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METHANE FLUX IN *PELTANDRA VIRGINICA* (ARACEAE) WETLANDS: COMPARISON OF FIELD DATA WITH A MATHEMATICAL MODEL[1]

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We present a mathematical model of the diffusive flux of methane through *Peltandra virginica*. Data on the diurnal changes in both the petiolar [CH_4] gradient and the values of the radial bulk exchange coefficient, E_r, are entirely consistent with this model and the assertion that changes in stomatal conductance regulate the rate of methane efflux in *P. virginica*. The differences between the values of E_r calculated for daytime and nighttime conditions are −40% for the submerged condition and −54% for the emergent condition. The axial diffusivity of CH_4 through the petiole of *P. virginica* is estimated in vitro to be 0.771 $cm^2\ min^{-1}$. Using our model, we estimate the equilibrium rate of methane efflux under daytime (97 ng $CH_4\ min^{-1}$ $petiole^{-1}$) and nighttime (65 ng $CH_4\ min^{-1}$ $petiole^{-1}$) emergent conditions. Numerical solutions of the model equations in the time domain offer a way of providing a dynamic model of the gas exchange responses of *P. virginica* to changing environmental conditions.

CH_4 is a minor constituent of the earth's atmosphere (Migeotte, 1948) and a small pool in the global carbon budget, but it is of major importance to the earth's atmospheric chemistry and radiative energy balance. Natural and constructed wetlands are thought to account for nearly 50% of the annual methane flux into the global atmosphere (Cicerone and Oremland, 1988). Vascular plants serve as important conduits for CH_4 emission from wetlands because they permit the microbially produced CH_4 to bypass the zone of microbial methane oxidation near the soil surface (Schütz, Seiler, and Conrad, 1989), but the processes and controls of gas transport through wetland plants are not well understood. It is commonly accepted that changes in stomatal aperture regulate the diffusive exchange of CO_2, H_2O, and O_2 (Cowan, 1977). On the other hand, Chanton et al. (1992) asserted that CH_4 flux from *Peltandra virginica,* a perennial aroid species common to freshwater marshes throughout eastern North America (Odum et al., 1984), is independent of stomatal aperture because net flux of CH_4 into a "phytochamber" did not vary under various environmental treatments (light, dark, high CO_2, ambient CO_2, and low CO_2). Here, we report an in situ, whole-plant application of the principles of gas flux porometry, based on the diffusion of naturally occurring CH_4 through *P. virginica.* Our results contradict those of Chanton et al. (1992) in that stomatal control of diffusive flux provides the best explanation of our observations.

We also describe a mathematical model of the diffusive flux of CH_4 through *P. virginica.* Methane concentrations within plants parameterize the model, showing the effect of changes in the radial bulk exchange coefficient of CH_4 (E_r) on the plant's internal CH_4 concentration gradient under daytime, nighttime, submerged, and emergent conditions. As stomata provide the only known variable resistance to radial flux from the petiole, we conclude that they control overall CH_4 efflux from *P. virginica.*

The model assumes that diffusion, and not mass flow, is the primary mechanism of gas flux in *P. virginica.* Botanists have long noted the highly developed aerenchyma, or air-space tissue, in wetland plants (Arber, 1920; Sifton, 1945, 1957). Aerenchyma permits the internal air space of the roots to be in continuous, or nearly continuous, gaseous connection with the atmosphere. Simple diffusion along gradients in partial pressures within the aerenchyma has been the accepted mechanism by which O_2 moves from the aerial portion of a plant to its roots, and CO_2 and CH_4 move in opposition to O_2 (Conway, 1937; Greenwood, 1967; Luxmoore and Stolzy, 1972). Armstrong (1979) provided a thorough review of diffusion as a ventilating process.

