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Methane emission to the atmosphere through emergent cattail (*Typha latifolia* L.) plants

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ABSTRACT

Methane (CH_4) produced microbially in sediments of marshes is emitted to the atmosphere primarily by flowing through and out of emergent aquatic plants. The magnitude of such emission rates and factors controlling those rates are not well understood. We evaluated CH_4 emission from the widely distributed aquatic emergent plant cattail (*Typha latifolia* L.) in several wetlands in the United States using a field gas-exchange system that concurrently estimated stomatal aperture (i.e., conductance) on the surface of leaves and net photosynthesis. We compared gas exchange among plants of different age and from sites with different soil and atmospheric conditions. The mean rate of CH_4 emission was 0.22 μmol m^{-2} [leaf] s^{-1}, which is 940 mg CH_4 m^{-2} d^{-1} on a ground-area basis, with individual rates ranging from 0.01 to 1.49 μmol m^{-2} [leaf] s^{-1}. For individual plants, we found emission rates were (i) highest for the part of the leaf about 1.0 m above the waterline and lower near the leaf tip and close to the leaf base, and (ii) highest near midday and lower soon after sunrise and towards sunset. We also found the ease that CH_4 moves in a sediment-plant-atmosphere continuum seems to increase with plant age. We propose that a series of factors influences CH_4 emission from *Typha latifolia* to the atmosphere; stomatal conductance and plant age are as important as the amount of microbially produced CH_4 in the wetland sediment.

1. Introduction

The discovery that wetlands emit CH_4 to the atmosphere has stimulated a large effort during the past decade to estimate the magnitude of the emission (Bartlett and Harriss, 1993 and references cited therein) and to establish links between emission rates and regional to global patterns in the atmospheric concentrations of CH_4 (Fung et al., 1991). Such linkages are central to studies of global climate change (Prinn, 1994) because CH_4 plays such a fundamental role in the chemistry and radiation budget of the earth's atmosphere (Ramanathan et al., 1985).

In particular, marshes dominated by emergent aquatic plants cover only 0.27×10^{12} m^2 globally (i.e., 5% of the world's wetlands) but account for about 21% of the 80 Tg emitted per year from all wetlands to the atmosphere (Aselmann and Crutzen, 1989). One explanation for this paradox (i.e., a relatively high emission rate of 250 mg CH_4 m^{-2} d^{-1}) is the finding in the 1970's that CH_4 produced microbially in marsh sediments was able to flow into, through and out of emergent aquatic plants (Dacey and Klug, 1979). Accordingly, emergent plants seem to enhance CH_4 emission to the atmosphere, as indicated by higher emission rates from vegetated than non-vegetated parts of marshes (Chanton and Dacey, 1991 and references cited therein; Chanton et al., 1992; Torn and Chapin, 1993). It is important, therefore, to consider emergent plants in studies of CH_4 emission to the atmosphere along with microbial production

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and consumption of CH_4 within the sediments (cf., Schütz et al., 1989; Chanton and Dacey, 1991). In this paper, we evaluated CH_4 emission from the aquatic emergent *Typha latifolia* to the atmosphere. This species is common and dispersed widely in North America from Alaska to Mexico (Hotchkiss, 1972). By sampling *Typha latifolia* in several wetlands we took advantage of natural variation in environmental conditions and plant physiology to (i) provide a reasonable regional estimate of CH_4 emission for a widespread wetland type (e.g., Whalen and Reeburgh, 1990; Moore et al., 1994), and (ii) provide insight into environmental factors that might regulate emission rates.

The perspective of this study is that CH_4 emission from *Typha latifolia* is a function of (i) the concentration gradient driving CH_4 transport in the soil-plant-atmosphere continuum and (ii) plant gas exchange characteristics (i.e., photosynthetic rates and stomatal conductance), which respond to natural fluctuations in ambient environmental conditions such as sunlight (i.e., photosynthetic photon flux density [PPFD], 0.4 to 0.7 μm), temperature and humidity (Knapp and Yavitt, 1995). We specifically addressed the following hypotheses.

(1) The rate of CH_4 emission from *Typha latifolia* to the atmosphere varies along the length of individual leaves (i.e., depth in the canopy) and among leaves of different age.

(2) The rate of CH_4 emission from *Typha latifolia* to the atmosphere varies during the course of the day.

(3) The rate of CH_4 emission from *Typha latifolia* to the atmosphere varies geographically, in particular, related to the length of the growing.

2. Materials and methods

2.1. Study sites

Between July 1992 and November 1993, we sampled *Typha latifolia* populations in nine sites (Table 1), which varied from relatively small seeps and sloughs to river bank and extensive open marsh systems. *Typha latifolia* was the dominant in each site, except possibly *Typha latifolia* × *domingensis* in Florida. At this site, we selected shoots with morphological and reproductive characteristics most similar to *Typha latifolia* (i.e., leaves greater than 1.5 cm in width; Smith, 1967).

2.2. Methodology for gas exchange, CH_4 concentrations and CH_4 emission

Stomatal conductance and net photosynthetic rates were measured with a field-portable, closed flow system (LI-COR model 6200, Licor Inc., Lincoln, Nebraska) and a 250 ml plexiglass cuvette. These measurements occurred within 30 s after closing the cuvette around individual leaves, assuring the CO_2 concentration in the cuvette decreased by no more than 5 to 10 μl liter^{-1} during these measurements. The leaves remained in the cuvette for an additional 3 min, and relative humidity and vapor pressure deficits were held at ambient levels by adjusting the portion of gas that flowed through a desiccant. Leaf and air temperatures were monitored with fine-wire thermocouples (± 0.1°C) and remained within 2°C of ambient conditions for the 3 min enclosure.

