Gas Transport and Pressures within **Potamogeton amplifolius and Potamogeton richardsonii**

BIOS 569 - Practicum in Aquatic Biology

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Abstract

This study examined internal transport of gases in submerged angiosperms. Aquatic vascular plants possess lacunae, air conduits which permit gas movement in both shoot-to-root and root-to-shoot directions. This transport of gases directly affects the abilities of plants to survive in their aquatic habitat. Through transport, plant roots receive oxygen needed for respiration. This process can also change the levels of methane released from the sediments to the aquatic environment and indirectly, to our outer atmosphere. To monitor this process, one directly dependent on photosynthetic oxygen production, a study of gas concentrations and pressures was conducted on two angiosperm species, Potamogeton amplifolius and Potamogeton richardsonii with an emphasis on alterations in light conditions. Experimental difficulties limited the experiment to examination of variations in lacunar CH_4 and CO_2 concentrations and flux rates. CH_4 release is potentially significant with respect to global warming since, molecule for molecule, atmospheric methane has 37 times greater a greenhouse effect than CO_2 (Bolin and Cook, 1983). Most of the data collected possessed too much variance to give it statistical significance. However, the sampling showed slightly higher lacunar CH_4 concentrations during the afternoon in both species. Photosynthetic utilization of stem lacunar CO_2 during the afternoon was also seen for both species. In terms of flux, afternoon conditions promoted a trend of higher CO_2 and CH_4 flows from root to stem.

Introduction

Submerged, aquatic plants exist at the interface between two very different microenvironments: the oxygenated, relatively nutrient-poor water surrounding the shoot of the plants and the oxygen deficient, nutrient-rich sediments surrounding their roots. In order for them to survive, they must possess the ability to cope with physiological stresses that this situation promotes. Internal transport of gases and nutrients within the submergent species satisfies this need.

Numerous studies have laid the foundation for this project through their illumination of the nature of the gas transport system in submersed angiosperms. A network of expanded, intercellular airspaces called lacunae has been determined to be the route for gas transport (Sculthorpe, 1967) (Fig.1: Appendix). These airspaces also serve to increase buoyancy, permitting plants to remain erect in the water column, maximizing the plant's exposure to light.

This study aimed to quantify the gas concentration and pressure variations within the lacunar system of two submersed species, *Potamogeton amplifolius* and *Potamogeton richardsonii* in both natural and artificial situations of varying light intensity. Light variations impact submersed plants due to photosynthesis. With respect to gas concentrations, photosynthesis during the day results in oxygen production and CO_2 consumption in the green, photosynthesizing tissues of the plants. The opposite occurs in the roots as respiration dominates metabolic activity. Therefore, lacunar gas flux consists of countercurrent exchange, with gases diffusing along their concentration gradients: O_2 down to the rhizosphere and CO_2 up into the shoot (Dacey, 1981)(Fig.2: Appendix).

Movement of CO_2 from roots to shoots can be vital for the health of submersed plants, especially for plants such as *Lobelia* which are obligate free CO_2 users (Wium-Anderson & Anderson, 1972). Diffusive boundary layers can limit aquatic plant productivity through the reduction of CO_2 exchange with the water (Smith & Walker, 1980).

Transport of photosynthetically produced oxygen has a number of effects. Anaerobic conditions occur just a few centimeters into the sediments of lakes due high microbial respiration. Lacunar gas transport provides for oxygen transfer to the respiring roots, permitting their survival in these sediments (Sculthorpe,1967). Oxygen can also be released from the roots to the sediments (Sand-Jensen, et al., 1982). This alters sediment oxidation/reduction potentials and directly affects microbial processes such as methane oxidation, nitrification, and oxidation of toxic, reduced materials (Anderson & Anderson, 1972; Wetzel, 1983).