Dacey and Klug (1979) suggested another ventilation mechanism entirely, i.e., pressurized, flow-through ventilation, whereby a gradient in total pressure may be generated within the leaf blades, petioles, and rhizomes of the pond lily, *Nuphar luteum* (Dacey, 1980, 1981; Dacey and Klug, 1982). This pressurization leads to a unidirectional flow of gases from the young leaves to the rhizomes and out through the older leaves. This flow, in turn, produces a distinctive CH_4 concentration gradient within the plant's aerenchyma, with high methane concentrations ([CH_4]) in the rhizome and older leaves, and low [CH_4] in the younger leaf petioles. Dacey and Klug (1979) and other researchers (Grosse and Schröder, 1984, 1986, 1987; Schröder, Grosse, and Woermann, 1986; Grosse and Mevi-Schütz, 1987; Armstrong and Armstrong, 1990) have established the presence of pressurized ventilation in other species, such as *Phragmites australis, Nuphar advenum, Nuphar lutea, Nelumbo nucifera, Nymphoides peltata, Victoria amazonica,* and *Alnus glutinosa.* This suggests that pressurized ventilation may be an important gas transport mechanism for diverse plant species, but our data do not support its presence in *P. virginica.* No evi-

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dence was found of the distinctive CH_4 concentration gradient expected in cases of pressurized flow. Our field measurements of the spatial and temporal variability of CH_4 in the soil-plant-atmosphere continuum are entirely consistent with the diffusive flux model.

MATERIALS AND METHODS

Site description—We sampled two sites in freshwater marshes on the Chickahominy River, a tributary of the James River, Virginia. Site 1 (37°18′45″N, 76°53′20″W) has a tidal range of approximately 0.7 m. Site 2, located just above Walker's Dam (37°24′20″N, 76°56′30″W), is nontidal. At both sites, *P. virginica* is the dominant plant species throughout the spring and summer (Odum et al., 1984).

Gas sample collection—For the petiolar aerenchyma of *P. virginica,* we carefully inserted a needle attached to a gas-tight syringe and withdrew 500 μl of gas over a period of approximately 15 sec. Dry gas samples obtained from underwater portions of the plants showed that no leakage occurred around the syringe. We sampled from the petioles and from the ambient air at several heights both within and above the plant canopy, recording the source and time of each sample. Between successive samples the syringes were flushed five times with ambient air. Immediately upon withdrawing the syringe, the gas samples were injected into N_2-flushed, 2-ml Wheaton borosilicate glass vials (volume = 2,750 μl) with butyl rubber stoppers. The vials were returned to the lab for analysis within 24 to 48 hr of sample collection.

We sampled biweekly from May through August of 1988 at Site 1 (tidal) to determine the natural variability of CH_4 in the soil-plant-atmosphere continuum and to estimate values for C_s and C_e, defined below. Petioles were sampled periodically from pre-dawn to sunset. The petioles were sampled within 10 cm of either their proximal or distal end. Measurements of leaf and air temperature and lacunar gas pressure (see below) were made at Site 1 during the 1988 growing season to test for the possibility of pressurized ventilation.

A more precise measurement of CH_4 concentration gradients was conducted in June and July of 1992. The CH_4 concentration gradients in submerged and emergent portions of petioles at Site 2 were sampled. Collections of the "daytime" samples were made between 1500 and 1800 hr. "Nighttime" samples were collected between 0300 and 0530 hr. This was done to maximize the time for the CH_4 concentration gradient to equilibrate to the diurnal change in stomatal aperture. Plants were sampled at a nontidal site in order to remove the transient effects of changing water levels. The water surface was the datum ($z = 0$) from which the location of each sample was measured. The sample locations are accurate to within 5 mm. Three samples were taken from each petiole, at elevations of either 0 cm, 10 cm, and 20 cm, or 0 cm, −5 cm, and −10 cm.

Porewater methane measurements—We determined $[CH_4]$ in the soil porewater with a porewater equilibrator (PWE) similar to that described by Hesslein (1976). A PWE consists of a 4-cm × 12-cm × 40-cm acrylic block with wells of approximately 15 cc milled into it. An array of 27 wells per block, with three wells at each of nine depths (ranging from 4 to 36 cm, in increments of 4 cm) was used. The wells were filled with deionized water and covered with a sheet of Versapor 200 (0.20 μm pore membrane filter, Gelman Sciences, Inc., Ann Arbor, MI) held by a faceplate and stainless steel nuts and bolts. Two PWEs were inserted into the marsh soil and allowed to equilibrate for 3 wk. Immediately upon collection, a 3-ml sample of the water in each well was removed by syringe and placed in butyl-rubber-stoppered 10-ml test tubes. The test tubes were shaken vigorously prior to analysis to degas the water. Aliquots of the headspace were analyzed by gas chromatography. The $[CH_4]$ of the porewater itself was calculated using Henry's Law.