We estimated CH_4 emission by taking 10-ml gas samples with plastic syringes (i) just before closing the cuvette, thus sampling ambient air at the same place in the plant canopy where the cuvette was placed, and (ii) from the cuvette headspace (405 ml total volume) 1, 2, and 3 min after closure. The syringes (20 cm^3 capacity, disposable polypropylene syringes, Becton Dickson Brand, Franklin Lakes, New Jersey, USA; equipped with 3-way nylon stopcocks, Baxter Healthcare Corporation, Edison, New Jersey, USA) served as storage vessels until gas analysis within 72 h of collection. We did several preliminary studies to confirm that the chamber did not leak (i.e., injecting CH_4 tracer into cuvette with and without plants). We also accounted for contamination in preliminary studies by injecting CH_4 into the cuvette and measuring recovery after 1 to 20 minutes. During the field studies, we filled several syringes with CH_4 standards of known concentration and analyzed them along with the *Typha latifolia* samples to correct for leakage or contamination from the sample syringes. Emission rates were calculated using the linear regression of concentration versus time ($r = 0.90$).

Following each gas exchange measurement, we collected separate <5-ml gas samples from (i) the air spaces within the leaf enclosed by the cuvette and (ii) the air spaces within the plant base below

Table 1. *Characteristics of sampling sites, with latitude, for CH_4 emission from Typha latifolia plants, including information on cumulative degree days and air and sediment temperatures at the time of the emission measurements*

Site	Type	Sampling date	Cumulative degree days*	Air temp. (°C)	Sed. temp. (°C) 2 cm	15 cm
Florida (25°50′ N)	slough					
predawn		27 Mar. 1993	289	21.0	21	21
midday		27 Mar. 1993		25.5	24	22
predawn		10 Jul. 1993	1,957	23.5	28	30
midday		10 Jul. 1993		32.7	31	30
predawn		20 Nov. 1993	4,313	21.0	21	20
midday		19 Nov. 1993		25.5	22	19
New Mexico (34°20′ N)	slough					
predawn		21 Jul. 1992	709	17.2	19	20
midday		20 Jul. 1992		34.5	22	20
Kansas-Cimmeron (37°20′ N)	slough					
midday		21 Jul. 1992	682	31.0	24	22
Kansas-Konza (39°11′ N)	seep					
predawn		23 Jul. 1992	612	19.6	20	20
midday		23 Jul. 1992		28.0	22	20
predawn		15 Aug. 1993	714	22.7	19	20
midday		15 Aug. 1993		32.0	20	20
New York (42°30′ N)	marsh					
predawn		31 Aug. 1992	184	17.0	18	19
midday		31 Aug. 1992		19.5	19	19
Wisconsin (43°04′ N)	marsh					
midday		2 Aug. 1993	367	25.5	23	23
Iowa (43°15′ N)	marsh					
predawn		24 Jul. 1992	218	13.9	19	19
midday		24 Jul. 1992		19.3	19	19
Minnesota-Cedar Creek (45°19′ N)	marsh					
predawn		25 Jul. 1992	178	17.0	19	18
midday		24 Jul. 1992		23.5	19	18
Minnesota-Whiteface Rv (47°10′ N)	marsh					
midday		25 Jul. 1992	42	19.5	19	18

* One degree-day is accumulated for each whole degree that the daily mean temperature is above 65°F. Values cumulated from 1 January.

the waterline, using plastic syringes and a 25 gauge needle (about 16 mm long).

We also sampled CH_4 dissolved in sediment pore waters ($n = 3$ per site). To access pore water, we inserted a small diameter (3.2 mm) stainless steel probe (open at both ends) to a depth of 2.5 cm. The top end of the probe was connected to a sampling syringe and 10 ml of water was slowly drawn into the syringe. The probe was pushed down to a depth of 25 cm, and an additional sample was collected. Dissolved CH_4 was extracted from the water sample by shaking vigorously for 2 min. The total amount of dissolved CH_4 in a given water sample was calculated (see Flett et al., 1976 for equations) and expressed as a partial pressure (at 20°C) by:

$$pCH_4 = C_w/\beta$$

where C_w is the concentration of dissolved gas (μl liter^{-1}) and β is the temperature-dependent Bunsen coefficient. For example, 1 μl liter^{-1} of dissolved CH_4 equals 27.7 μatm of pCH_4 at 20°C.

Concentrations of dissolved CH_4 may exceed equilibrium with CH_4 in the gas phase (Pauss et al., 1990); therefore, the calculation of pCH_4 may be too low assuming Henry's law. Nevertheless, the calculation is necessary to present data from air samples and waterlogged sediment in comparable units to estimate concentration gradients in the ecosystem. Sediment temperatures were measured at both the 2- and 25-cm depths with a thermistor ($\pm 0.5°C$).

2.2. *Studies and surveys of sites*

We carried out several studies in order to understand CH_4 emission to the atmosphere as a function of position along *Typha latifolia* leaves, light level, as well as geographical region of the wetland. These studies were as follows:

(1) At three sites (Wisconsin, Kansas-Konza Prairie, and Florida), we selected mature leaves that showed little evidence of senescence (brown edges or tips) and, at midday (1100 to 1400 h) in midsummer with PPFD $> 1500\ \mu mol\ m^{-2}\ s^{-1}$, made measurements of gas exchange, CH_4 concentrations and CH_4 emission on 6 to 10 cm^2 parts of an individual leaf at three heights (i) 0.40 ± 0.05 m above the waterline (hereafter: base of the leaf), (ii) 1.0 ± 0.2 m above the waterline (hereafter: mid leaf), and (iii) 1.6 ± 0.2 m above the waterline (hereafter: leaf tip). Measurements were made on three individuals at each leaf location. All leaves were exposed to full sunlight for a sufficient period of time prior to measurement to allow for physiological adjustment.

(2) At the site in New York, we measured gas exchange, CH_4 concentrations and CH_4 emission for the outer most (oldest) and the inner most (youngest) leaf on four different shoots to evaluate exchanges and concentrations as a function of leaf age. From April to November 1992, we also sampled CH_4 concentrations in plant leaves and bases as well as in sediment pore waters using methods mentioned above. We sampled four populations and 4 to 8 plants per population.

(3) At the Kansas-Konza Prairie and Florida sites, on a cloudless day in midsummer, we measured gas exchange, CH_4 concentrations and CH_4 emission every 2 to 3 h from sunrise to sunset. We made measurements only for leaf tips at the Florida site. At the Konza site, in addition to the measurements at the leaf tip, we also made measurements at the mid leaf and base of the leaf in the morning (830 h) and again near noon (1130 h).