Methane transport is a potentially important function of lacunae in submerged angiosperms. With respect to global warming, recent studies have shown that, molecule for molecule, methane has 37 times the effect of CO_2. Methane tends to accumulate in the chemically reduced environment of the sediments. Changes in rates of plant photosynthesis may affect its transport from the substrate (Dacey, 1981) (Fig.2: Appendix). For example, methane oxidation, affected by bacterial action in the rhizosphere, may increase during the day due to higher transport rates of oxygen to the sediments (Kemp and Murray, 1986). Although plants receive no nutritional benefits from methane, they can function as conduits, releasing methane from sediments to the atmosphere. Little specific data documenting this process exists, and its examination was a major goal of this project.

Not only does photosynthesis alter gas concentrations within the lacunae, it also strongly influences gas pressures. Photosynthetic O_2 production can pressurize internal gas spaces (Carlton R.G., personal communication). Dale (1984) and Sculthorpe (1967) theorized that this condition maintained lacunar structure in the presence of external hydrostatic pressures and also facilitated development of new openings during plant growth. However, recent studies have shown that even during the day, aquatic plants do not necessarily have positive pressures within their lacunae relative to the surrounding hydrostatic pressure (Carlton, personal communication). This contradiction warranted study, and thus efforts were made to examine lacunar pressures in the two Potamogeton species.

Materials and Methods

Of the principle aspects of this experiment, only one worked well enough mechanistically to provide data for analysis: the in situ study of lacunar gas concentrations. The study was conducted on fair weather days in July, 1991. The site of the study was Tenderfoot Lake on the property of the University of Notre Dame Environmental Research Center (UNDERC) in Gogebic Co. in the upper peninsula of Michigan. Sampling was accomplished using 1-ml glass syringes equipped with 1/2 inch, 25 gauge needles. In the early morning and in the middle of the afternoon, samples were taken from similarly sized, outwardly healthy specimens of both Potamogeton amplifolius and Potamogeton richardsonii growing at a depth of approximately 1.5m. First, a small plastic clamp was carefully tightened around the stem of each plant just above the sediment surface to cut off gas exchange between the root and stem. Then, the plant was brought to the surface where it was sampled. Approximately 100 microliters of gas was withdrawn from the lacunar gas spaces from the root and midpoint of the shoot. Syringes were shaken out to remove any water from the sample which could interfere with results and then stuck into large rubber stopper to prevent sample contamination. Length measurements were then taken of the sampled plants for later use in flux calculations.

Samples were then injected into a Hewlett-Packard 5890A Gas Chromatograph equipped with a Porapak Q column and thermal conductivity detector. The aforementioned column does not separate oxygen from nitrogen, so only CH_4 and CO_2 quantified. Output signals from the detector were processed by a Hewlett- Packard 3396 recording integrator. Detector calibration was accomplished using standard gas mixtures.

To analyze the data, areas of gas peaks were compared to the areas of the gas in the standard. By relating the standard area of the particular gas peak to the sample's peak area for that gas, each gas's molar concentration was obtained. From an ideal gas value of 22.4 mol per liter of gas, the standard's molar concentrations of CH_4 and CO_2 were determined. Then, the ratio of sample to standard permitted calculation of sample molar concentrations for the two gases. Flux rates of each gas for individual plants were then calculated using the formula:

$$J = D_s dC/dx$$

where J equals flux in $mol/cm^2/s$, D_s is the diffusion coefficient of the gas in air (interpolated from values given in the Handbook for Physics and Chemistry), dC is the difference in molar concentration between the root and stem, and dx represents the distance between root sampling site and stem sampling site.

Means were calculated for root and stem CH_4 and CO_2 concentrations for both Potamogeton species in the morning and afternoon. Error bars displayed were +/- 2 standard errors of the mean (giving confidence intervals of approximately 95%). Analysis of gas flux was done in a similar fashion, with means and errors calculated for the morning and afternoon samples and compared between species.

Two other aspects of this experiment failed due to equipment difficulties. Investigation of lacunar gas pressures was a major goal of this study. It involved the use of a micromanometer which consisted of a ruler and capillary tube attached to a piece of plexiglass (Fig. 3: Appendix). At one end, the tube was blocked by a glob of glue. The other end was connected to a small length of flexible tube which at the opposite end, possessed a 25 gauge needle for insertion into the plant. The liquid (red-colored water) contained within the tubing, and which partially filled the capillary, was designed to move depending on the pressure to which the needle opening was exposed. When the needle was inserted into the plant, the meniscus was supposed to move either to the left or right depending on the pressure within the plant's lacunar system (Fig. 3: Appendix).