Temperature measurements—Measurements of leaf, air, and water temperatures were made with an Omega model HH23 temperature meter. Leaf temperatures at the midrib were measured by inserting a 33-gauge, Type T thermocouple (Omega, Stamford, CT). Air and water temperatures were measured with a multipurpose Type T thermocouple.

Pressure measurements—Pressure measurements were made with a Gilmont model G1500A micromanometer (Gilmont Instruments, Inc., Great Neck, NY) with isooctane as the manometric fluid for increased sensitivity. When used for difference measurements this system has an accuracy of ± 5 Pa. Gas pressure within the aerenchyma was measured by inserting a 22-gauge needle connected to the manometer by 2 m of $\frac{1}{16}$-in.-diameter teflon tubing.

In vitro experimental procedure—We made in vitro measurements to determine axial diffusivity (D_a) with the apparatus shown in Fig. 1. The "source" flask was filled with a standard mixture of 987 ppm CH_4 in N_2 (Scott Specialty Gases, Plumsteadville, PA), and the "sink" flask was flushed with N_2 prior to each run. Tygon tubing (1 m long, 0.8 mm [$\frac{1}{32}$″] inside diameter), connected to each flask and open to the atmosphere, maintained ambient pressure in both flasks during sampling and provided a sufficient barrier to diffusive loss of the tracer gas during the 1 hr run time. Entire plants were brought to the lab, and their roots were washed free of soil. They were allowed to stand overnight in a bucket of water sparged with N_2 to remove any residual CH_4. The following day, a 5-cm- or 10-cm-long segment of petiole was excised, coated with silicone grease, surrounded by a sleeve of tygon tubing, and sealed to the apparatus as shown in Fig. 1. Samples of 100 μl each were taken from the "source" flask at the initial and final times and of 500 μl from the "sink" flask at 5-min intervals for 1 hr. All samples were analyzed immediately by gas chromatography.

Gas sample analysis—All CH_4 analyses were done on a Varian model 3700 gas chromatograph (1 m Poropak Q 100/120 mesh, N_2 carrier gas flow rate of 30 ml min^{-1}, column temperature 60 C, flame ionization detector). A mixture of 987 ppm CH_4 in N_2 (Scott Specialty Gases, Plumsteadville, PA) was used as a standard. The vial volume was used to determine the dilution factor for the calculation of $[CH_4]$ in the field samples.

Model derivation—As a first approximation, the plant can be represented by a tube connecting a lower compartment (i.e., the soil) with $[CH_4] = C_s + C_e$ to an upper compartment (i.e., the atmosphere) with $[CH_4] = C_e$. The axial diffusivity and radial bulk exchange coefficient of CH_4 are given by D_a and E_r, respectively. C(z) defines the $[CH_4]$ in the tube (i.e., the plant) at a given distance, "z," from the lower compartment. The model assumes that both the upper and lower compartments are well mixed, and that there is no radial gradient in $[CH_4]$ within the tube.

The rate of change of $[CH_4]$ over time is given by:

$$\frac{\partial C}{\partial t} = D_a \frac{\partial^2 C}{\partial z^2} - E_r[C(z) - C_e] \quad (1)$$

When the system is at equilibrium:

$$\frac{\partial C}{\partial t} = 0 \quad (2)$$

Therefore, Equation 1 can be rearranged as:

$$\frac{\partial^2 C}{\partial z^2} = \frac{E_r}{D_a}[C(z) - C_e] \quad (3)$$

The variable "F" is defined as:

$$F = \sqrt{\frac{E_r}{D_a}} \quad (4)$$

Substituting Equation 4 into Equation 3 yields:

$$\frac{\partial^2 C}{\partial z^2} = F^2[C(z) - C_e] \quad (5)$$

A solution for C(z), given the boundary conditions that $C(0) = C_s + C_e$, and $C(\infty) = C_e$ is:

$$C(z) = C_e + C_s e^{-Fz} \quad (6)$$

This can be shown by taking the derivatives of C(z) with respect to z.

$$\frac{\partial C}{\partial z} = -FC_s e^{-Fz} \quad (7)$$

$$\frac{\partial^2 C}{\partial z^2} = F^2 C_s e^{-Fz} \quad (8)$$

Substituting the right-hand side of Equation 6 into Equation 5 yields:

$$\frac{\partial^2 C}{\partial z^2} = F^2[(C_e + C_s e^{-Fz}) - C_e] \quad (9)$$

The C_e terms in Equation 9 cancel, proving the equivalence of Equations 5 and 8.