In conjunction with the measurements at the Kansas-Konza Prairie site, we also altered sunlight level experimentally in order to determine its effect on gas exchange and CH_4 concentrations and emission. For three mature leaves, we made measurements in full sunlight at midday (1230 h) in August; after that, the gas exchange cuvette was opened and flushed with ambient air and the entire shoot was shaded for 60 min with neutral density screen, which reduced PPFD to $350\ \mu mol\ m^{-2}\ s^{-1}$, before the measurements were made in the shade.

(4) In midsummer at each site, we measured gas exchange, CH_4 concentrations and CH_4 emission at midday (1100 to 1400 h) and at ambient temperature and humidity with levels of PPFD $> 1500\ \mu mol\ m^{-2}\ s^{-1}$, except at the Minnesota-Whiteface River and Iowa sites where cloudcover constrained high PPFD measurements. At each site, we measured gas exchange only for leaf tips on three to nine mature leaves that showed little evidence of senescence (brown edges or tips).

At each site, except Kansas-Cimmeron River and Minnesota-Whiteface River, we measured gas exchange, CH_4 concentrations and CH_4 emission about 1 h before sunrise when PPFD was $< 30\ \mu mol\ m^{-2}\ s^{-1}$. The plants were within 2 m of the those used for the midday measurements.

(5) At the Florida site, we measured gas exchange, CH_4 concentrations and CH_4 emission for leaf tips in the spring (March) and again in the late autumn (November) in order to compare to similar measurements made in midsummer.

2.3. *Data analyses*

Methane in air samples was analyzed with a gas chromatograph (Perkin Elmer, Inc., model Sigma 3B), equipped with a flame ionization detector and a 3-m Poropak-Q (80/100 mesh) column maintained at 35°C, with He carrier gas at 35 ml min^{-1}. We quantified CH_4 concentrations by comparing peak areas for samples and several standards (0.9987 to 10,300 $\mu l\ liter^{-1}$ CH_4 in N_2; Scott Specialty Gases, Plumsteadville PA). Standards bracketed every 5–10 samples. Analytical precision was $< 0.2\%$ for the lowest standard, and analytical accuracy was always within 2%. With this

system, we could measure a minimum emission rate of 0.01 μmol m^{-2} [leaf] s^{-1}.

We examine relationships among CH_4 emission versus stomatal conductance, net photosynthesis, and CH_4 concentration in plant leaves using correlation analysis. Significance differences among measurements (e.g., among positions on the leaf, among sites) were determined by analysis of variance at a significance level of 0.05.

3. Results

3.1. Patterns along individual Typha latifolia leaves

We measured CH_4 emission along *Typha latifolia* leaves at the Wisconsin, Kansas-Konza Prairie, and Florida sites. During the measurements (i.e., in midsummer and under full sunlight at 1300 h) pCH_4 in sediment pore water at the 0.20 depth (mean = 43.8 matm) was 10 times higher than pCH_4 in sediment pore water at the 0.05 m depth (mean = 4.37 matm) and 100-times higher than the concentration of CH_4 in air spaces of *Typha latifolia* stems below the waterline (mean = 462 μl $liter^{-1}$) (Fig. 1). Methane concentrations inside *Typha latifolia* leaves were significantly higher near the base of the leaf than near the middle and leaf tip, except at the Wisconsin site, and, in particular, were higher than the concentration of CH_4 in ambient air surrounding the plants.

The rate of CH_4 emission from *Typha latifolia* leaves to the atmosphere varied significantly for the three positions along the leaf, with a mean emission rate of 0.075 μmol m^{-2} [leaf] s^{-1} for both the leaf tip and base of the leaf and a rate 4.4-times higher (0.33 μmol m^{-2} [leaf] s^{-1}) for the middle part of the leaf (Fig. 2). The only difference among the sites was a significantly higher emission rate of 0.17 μmol m^{-2} [leaf] s^{-1} for the base of

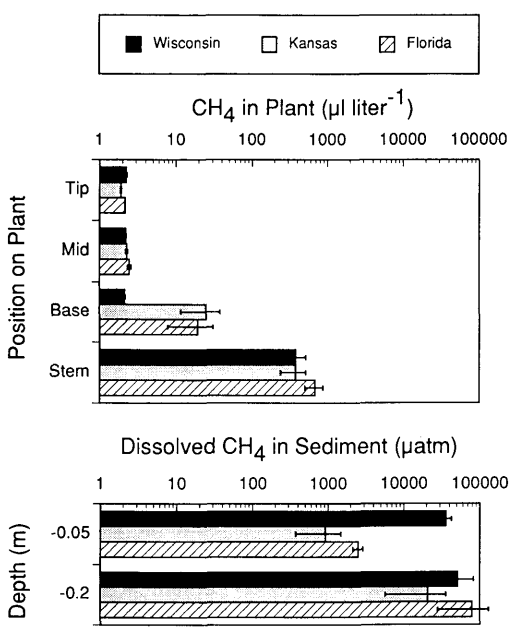

Fig. 1. Methane concentrations at different locations inside Typha latifolia plants (top panel) and in sediments of Typha latifolia wetlands (bottom panel) in Wisconsin, Kansas and Florida. Values are the mean of three measurements. Error bars indicate one SE.

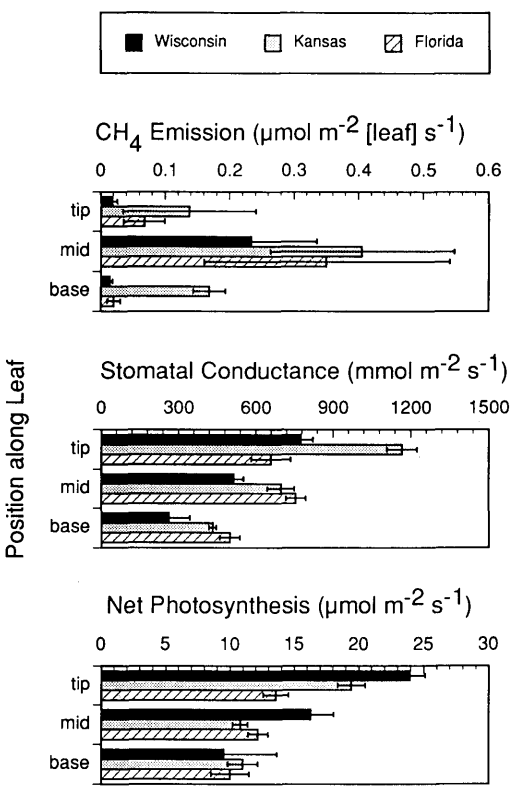

Fig. 2. Rates of CH_4 emission, stomatal conductance, and net photosynthesis made at midday (1300 h) under full sunlight (i.e., no cloudcover) for three locations along Typha latifolia leaves in wetlands in Wisconsin, Kansas and Florida. Values are the mean of three leaves. Error bars indicate one SE.