The direction of movement was to provide only qualitative information about lacunar pressure. To get a rough quantitative value for the pressure, an estimation of lacunar volume within the stem was required. Estimates of lacunar cross-sectional areas, caliper measurements of stem diameter at the base, middle, and top of an average plant, and a measurement of stem length were made. Diameters would have been averaged and combined with length and lacunar area measurements to obtain allometric conversion factors for estimation of lacunar volumes. These volumes were to have been used to approximate lacunar pressure.

These calculations could not be made because lacunar pressure changes were never quantified. When sampling plants in situ, the manometer did not function properly. The meniscus would respond to pressure changes caused by increasing hydrostatic pressure, but would rarely change position when inserted in the plant. It is possible that pressure variations were not great enough for the manometer to detect. However, upon surfacing, the meniscus would often not return to its previous level, indicating possible clogging of its needle with plant stem material. Larger gauge needles were tried in an effort to eliminate clogging, but the effort was unsuccessful. Frequent needle replacement also was attempted, but little improvement was noted, and this aspect of the experiment was left uncompleted due to time limitations.

The laboratory work of this investigation was the transplanting of aquatic, submerged angiosperms into 7- cm-internal diameter, 3-mm-thick polycarbonate cylinders, divided into two water/gas tight sections (Fig. 4: Appendix). Plants were carefully uprooted, and any root bound sediments were washed away. Plants were then placed in cylinders with roots in one section and stems in the other. This was accomplished using opaque, gray-colored, 1/8 inch PVC dividing plates, designed to prevent light penetration to the root area. Mating surfaces were sealed with petroleum jelly. Black plastic was wrapped around the root section to prevent light infiltration. Two 1/4 inch rubber septa in each cylinder section permitted two-way flow during sampling. Figure 4 (Appendix) shows the entire system conceptually, while Figure 5 (Appendix) examines the divider system itself.

When tested for gas exchange without a plant, the cylinder system did not adequately separate the root and shoot sections. Instead of PVC, a more flexible plastic material which was presumed to be resistant to gas diffusion was used as the divider for the small cylinder. This material could have been quite permeable to the gases under study. In addition, sealing of the cylinders was done using black rubber stoppers. The sealing process pressurized the sections internally and may have caused the gas exchange between sections observed in testing. Attempts were made to minimize the pressure variations through the use of a pressure release in one of the side septa of each section. These efforts were unsuccessful, and further studies on the system were not allowed due to time restrictions.

Results

Tables 1 and 2 represent mean CH_4 and CO_2 concentrations within the roots and shoots of P. amplifolius and P. richardsonii respectively. Concentrations are calculated for the morning and afternoon. The tables also include mean flux values for both species in the morning and afternoon.

The data depict temporal alterations in lacunar gas composition between roots and stems in both species. P.amplifolius showed statistically significant, higher levels of both CH_4 and CO_2 in the root in both morning and afternoon samples. A general trend toward increased CH_4 levels in both root and shoot during the afternoon was observed. Mean concentration increased from morning levels of 0.088 mmol/L and 2.971 mmol/L in the stem and root respectively to afternoon levels of 0.308 mmol/L and 5.493 mmol/L (Figs. 6 & 7). However, variance was such that the trend was not statistically significant. The data also show a decrease in CO_2 concentration in the stems of P. amplifolius from 0.211 mmol/L in the morning to 0.075 in the afternoon (Figs. 6 & 7). CO_2 concentrations in the lacunar spaces of the root did

Table 1. Temporal variations in mean lacunar methane and carbon dioxide concentrations and fluxes in Potamogeton amplifolius. Flux calculations are made from data on individual plants, not from mean concentrations.