When applying this physical model of gas diffusion to *P. virginica,* it is necessary to consider the influence of the relevant biology. The petiole and leaf blade of *P. virginica* are covered with stomata, controlling the diffusive exchange of CO_2, O_2, and H_2O. We reason that if changes in the stomatal aperture are able to control the diffusive exchange of CO_2, O_2, and H_2O, they should also control the diffusive exchange of CH_4. We would expect to see both a diurnal increase in the value of E_r coincident with the diurnal stomatal opening, and a marked decrease in the values of E_r for the submerged vs. emergent portions of the petiole.

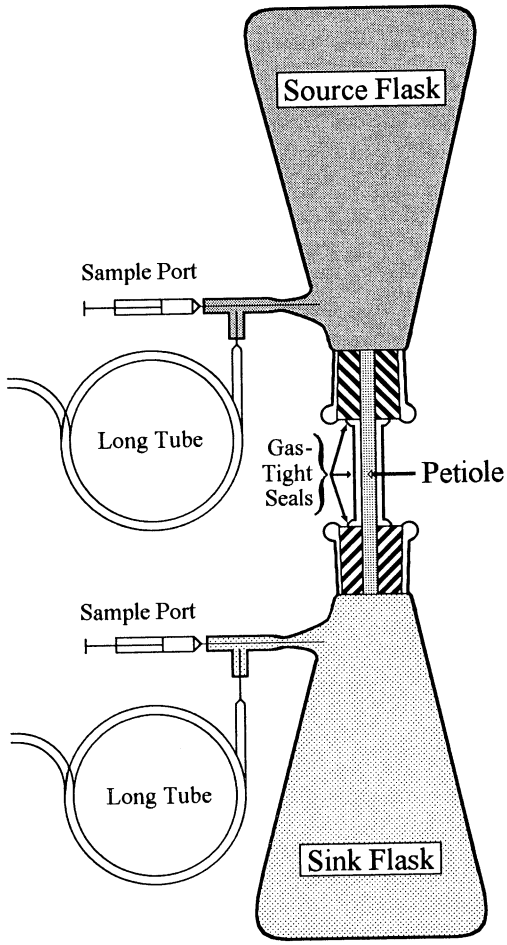

Fig. 1. The experimental apparatus for the determination of D_a in vitro. Volume of the "source" flask = 590 ml, "sink" flask = 150 ml. The "sink" flask was continuously stirred with a magnetic stirring bar.

Parameter estimation—D_a, E_r, C_s, and C_e must be estimated to apply this model. For E_r and D_a, we measured the $[CH_4]$ gradient in plants at Site 2 and normalized to the $[CH_4]$ at the water surface, therefore $C_s + C_e = C(0) = 1$. Since $C_e \ll C_s$, little error will be introduced at this point by reducing Equation 6 to:

$$C(z) = e^{-Fz} \quad (10)$$

The values of the parameter "F" in Equation 10 were fit to these data using the SPSS's Nonlinear Regression (NLR) program, an iterative least squares program which also estimates the asymptotic standard error and r^2. This provides estimates of "F" under four conditions—daytime emergent, daytime submerged, nighttime emergent, and nighttime submerged. The in vitro measurements of axial diffusion through a segment of a petiole were used to estimate the value of D_a, which is assumed to remain constant, by fitting the data to Fick's First Law:

$$J = -DA\frac{\partial C}{\partial L} \quad (11)$$

TABLE 1. The distribution of CH_4 in the soil-plant-atmosphere continuum of *P. virginica*, measured during May through August of 1988 at a tidal freshwater marsh on the Chickahominy River, Virginia.