the leaf at the Kansas-Konza Prairie site versus about 0.02 μmol m^{-2} [leaf] s^{-1} for leaf bases at the Wisconsin and Florida sites. Concomitant measurements of stomatal conductance and net photosynthesis (Fig. 2) indicated a significant reduction in rates of both processes as the measurement sites decreased from the tip to the base of the leaf.

3.2. *Patterns among leaves of different age*

At the site in New York, we assessed how CH_4 emission varied among the oldest and youngest leaf on the same *Typha latifolia* plant (Table 2). Stomatal conductance and net photosynthetic rates were significantly lower (i.e., >30%) for the youngest than oldest leaf. However, mean rates of CH_4 emission did not vary significantly ($p > 0.20$) as a function of leaf age, although the concentration of CH_4 within the leaf was higher for the youngest than oldest leaf.

3.3. *Patterns during the course of the day*

At the Kansas-Konza Prairie and Florida sites where we measured CH_4 emission from the tip of *Typha latifolia* leaves to the atmosphere periodically during the course of the day in midsummer, the highest emission rate occurred in the mid to late morning (Fig. 3). In particular, emission rates were low in the afternoon. At the Kansas-Konza Prairie site, the emission rate for the middle and base of leaves also was higher near noon than early in morning (Table 3).

At both sites, CH_4 concentrations inside the tip of *Typha latifolia* leaves were maximum in early morning and decreased during the course of the day (Fig. 3). This pattern in concentration during the course of the day was even more pronounced for the plant below the water line than inside the leaf tip. Conversely, pCH_4 in sediment pore water seemed to increase during the course of the day; hence, there was a much stronger concentration gradient for CH_4 in the sediment-plant-atmosphere continuum early in the morning than after noon.

We assessed the response of CH_4 emission to shade-induced stomatal closure at midday by shading leaf tips at the Kansas-Konza Prairie site for 60 minutes (Table 4). Notably, emission rates did not differ significantly for the sun and shade measurements; however, stomatal conductance and net photosynthetic rates were significantly

Table 2. *Net photosynthesis, stomatal conductance, and CH_4 emission for the oldest and youngest leaves on Typha latifolia plants in a wetland in New York. Measurements took place at midday in July 1992; data are mean $\pm SE$ ($n = 3$)*

	Oldest leaf	Youngest leaf
Net photosynthesis (μmol m^{-2} s^{-1})	20.2* $\pm$ 0.7	9.0* $\pm$ 1.9
Stomatal conductance (mmol m^{-2} s^{-1})	340* $\pm$ 31	180* $\pm$ 19
CH_4 emission (μmol m^{-2} [leaf] s^{-1})	0.14 $\pm$ 0.05	0.15 $\pm$ 0.09
CH_4 in plant leaf (μl $liter^{-1}$)	2.42 $\pm$ 0.25	2.93 $\pm$ 0.30

* $p < 0.05$ for pairwise comparison.

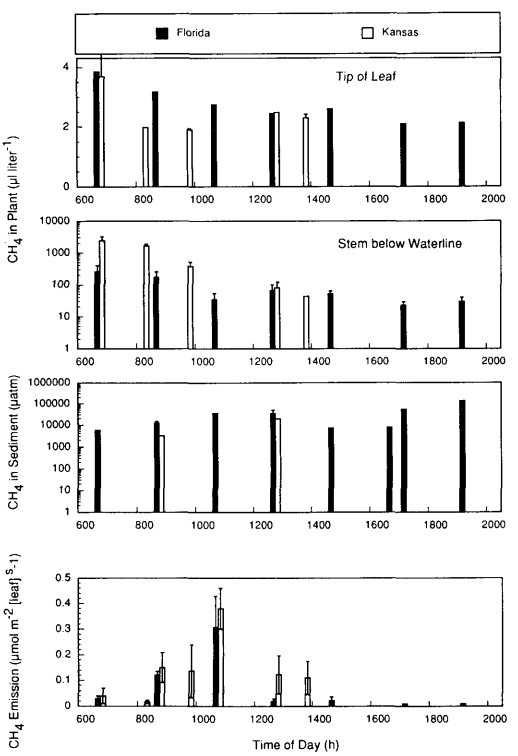

Fig. 3. Methane concentrations at two locations inside Typha latifolia plants and at the 2.5 cm depth in sediments of the wetland, as well as mean rate of CH_4 emission from Typha latifolia leaves to the atmosphere, during the course of a day in wetlands in Kansas and in Florida. Values are the mean of three measurements. Error bars indicate one SE.

Table 3. *Net photosynthesis, stomatal conductance, and CH_4 emission for two positions along Typha latifolia leaves in a wetland in Kansas; measurements took place in the morning and again near noon in August 1993; data are mean $\pm$ SE ($n = 3$)*

	Middle of leaf		Base of leaf	
	8:30 h	11:30 h	8:30 h	11:30 h
Net photosynthesis (μmol m^{-2} s^{-1})	9.5 $\pm$ 0.5	11.0 $\pm$ 1.0	8.9 $\pm$ 0.4	11.5 $\pm$ 1.1
Stomatal conductance (mmol m^{-2} s^{-1})	640 $\pm$ 65	720 $\pm$ 50	345 $\pm$ 35	450 $\pm$ 25
CH_4 emission (μmol m^{-2} [leaf] s^{-1})	0.1* $\pm$ 0.05	0.41* $\pm$ 0.14	0.1* $\pm$ 0.05	0.17* $\pm$ 0.03
CH_4 in plant leaf (μl $liter^{-1}$)	2.00* $\pm$ 0.01	2.27* $\pm$ 0.07	282 $\pm$ 188	25 $\pm$ 13

* $p < 0.05$ for pairwise comparison.

higher for leaves in the sun than when exposed to shade, as expected. The CH_4 concentration inside the tip of *Typha latifolia* leaves exposed to shade was slightly higher than that inside the tip under full sunlight. However, the concentration was 3.3 times higher within the middle of the leaf when exposed to shade than at the same sampling location in the sun, suggesting that concentrations inside the leaf were beginning to increase.

