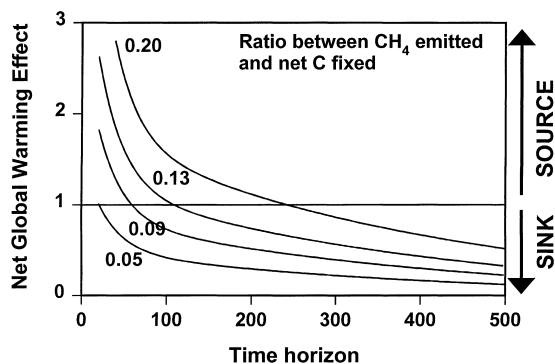


Fig. 5. The relative net radiative forcing (relative to CO₂) over time for wetlands where the molar ratio between CH₄ emitted and net C fixed is 0.20, 0.13, 0.09 and 0.05, respectively. Whiting and Chanton (1997) reported that the ratio between CH₄ emitted and net C fixed for a range of wetlands generally varies between 0.05 and 0.13. In the present study, a ratio of 0.09 for a temperate *Phragmites* wetlands was found. When the curves are located above 1, the wetland can be regarded as a source for greenhouse gases and so will increase the global warming, and if the curves are located below 1, the wetland can be regarded as a sink for greenhouse gases and thus will attenuate the global warming.

The common perception of wetlands as contributors to global warming nevertheless appears to be a consequence of the short time scales of most studies of their gas exchange. The lifetime of natural wetland ecosystems varies from hundreds to thousands of years (Thompson and Hamilton, 1983), and in this context their overall function is as a sink in global warming effects, unless they have a very low net carbon fixation relative to their CH₄ emission. The case for created wetlands is that they are likely to be net contributors to global warming early in their lifetime, but can become net sinks as they age, again depending on the net C fixation and molar ratio. Management practices should therefore act to favor net carbon fixation and accumulation in both natural and created wetlands as much as possible, if climate change issues are under consideration.

4. Conclusions

The primary productivity of *P. australis* wetlands is high, and the fate of the carbon they fix varies seasonally and diurnally. Approximately 50% of the net primary production is respired to CO₂ and CH₄ in the sediment, with methanogenesis limited primarily by organic matter availability in the growing season and temperature at other times. Diffusion across the water interface and bubble ebullition are insignificant mechanisms of CH₄ release to the atmosphere in *P. australis* wetlands, with the major mechanism being internal plant transport — especially the diurnal convective gas flow. The resulting annual pattern is a net molar C uptake during the growing season, with a small net molar C release as CH₄ and CO₂ in the winter; CH₄ release is about 4% of photosynthetic CO₂ fixation and 9% of the net C fixation in the wetland. On the basis of current GWP values for CH₄ relative to CO₂ and the molar ratios, the *P. australis* wetland illustrated can be viewed as net sources of greenhouse gases

over timescales <60 years, but net sinks over longer timescales. Wetlands may therefore be regarded as a source for greenhouse gases and so increase the global warming in evaluated over a relatively short time horizon (decades), but as a sink for greenhouse gases, and thus, attenuating global warming if evaluated over longer time horizons (>100 years).

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