Source	[CH_4] ± SE [b](mg/liter)	*N*	[a]z ± dz (cm)
Soil porewater	[c]3.397 ± 0.034	27	−20 ± 16
Petioles (basal end)	2.422 ± 0.530	47	5 ± 5
Petioles (distal end)			
Nighttime	0.053 ± 0.010	73	80 ± 20
Daytime	0.033 ± 0.001	108	80 ± 20
Air within plant canopy	[d]0.033 ± 0.004	20	30 ± 20
Air above plant canopy	0.031 ± 0.006	75	200 ± 50

[a] z ± dz represents the elevation from the marsh surface at which samples were taken ± the estimated range of uncertainty.
[b] Concentrations converted from ppmv assuming STP.
[c,d] Values used for $C_s + C_e$ and C_e, respectively. Therefore, C_s is estimated as 3.364 mg/liter.

where "A" is the petiole's cross-sectional area, "∂L" is the length of the petiole, and "∂C" is the average [CH_4] difference between the chambers. Values of E_r were then calculated from Equation 4 using D_a and the estimates of "F."

The values of C_s and C_e were estimated from the average [CH_4] in the soil porewater and canopy air measured at Site 1.

RESULTS

Methane in the soil-plant-atmosphere continuum—The CH_4 distribution within the soil-plant-atmosphere continuum is shown in Table 1. These data were collected at Site 1 during May through August of 1988. Note the high values for both soil porewater and basal petiole end samples, as well as the variability in the basal end samples. The mean values of the porewater and basal petiole end samples are not significantly different (*t*-test, $\alpha = 0.05$). There is a steep within-petiole [CH_4] gradient, and a slight [CH_4] gradient in the ambient air, with [CH_4] decreasing with distance from the soil surface. The petiolar [CH_4] was greater at night than during the day. The change from nighttime to daytime regimes occurred within 2 hr following sunrise.

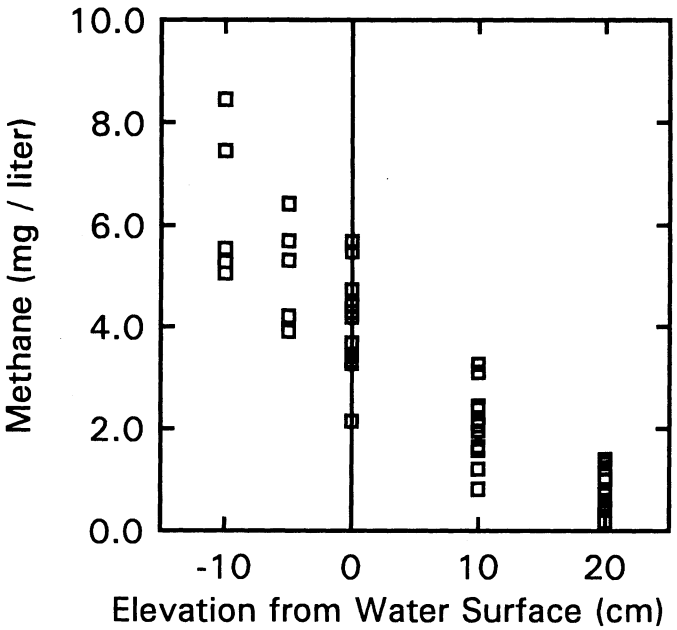

Fig. 2. In vitro determination of D_a, the coefficient of axial diffusion of CH_4 through the petioles of *P. virginica*. Squares and triangles are from separate runs with petiole segments of the cross-sectional areas and lengths indicated. Solid symbols, "source" flask; open symbols, "sink" flask.

TABLE 2. Model parameters fit to the data in Fig. 4 and the values of E_r calculated therefrom assuming $D_a = 0.771$ cm^2 min^{-1}.

Condition	F ± 1 SE (cm^{-1})	*N*	r^2	E_r (min^{-1})
Daytime				
Emergent	0.0752 ± 0.0038	33	0.94	0.00436
Submerged	0.0359 ± 0.0022	15	0.86	0.00099
Nighttime				
Emergent	0.0509 ± 0.0082	15	0.70	0.00199
Submerged	0.0282 ± 0.0021	18	0.78	0.00061

Temperature and pressure differentials—The leaf-to-air temperature differential, measured biweekly, was as great as 5 C, with an average ΔT of 2.8 C. These positive ΔT values occurred only for daytime measurements. All measurements made at night showed leaf temperatures equal to that of the surrounding air. Repeated attempts were made to measure a difference between the lacunar gas pressure and ambient atmospheric pressure. No ΔP greater than 50 Pa was ever recorded.