Table 4. *Rates of CH_4 emission and gas exchange characteristics under sun and shade conditions for tips of Typha latifolia leaves in Kansas; sun measurements were made in full sunlight at midday (1230 h); after that, the plants were shaded for 60 min before the shade measurements were made; data are mean (+1 SE); $n = 3$*

	Sun	Shade
Methane emission (μmol m^{-2} [leaf] s^{-1})	0.11 $\pm$ 0.06	0.12 $\pm$ 0.07
Methane concentration (μl $liter^{-1}$)		
tip	2.29 $\pm$ 0.12	2.48 $\pm$ 0.23
mid	2.58* $\pm$ 0.18	8.44* $\pm$ 1.85
PPFD (μmol m^{-2} s^{-1})	> 1500	350
Stomatal conductance (mmol m^{-2} s^{-1})	593* $\pm$ 52	371* $\pm$ 7
Net photosynthesis (μmol m^{-2} s^{-1})	22.8 $\pm$ 1.2	9.6* $\pm$ 0.4

* $p < 0.05$ for comparison between sun and shade conditions.

3.4. *Extensive survey of study sites*

For the extensive survey of sites (Fig. 4), pCH_4 in sediment pore water (mean = 15.9 matm) varied from < 2 matm at sites in New Mexico and Kansas to values of 7.0 to 82.7 matm at the other sites. The concentration of CH_4 in *Typha latifolia* parts below the waterline (mean = 1038 μl $liter^{-1}$) varied from 8.1 μl $liter^{-1}$ at midday in the New Mexico site to 5,400 μl $liter^{-1}$ at predawn in the Iowa Site. The data did show that CH_4 concentrations in stems of *Typha latifolia* below the waterline were at least 2-times higher for predawn than for midday measurements, except at the Kansas-Konza Prairie site. The concentration of CH_4 in *Typha latifolia* leaves (mean = 3.76 μl $liter^{-1}$) was always higher than the concentration in ambient air (mean = 2.56 μl $liter^{-1}$); hence, there was always a leaf-to-air concentration gradient for CH_4.

Among the sites in the extensive survey (Fig. 4), the mean rate of CH_4 emission from *Typha latifolia* leaves to the atmosphere was 0.22 μmol m^{-2} [leaf] s^{-1}, with individual measurements ranging from < 0.01 to 1.49 μmol m^{-2} [leaf] s^{-1}. At midday, the site in Iowa had the highest mean emission of 0.69 μmol m^{-2} [leaf] s^{-1} and the northern most site had the lowest mean emission of 0.01 μmol m^{-2} [leaf] s^{-1}. Comparison of measurements made at predawn versus midday at the same site indicated that the CH_4 emission rate

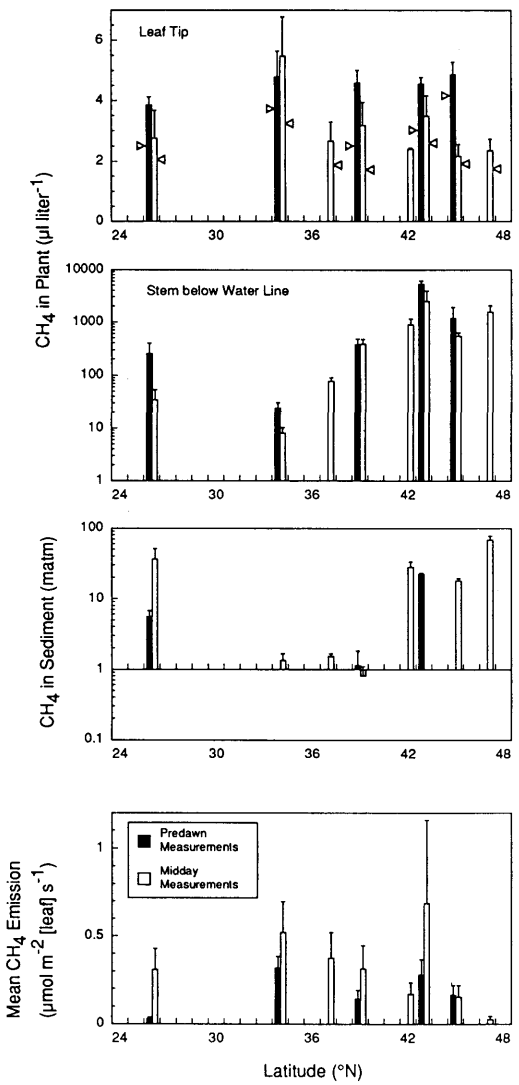

Fig. 4. Methane concentrations at two locations inside Typha latifolia plants and at the 2.5 cm depth in sediments of the wetland, as well as mean rate of CH_4 emission from Typha latifolia leaves to the atmosphere, for sites arranged according to latitude. All measurements took place in midsummer in 1992 or 1993. Values are the mean of three measurements. Error bars indicate one SE.

at midday was about 80% greater than predawn estimate, except for equal midday and predawn estimates at the Minnesota-Cedar Creek site.

Stomatal conductance (to water vapor) was consistently low at predawn among the four study sites (mean = 300 mmol m^{-2} s^{-1}, range = 260 to 325 mmol m^{-2} s^{-1}), presumably and partially the result of low PPFD (5 to 75 μmol m^{-2} s^{-1}) at this time (cf., Knapp and Smith, 1990). In contrast, mean stomatal conductance in full sunlight (> 1500 μmol m^{-2} s^{-1}) was 750 mmol m^{-2} s^{-1}, with individual values ranging from 225 to 945 mmol m^{-2} s^{-1}. Conversely, midday estimates of net photosynthetic rates were relatively similar, at least, among the six sites where gas exchange was measured under full sunlight.