Morning 8am

Mean Concentrations: std=standard deviation		CH4	CO2
stem	mean>	0.088 mmol/L	0.211 mmol/L
	std>	0.069	0.078
root	mean>	2.971 mmol/L	0.628 mmol/L
	std>	1.918	0.120
Flux	mean>	0.0113 umol/cm2/s	0.0015 umol/cm2/s
Calc.	std>	0.0014	0.0006

Afternoon 3pm

Mean Concentrations: std=standard deviation		CH4	CO2
stem	mean>	0.308 mmol/L	0.075 mmol/L
	std>	0.279	0.012
root	mean>	5.493 mmol/L	0.877 mmol/L
	std>	3.757	0.332
Flux	mean>	0.0311 umol/cm2/s	0.0026 umol/cm2/s
Calc	std>	0.0266	0.0011

Table 2. Temporal variations in mean lacunar methane and carbon dioxide concentrations and fluxes in Potamogeton richardsonii. Flux calculations are made from data on individual plants, not from mean concentrations.

Morning 8am

Mean concentrations: std=standard deviation		CH_4	CO_2
stem	mean>	0.208 mmol/L	0.477 mmol/L
	std>	0.162	0.239
root	mean>	1.304 mmol/L	0.465 mmol/L
	std>	0.538	0.152
Flux Calc.	mean>	0.0064 umol/cm2/s	0.0004 umol/cm2/s
	std>	0.0031	0.0002

Afternoon 3pm

Mean Concentrations: std=standard deviation		CH_4	CO_2
stem	mean>	0.349 mmol/L	0.055 mmol/L
	std>	0.200	0.007
root	mean>	1.700 mmol/L	0.949 mmol/L
	std>	0.383	0.178
Flux Calc.	mean>	0.0102 umol/cm2/s	0.0036 umol/cm2/s
	std>	0.0032	0.0008