In vitro determination of D_a—Two separate determinations of D_a were made using petioles from different plants. Although the [CH_4] in the "source" chamber decreased slightly during the hour, this did not seem to affect the linearity of the methane flux into the "sink" chamber (Fig. 2). The values of D_a calculated using the dimensions of the petiole segments given in Fig. 2 are 0.745 cm^2 min^{-1} for the 5-cm petiole segment and 0.797 cm^2 min^{-1} for the 10-cm petiole segment. For the sake of comparison, the diffusivity of CH_4 in air at 0 C and 760 mm Hg is 11.76 cm^2 min^{-1} (Gray, 1972) and that of CH_4 in H_2O at 25 C is 0.000894 cm^2 min^{-1} (Lide, 1990). An average value of $D_a = 0.771$ cm^2 min^{-1} was used to calculate the values of E_r shown in Table 2.

Methane distributions and model fit—There was considerable between-petiole variability in [CH_4] at Site 2 (Fig. 3). We normalized, therefore, the data from each individual petiole the [CH_4] measured at the water surface in that petiole. This results in a value of C(0) = 1 for all petioles. The normalized data for both daytime and nighttime samplings, presented along with the model and its 95% confidence intervals in Fig. 4, illustrate the variance reduction of the normalization. Model parameters and their error estimates are presented in Table 2. Note the pronounced shift in the value of E_r from daytime to nighttime conditions (Table 2).

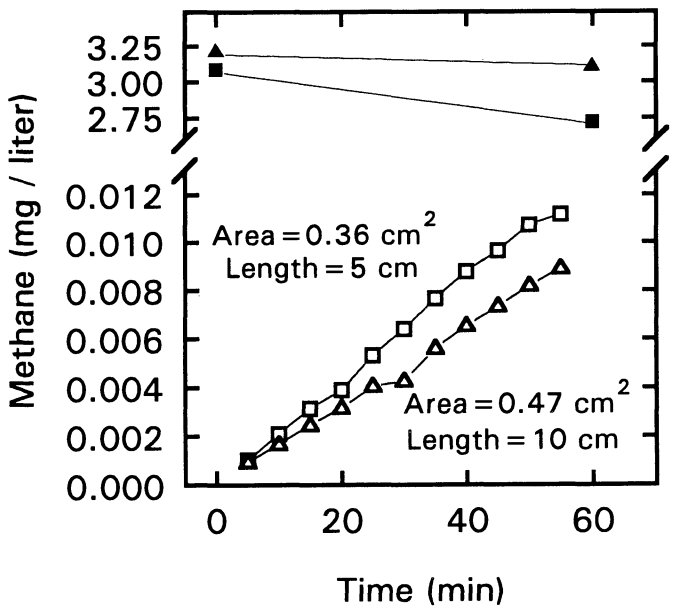

Fig. 3. Daytime lacunar CH_4 concentrations in the petioles of *P. virginica*, sampled during June and July of 1992 at a nontidal freshwater marsh on the Chickahominy River, Virginia.