3.5. *Patterns in spring, summer and autumn*

At the Florida site, we measured the same plants in the spring (March) and again in late autumn (November) in order to compare to the measurements from midsummer (Fig. 5). The concentra-

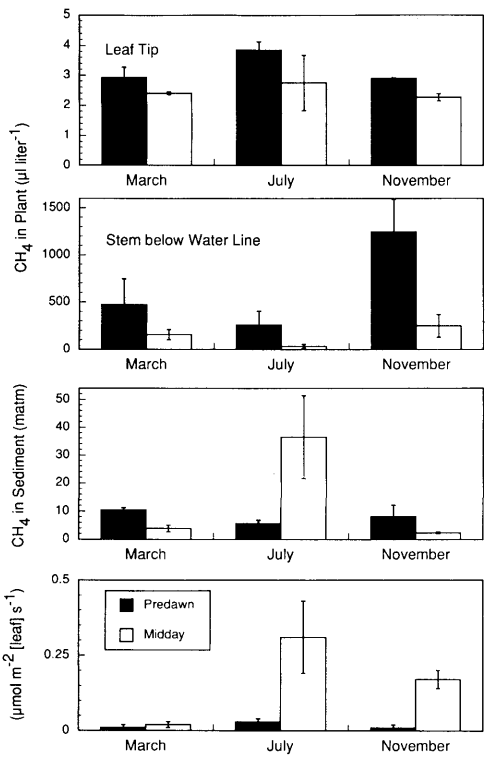

Fig. 5. Methane concentrations at two locations inside Typha latifolia plants and at the 2.5 cm depth in sediments of the wetland, as well as mean rate of CH_4 emission from Typha latifolia leaves to the atmosphere, as a function of sampling date in the wetland in Florida. Values are the mean of three measurements. Error bars indicate one SE.

tion of CH_4 within *Typha latifolia* plants and pCH_4 in the sediments did not vary significantly among the three sampling dates, despite the variance in the measurements. For example, the concentration of CH_4 in plant stems below the water line ranged from 30 to $>1600\ \mu l\ liter^{-1}$ in the data set. Further, pCH_4 in the sediment ranges from <1 matm to >40 matm in July. We did, however, find midday rates of CH_4 emission from *Typha latifolia* to the atmosphere varying significantly among the sampling dates, with rates in July greater than those in November, which were greater than those in March.

4. Discussion

4.1. Patterns among plant parts

In theory, CH_4 should flow from the sediment to and through an emergent aquatic plant along a concentration gradient; hence, the gradient drives diffusion through pores on the surface of leaves and stems to the atmosphere. There is some question whether the pores are stomata, which undergo opening and closing during the day, or micropores that remain open (see below). *Typha latifolia* also has supplemental gas flow by throughflow convection (i.e., pressurization), generated by gradients in temperature and water vapor pressure between internal lacunae and the surrounding atmosphere (Bendix et al., 1994). The highest flow rate seems to occur at the lowest ambient relative humidity and is independent of light level. Therefore, rates and controls of CH_4 emission from emergent aquatic plants to the atmosphere may vary in response to several factors, including (i) changes in concentration gradients, (ii) gas flow rate, and (iii) resistance along the flow path.

The maximum rate of CH_4 emission at the middle part of the *Typha latifolia* leaf coincided with intermediate values for plant gas exchange (e.g., net photosynthesis, stomatal conductance), which decreased from the tip to the base of the leaf (Fig. 2), as well as CH_4 concentration within the leaf that decreased from the base to the tip (Fig. 1). This suggests that neither gas exchange characteristics of leaves nor CH_4 concentration inside the leaf lacunae alone explain the variation in emission rates along the length of the leaf, and, accordingly, correlation between emission rates and stomatal conductance and CH_4 concentrations measured along the length of the leaf were not statistically significant (both p's > 0.30).

On the contrary, we can assess leaf-level variation in emission rates by the combination of stomatal conductance and the CH_4 concentration gradient using Ohm's law analogy for Fick's law that describes diffusive gas flow. We assumed for the calculation the concentration gradient from the leaf lacunae to the atmosphere drives CH_4 emission by diffusion out of stomata on the surface of the leaf; therefore, the rate of CH_4 emission by diffusion is given by:

$$J_{CH_4} = \Delta C_{CH_4} / R_{CH_4},$$

where (i) J_{CH_4} is the emission rate per unit of leaf area; (ii) ΔC_{CH_4} is the measured leaf-to-air CH_4 concentration gradient; and (iii) R_{CH_4} is the total leaf resistance to CH_4 diffusion, which is the measured resistance to water vapor diffusion corrected by the ratio of diffusion coefficients for water vapor and CH_4 (D_{H_2O}/D_{CH_4}).

We found a significant and positive correlation between the predicted and measured emission rates for data from the leaf tip and the middle of the leaf ($r = 0.812$, $n = 6$, $p = 0.047$). However, Fick's law predicted emission rates of 4.0 to $8.3\ \mu mol\ m^{-2}\ [leaf]\ s^{-1}$ at the base of the leaf, which were considerably higher than the measured rates (Fig. 2). The reason for the discrepancy is unclear; however, it seems the measured leaf-to-air concentration gradient for CH_4 at the base of the leaf is much higher than that supporting the actual emission rate. The leaf is the thickest at the base (cf., Constable et al., 1992), and the syringe needle might have collected gas from lacunae far removed from pores on the leaf surface, i.e., compared to the gas sampled from lacunae closer to surface pores for the thinner more-distal parts of the leaf.