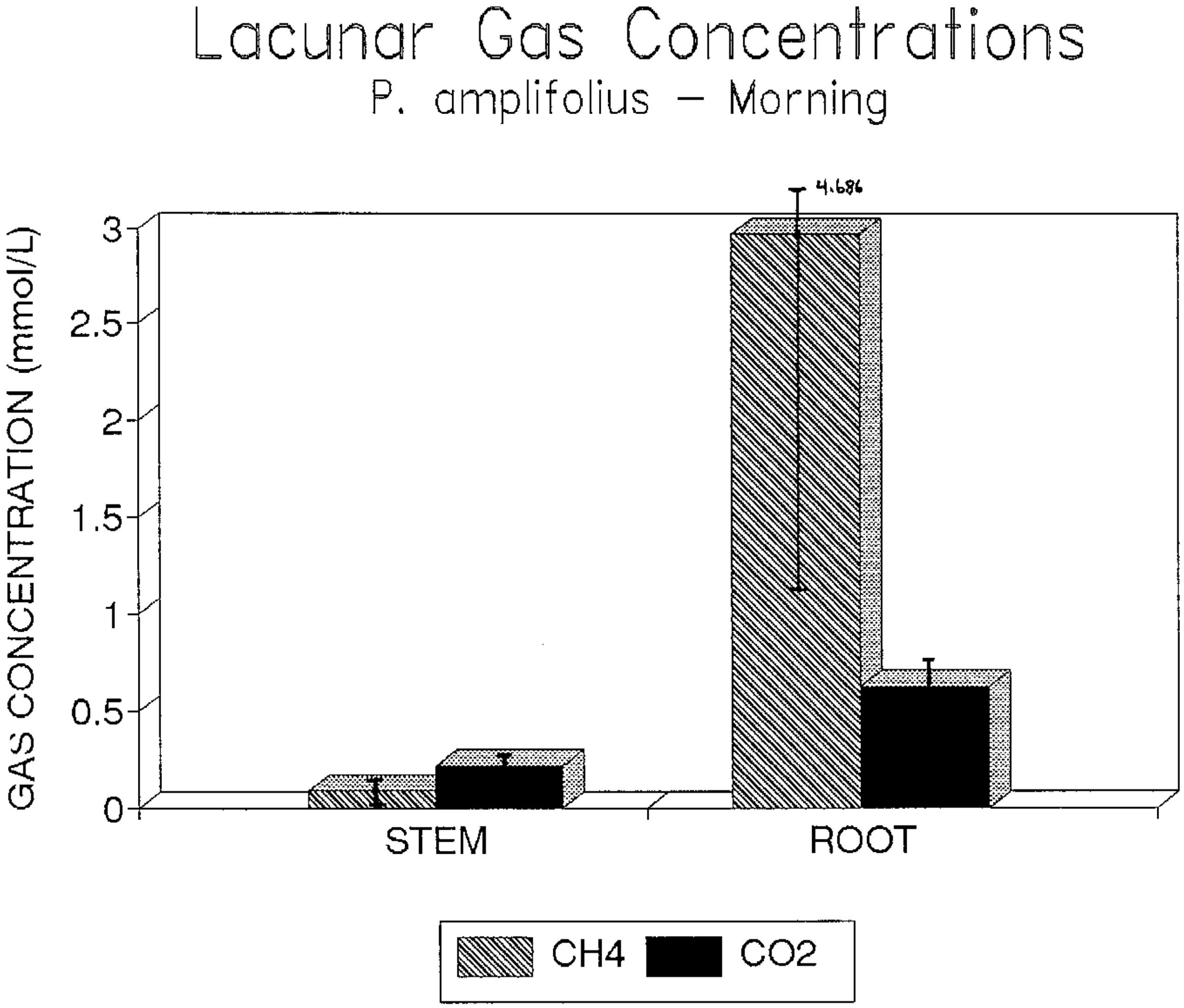

Fig. 6. Morning mean lacunar CH_4 and CO_2 concentrations within the stem and root of Potamogeton *amplifolius* (units = mmol/L).