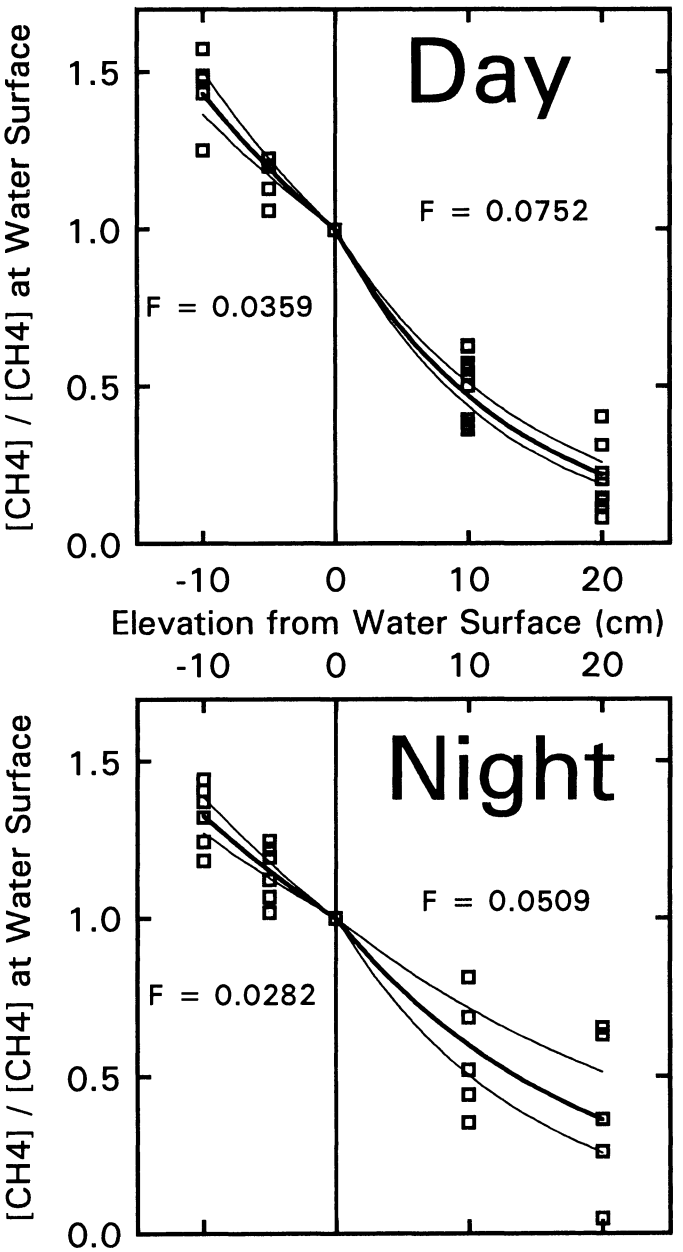

Fig. 4. Daytime and nighttime normalized lacunar CH_4 concentration gradients in the petioles of *P. virginica*, sampled during June and July of 1992 at a nontidal freshwater marsh on the Chickahominy River, Virginia.

DISCUSSION

Methane in the soil-plant-atmosphere continuum—The data in Table 1 illustrate the steep gradient for diffusion of CH_4 in the soil-plant-atmosphere continuum. Other researchers have documented similar distributions for other plant species. Sebacher, Harriss, and Bartlett (1985) surveyed lacunar [CH_4] in 14 rooted, freshwater macrophyte species, and found on average a 97% drop in [CH_4] 30 cm above the water line relative to [CH_4] at the water line. Their results for *P. virginica* (0.538 mg CH_4/liter at $z = 0$, <0.001 mg CH_4/liter at $z = 30$) are consistent with our own. Our model suggests that the primary controls of lacunar [CH_4] at the water surface in *P. virginica* are the [CH_4] in the soil, the distance between the soil and the water surface, and the status of the petiolar stomata. Sebacher, Harriss, and Bartlett (1985) do not report the depth of inundation at their sampling site, and they took samples only during sunny daylight hours. Our Site 1 experiences tidal inundation of approximately 70 cm twice daily. The basal petiole ends have highly variable lacunar [CH_4] because they experience these fluctuating water levels and are in the steepest portion of the [CH_4] gradient where small uncertainties in the sampling location would have the greatest effect on measured [CH_4]. The distal petiole ends are not typically inundated and exhibit significantly less variability.

We also demonstrate a small but significant diurnal change in the lacunar [CH_4] of the distal end of the petiole. A similar phenomenon was noted by Knapp and Yavitt (1992) for *Typha latifolia*.

At our nontidal Site 2, the depth of inundation is approximately 30 cm, but because of the hummocky growth form of *P. virginica*, the depth between adjacent plants varies by as much as 10 cm. It is this variability in the depth of inundation that we believe is primarily responsible for the variability of the data presented in Fig. 3. Normalization of the data from each petiole to the [CH_4] at the water line for that petiole (Fig. 4) reduced the variance considerably.

Temperature and pressure differentials—We routinely measured daytime leaf-to-air temperature differentials as great as 5 C with an average ΔT of 2.8 C. For plants exhibiting pressurized ventilation, theory predicts a pressurization of the lacunar gas as a result of the temperature differentials between the leaves and air. No pressurization of the magnitude reported by Dacey (1981) for *Nuphar* (circa 200 Pa) was ever observed. In fact, no ΔP greater than 50 Pa was ever recorded, and the effect of heating

on the manometer was suspect in all positive pressurizations measured. Our data, when taken in concert with the fact that no evidence was found of the distinctive CH_4 concentration gradient expected in cases of pressurized flow, lead us to conclude that pressurized ventilation does not occur in *P. virginica*. Our field measurements of the spatial and temporal variability of CH_4 in the soil-plant-atmosphere continuum are, however, entirely consistent with the diffusive flux model.