Nevertheless, our findings suggest that CH_4 released from the upper 2/3 of the leaf occurs through stomata; hence, stomatal conductance does play a regulatory role in CH_4 emission. This disagrees with findings for rice (Nouchi et al., 1990) and some other emergent plants (e.g., Harden and Chanton, 1994) but agrees with others (Morrissey et al., 1993; Frye et al., 1994). Chanton and Dacey (1991) argue against stomatal conductance as a regulator of CH_4 emission. They hypothesize the highest resistance to CH_4 flow in the sediment-plant-atmosphere continuum occurs

at the surface of fine roots, where there is the largest concentration gradient, and thus stomatal resistance is too small to regulate the overall rate of emission to the atmosphere. However, Frye et al. (1994) showed in a mathematical model that CH_4 release through stomata is consistent with CH_4 flow in a sediment-plant-atmosphere continuum.

There is a common belief that CH_4 escapes from emergent aquatic plants to the atmosphere only through old and dead leaves or damaged shoots (cf., Dacey, 1981; Sorrell and Boon, 1994). The basis for the hypothesis is the throughflow convection of gases in the plant in which the pressure initiates in one part of the plant, while gases vent to the atmosphere where there is much less resistance to gas flow. However, Tornbjerg et al. (1994) showed that air entered middle-aged leaves on *Typha latifolia* plants, was convected down the leaf to the part of the plant below ground, and from there it was vented back to the atmosphere through both the oldest and youngest leaves. Therefore, our finding that rates of CH_4 emission to the atmosphere did not differ significantly among the oldest and youngest leaves on an individual shoot (Table 2) supports the assertion.

Our finding the highest emission rate near noon and much lower rates in the early morning and late afternoon corroborates the diurnal pattern reported by Chanton et al. (1993) for *Typha latifolia* in Florida. They contend that emission rates fluctuate during the course of the day because there is an accompanying diurnal pattern in the convective gas flow rate through *Typha latifolia*, presumably, as relative humidity of the atmosphere changes. Accordingly, for our two sampling dates (Fig. 3), relative humidity was nearly 100% at night and at sunrise then decreased to about 50% by 1000 h; after that, relative humidity increased to 75% in the afternoon, before reaching close to 100% by sunrise. Consequently, gas flow rate increased between sunrise and midmorning because relative humidity decreased during this part of the day; after that, higher relative humidity in the late afternoon and at night decreased the emission rate for CH_4.

Chanton et al. (1993) were able to disrupt the pattern in emission by experimentally shading whole plants, albeit, they may have caused a secondary effect on relative humidity. Our experimental, short-term (e.g., 60 min) shading of individual shoots did not affect the rate of CH_4 emission, which is consistent with no light effects on convective gas flow rate (Bendix et al., 1994). While shading caused a decrease in stomatal conductance, the CH_4 concentration gradient from leaf lacunae to the atmosphere did increase at the same time, which maintained the rate of CH_4 emission to the atmosphere.

Previous studies of gas concentrations within the lacunae of emergent plants have found the highest concentrations of gas (other than O_2) at night followed by decreasing concentrations during the course of the day (Brix, 1988; Constable et al., 1992; Frye et al., 1994). In the present study, the highest CH_4 concentration within stems and leaves of *Typha latifolia* at sunrise are consistent with those findings, even though the highest rate of CH_4 emission to the atmosphere occurred later in the daytime.

4.2. *A regional estimate*

Our extensive survey of sites covered more than 21° of latitude, providing the means for a reasonable regional estimate of CH_4 emission to the atmosphere. Assuming *Typha latifolia* has a leaf-area index of 5 ($m^2\,m^{-2}$; cf., Wetzel, 1983), our measurements extrapolate to a mean emission rate of 950 mg CH_4 $m^{-2}\,d^{-1}$ (range among sites = 43 mg CH_4 $m^{-2}\,d^{-1}$ to as high as 6 g CH_4 $m^{-2}\,d^{-1}$). The mean estimate is substantially higher than the global mean rate of CH_4 emission for marshes of 238 mg CH_4 $m^{-2}\,d^{-1}$, as summarized by Aselmann and Crutzen (1989).

Further, we can estimate the amount of CH_4 emitted from sediment pore water to the atmosphere supported by diffusion with the following equation:

$$F = k(C_w - C_e),$$

where F is the emission rate of CH_4 per unit area, k is the gas exchange coefficient (conservatively assumed to be 2×10^{-3} cm s^{-1}), C_w is the concentration of CH_4 measured in the sediment pore water, and C_e is the atmospheric CH_4 equilibrium concentration (atmospheric CH_4 concentration times β). Estimates ranged from low values of about 30 mg CH_4 $m^{-2}\,d^{-1}$ for sites in New Mexico and Kansas to as high as 2.8 g CH_4

$m^{-2} d^{-1}$ at Whiteface River site in northern Minnesota. These results corroborate earlier indications that marshes dominated by *Typha latifolia* are extraordinary sources of atmospheric CH_4 (cf., Swain, 1973; Chanton et al., 1993).

Our measurements also provide a partial picture of the controls on CH_4 emissions from *Typha latifolia*. The mean rate of CH_4 emission for each site did not correlate significantly (all p's > 0.10) with either stomatal conductance, net photosynthesis, or CH_4 concentration in *Typha latifolia* leaves and bases and in sediment pore waters at the given site, as expected. Further, the lower emission rates for the predawn than midday measurements were consistent with our findings for CH_4 emission rates during the course of the day (see above). It is notable, that the definition of predawn is somewhat arbitrary; although, we sampled at least one hour before the sun rose above the horizon at each site, in some measurements there was enough light in the sky (25 to 75 μmol $m^{-2} s^{-1}$) in order to support positive photosynthetic rates and relatively high values of stomatal conductance. This accounts for the large variation in stomatal conductance at predawn.

We did find a significant correlation between mean CH_4 emission rates predicted with Fick's law and the measured estimates (Fig. 6). Further, our measurements showed a strong positive correlation between the mean CH_4 emission rate and cumulative degree days on the sampling date at each site (Fig. 6). Cumulative degree days is a surrogate for plant age, suggesting that older plants emitted CH_4 at a higher rate than younger plants. For example, plants in the sites in Florida, New Mexico and Kansas were older than plants in Minnesota when sampled, as indicated by cumulative degree days (Table 1) at that time. It also is possible that the elegant network of baffles in *Typha latifolia* leaves (Rowlatt and Morshead, 1992), conferring plant structure, offers resistance to methane transport through lacunae; however, the resistance lessens as the plant ages (Constable et al., 1992). Therefore, older plants are more efficient at CH_4 transport and emission, whereas CH_4 accumulates in plant bases of younger plants.