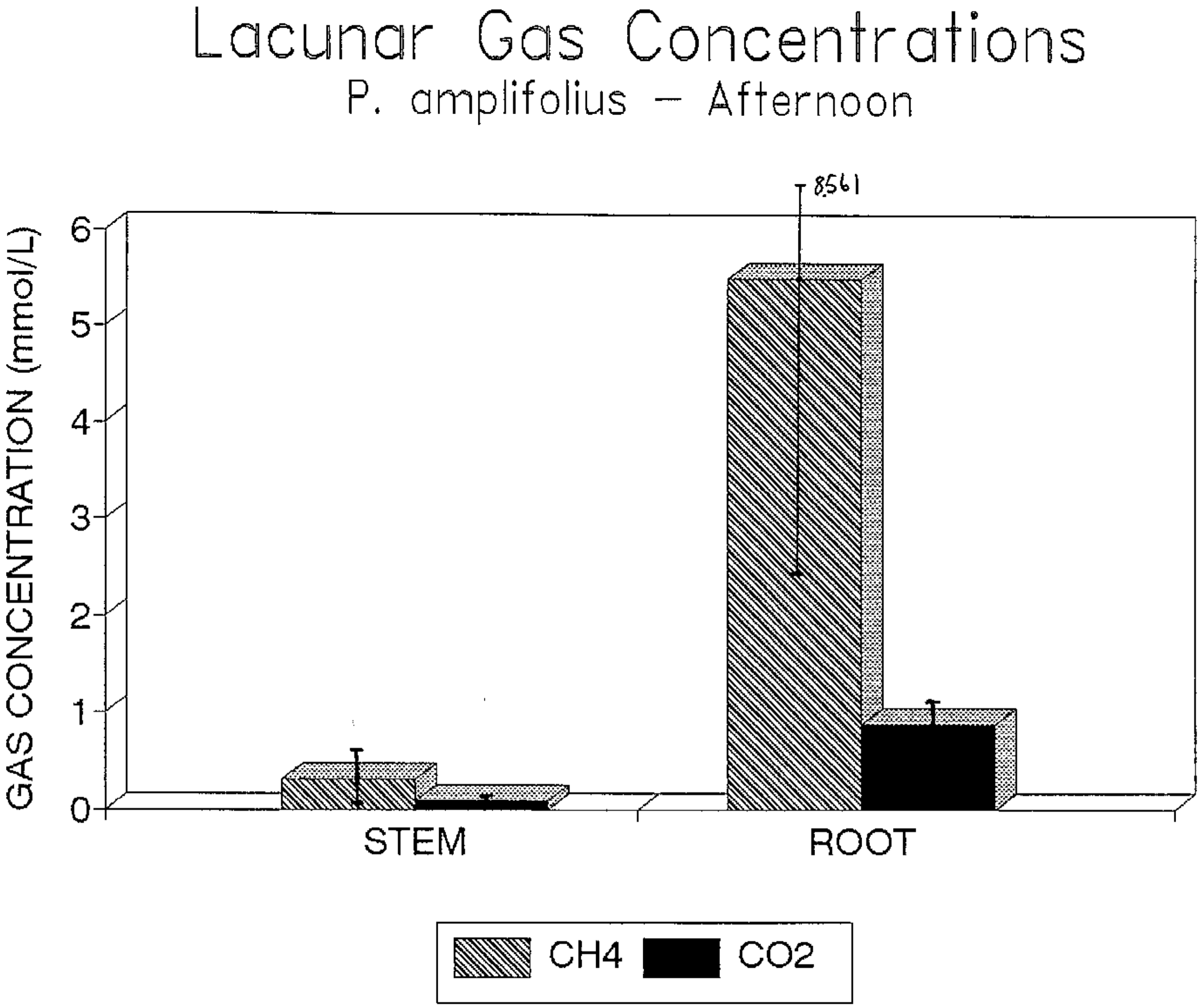

Fig. 7. Afternoon mean lacunar CH_4 and CO_2 concentrations within the stem and root of <u>Potamogeton amplifolius</u> (units = mmol/L).

not vary greatly during the day but perhaps were slightly higher in the afternoon (Figs. 6 & 7).

P. richardsonii showed the same higher CH_4 concentrations in the root compared to the stem seen in P. amplifolius. However, methane levels were generally lower in both sampling sites in P. richardsonii. Mean morning CH_4 concentrations were 0.208 mmol/L in the stem and 1.304 mmol/L in the root, while afternoon levels were 0.349 mmol/L and 1.700 mmol/L respectively (Figs. 9 & 10). For CO_2, in the morning, root and stem levels were nearly identical at mean concentrations of approximately 0.470 mmol/L (Fig. 9). However, in the afternoon, CO_2 rose to 0.949 mmol/L in the roots and fell to 0.055 mmol/L in the stems (Fig. 10).

In terms of CH_4 flux in the two species, P. amplifolius had greater flux than P. richardsonii during the morning and the afternoon (Figs. 8 & 11). Both species demonstrated higher CH_4 flux in the afternoon compared to morning (Figs. 8 & 11). Throughout the day, CO_2 flux was generally lower than CH_4 flux in the two species. P.richardsonii showed a clear CO_2 flux increase in the afternoon (Fig. 11). Flux levels of CO_2 in P.amplifolius rose slightly in the afternoon, but the increase was not statistically significant (Fig. 8).

Discussion

Photosynthetic production of oxygen during the day increases oxygen transport to the sediments thus increasing aerobic processes by bacteria in the rhizosphere (Kemp & Murray, 1986). Methane oxidizing bacteria in the rhizosphere use O_2 to oxidize CH_4 to CO_2 which can be utilized by the bacteria. CH_4 oxidation in the rhizosphere should result in lower CH_4 concentrations and fluxes in the two Potamogeton species during daylight hours. At night or in the early morning, lower oxygen transport should result in decreased CH_4 oxidation, which may increase CH_4 concentrations and fluxes within the plants.