Model fit—Our [CH_4] data (Fig. 4) enable us to estimate the values of "F" under daytime, nighttime, submerged, and emergent conditions (Table 2), because we sampled at more than two locations in each plant. In the case of axial diffusion through a tube that is radially impervious to CH_4, the [CH_4] gradient would be linear, and two sample locations would suffice to determine its value. If, however, one would like to consider the effect of radial losses in the system, then at least three sampling locations are required to estimate the nonlinearity of the gradient. We chose not to use more than three because of the effect withdrawing more gas from the aerenchyma might have on the gradient measured. The changes between the values of E_r calculated for daytime and nighttime conditions (−40% for submerged, −54% for emergent) are in reasonable agreement with the magnitude of the changes in stomatal conductance of water vapor (up to 42%) observed by Knapp and Yavitt (1992) for *Typha latifolia* under various treatments. Thus, it is reasonable that the changes in E_r we observe are entirely due to changes in stomatal conductance.

Model utility—Our model of CH_4 flux through *P. virginica* offers several insights into the rates and controls of CH_4 emissions from plants. According to the mass balance constraints of the model, the rate at which CH_4 crosses the $z = 0$ boundary of the model must be equal to the total loss of CH_4 from all other parts of the plant combined. Knowing values of "F" and C_s, Equation 7 can be solved for $z = 0$. Then, using Equation 11, a measure of the cross-sectional area of the plant, and an estimate of D_a, an equilibrium flux rate can be calculated. Using our values for C_s, D_a, a cross-sectional area of 0.5 cm^2, and values for "F" under the emergent conditions, we estimate flux rates of 97 ng CH_4 min^{-1} $petiole^{-1}$ during the day and 65 ng CH_4 min^{-1} $petiole^{-1}$ at night. This somewhat counterintuitive result that the CH_4 flux rate is higher when the average lacunar [CH_4] is lower can now be understood in light of the physical transport principles involved. Furthermore, the relatively high methane flux at night suggests one or more of the following: the stomata may not close tightly at night, the petiolar epidermis may be somewhat permeable to methane, or there may be micropores in the petiole, similar to those suggested by Nouchi, Mariko, and Aoki (1990) for rice plants.

The results presented thus far rely upon the simplifying assumption of equilibrium, i.e., the left hand side of Equation 1 equals zero. In the real world, however, the system is not in equilibrium. The tide fluctuates; the stomata open and close; [CH_4] rises and falls. These dynamic processes are evident in the variability of [CH_4] measured in the basal ends of petioles (Table 1). Nonequilibrium, analytical solutions of Equation 1 would have complex boundary conditions that would be difficult to specify in the real world. Although the CH_4 distributions we measured are static, D_a and E_r imply time. Therefore, numerical solutions of Equation 1 in the time domain are possible and permit the nonequilibrium boundary condition problems to be circumvented. Preliminary results of such simulations support the hypothesis of Knapp and Yavitt (1992) that the rate of methane emission should be highest just after sunrise when the high [CH_4] which has built up due to stomatal closure overnight is released to the atmosphere.

In conclusion, we have presented a mathematical model of the relevant physical transport processes to the flux of methane through *P. virginica*. This model has allowed us to estimate the magnitude of the biological control of the system. Our data on the diurnal changes in both the lacunar [CH_4] gradient and the values of the radial bulk exchange coefficient, E_r, are entirely consistent with a diffusive flux model where the principal control of the diffusive efflux of CH_4 is exerted by the stomata. The model also permits estimates of the equilibrium rate of methane efflux under daytime (97 ng CH_4 min^{-1} $petiole^{-1}$) and nighttime (65 ng CH_4 min^{-1} $petiole^{-1}$) emergent conditions. Numerical solutions of the model equations in the time domain offer a way of providing a dynamic model of the gas exchange response of *P. virginica* to changing environmental conditions.

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