Certainly, other factors play a role in a seasonal cycle of CH_4 emissions such as changes in the rates of methanogenic activity and root growth. Further, the oxidation of CH_4 by micro-organisms inhabiting wetland soil and sediments, which limits the amount of CH_4 available for emission, may change seasonally. For example, King (1994) and King and others (King et al. 1990) have shown that *Typha latifolia* roots support CH_4-oxidizing bacteria that display the higher activity in late summer (August–September) than earlier in the growing season. Such activity seemed more sensitive to the oxygen (O_2) concentration of the sediment than the CH_4 concentration.

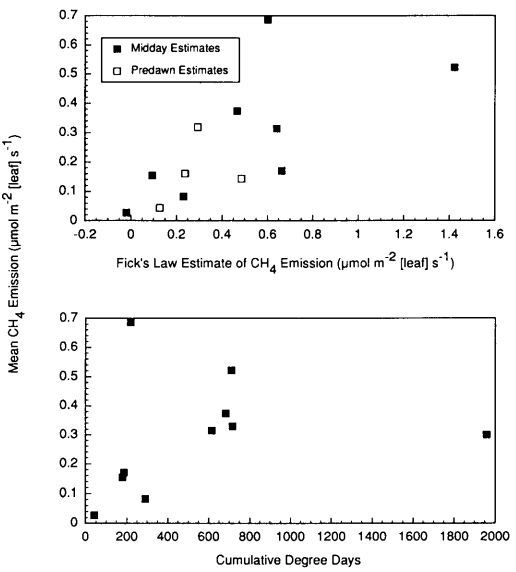

Fig. 6. Correlation between measured rates of CH_4 emission from Typha latifolia leaves to the atmosphere and rates predicted with Fick's law as well as cumulative degree days for several wetlands sampled in midsummer. Values are the mean of three measurements at each site.

Notwithstanding, the hypothesis that plant-age influences rates of CH_4 emission from *Typha latifolia* has important consequences depending on the magnitude of predicted climatic change. One scenario suggests warmer nighttime temperatures (cf., Karl et al. 1991), as well as lengthening of the growing season. A longer growing season could sustain high emission rates well into autumn. At this time of year, tropospheric CH_4 has crucial effects on the Earth's radiation budget since natural, chemical processes that destroy tropospheric CH_4 are seasonally weak (Tie et al., 1992) in autumn.

4.3. *Hypotheses of controls*

We envision a hierarchy of factors influence CH_4 emission from *Typha latifolia* to the atmosphere (Fig. 7), including (i) microbial production of CH_4, (ii) CH_4 transport in the sediment-plant-atmosphere continuum, and (iii) stomatal conductance. For example, at night when stomata are essentially closed (Knapp and Yavitt, 1992) and when convective gas flow is slow, the sediment-to-plant concentration gradient drives CH_4 influx by diffusion and CH_4 concentrations increase within the plant. After sunrise, as gas flow rates and stomatal conductance increase, CH_4 emission to the atmosphere increases progressively; hence, there is a stomatal control of CH_4 emission during this part of the day. In the afternoon, CH_4 emission is limited by convective gas flow.

We also suggest a sequence of factors probably controls CH_4 emission from *Typha latifolia* to the atmosphere seasonally, including (i) variation in the rates of production and consumption of CH_4 by micro-organisms, (ii) followed by changes in the resistance to gas flow through the young *Typha latifolia* plants in the spring and summer, and (iii) possibly stomatal control as the principal regulator of CH_4 emission from older plants. As a result, the highest emission rates from *Typha latifolia* might occur late in the growing season. For example, the growing season in Florida starts in July to September in response to the autumn rainy season; hence plants in July are oldest, and we found the highest emission rates at that time of the year (Fig. 5).

These predictions point to important processes and mechanisms that control CH_4 emission from *Typha latifolia* plants to the atmosphere, especially, at the level of individual leaves. With almost certain changes in air temperature, concentration of atmospheric CO_2, cloudcover and relative humidity expected from climatic change, plants will be affected in complex ways (Eamus, 1991), and our data suggest there will be consequential effects on CH_4 emission either directly (e.g., through changes in stomatal conductance) or indirectly (e.g., through changes in gas flow rates). Process models of biosphere-atmosphere interactions have progressed in their development to now consider how biophysical elements change as a function of depth in plant canopies (cf., Sellers et al., 1992), and including fluxes of atmospheric trace gases in such models should be possible.

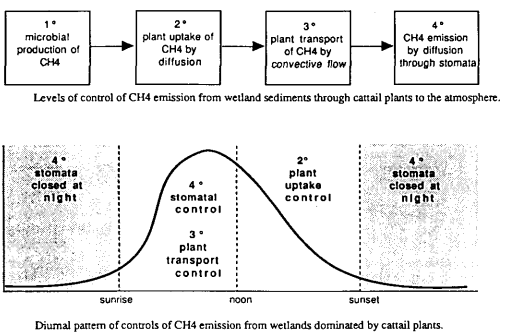

Fig. 7. Relationships among the factors that largely control CH_4 emission from Typha latifolia leaves to the atmosphere. The top panel shows the hierarchical arrangement of the factors, and the bottom panel shows idealized time course changes in CH_4 emission, with the factor responsible for the rate-limiting step shown.

4.4. *Implication*

Finally, CH_4 emission to the atmosphere from all sources is now (Crutzen, 1991) set at 505 ± 105 Tg yr^{-1}. Natural wetlands and rice paddies account for about 42% of the total. Marshes are a relatively minor component of the world's wetland area, yet they seem to account for $4 - 31$ Tg CH_4 yr^{-1} (Aselmann and Crutzen, 1989). Our results for *Typha latifolia* are interesting because marshes are increasingly being managed in such a way (e.g., by eutrophication, increased sedimentation from soil erosion, for waste water treatment) that leads to the loss of biodiversity and replacement by monospecific stands of plants such as *Typha latifolia*. Our data provide additional evidence how human-accelerated environmental change continues to perturb the global budget for atmospheric CH_4.

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