The data on temporal variations from the in situ study do not support expectations higher lacunar CH_4 flow in the morning. Concentrations of methane in both root and shoot for both species were lower in the morning than in the afternoon. CH_4 flux calculations also indicated lower gas flows in the morning. One possible explanation was the sampling times. Ambient light intensity was increasing during early morning sampling. This increase could have promoted photosynthetic production and transport

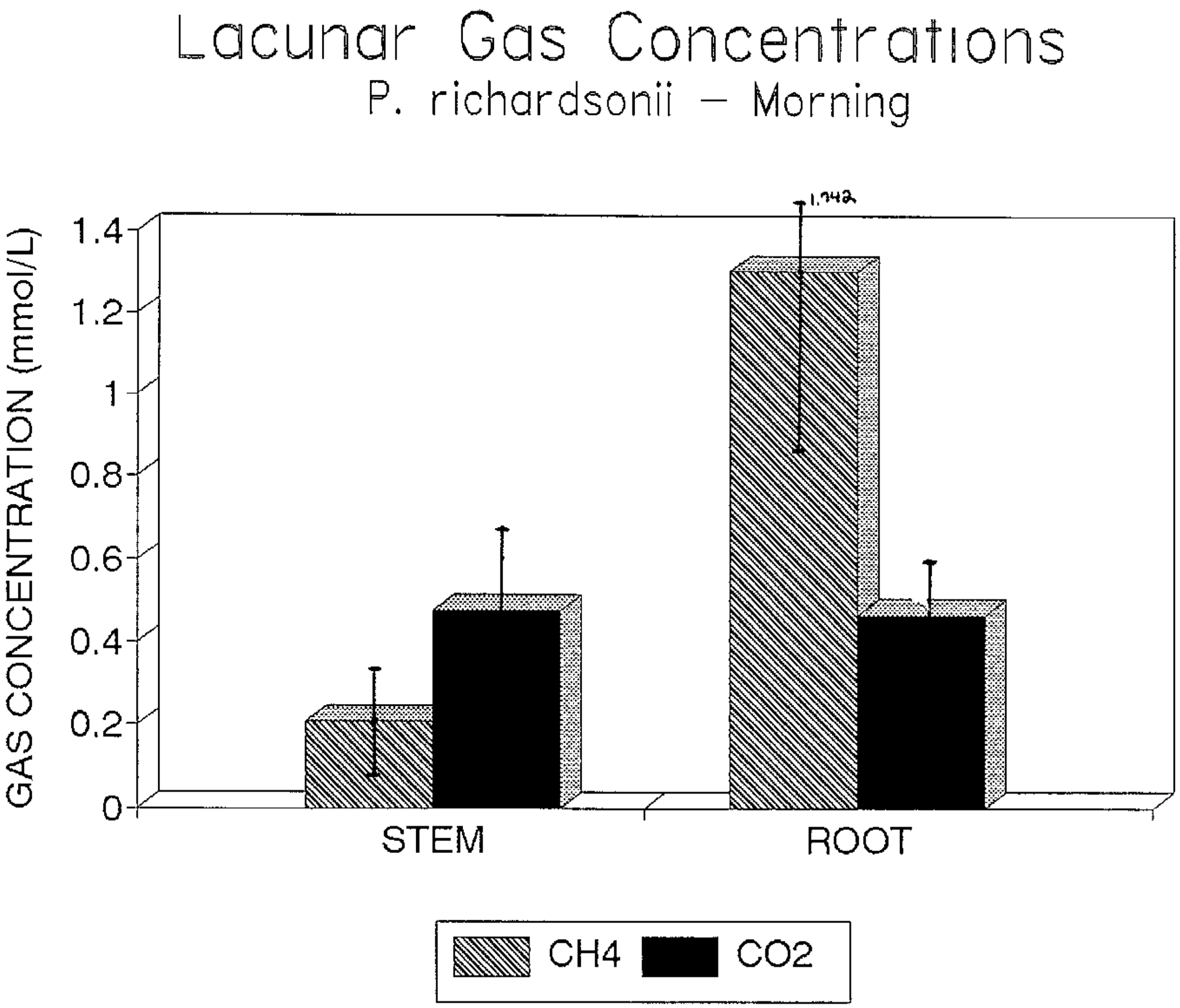

Fig. 9. Morning mean lacunar CH_4 and CO_2 concentrations within the stem and root of Potamogeton richardsonii (units = mmol/L).

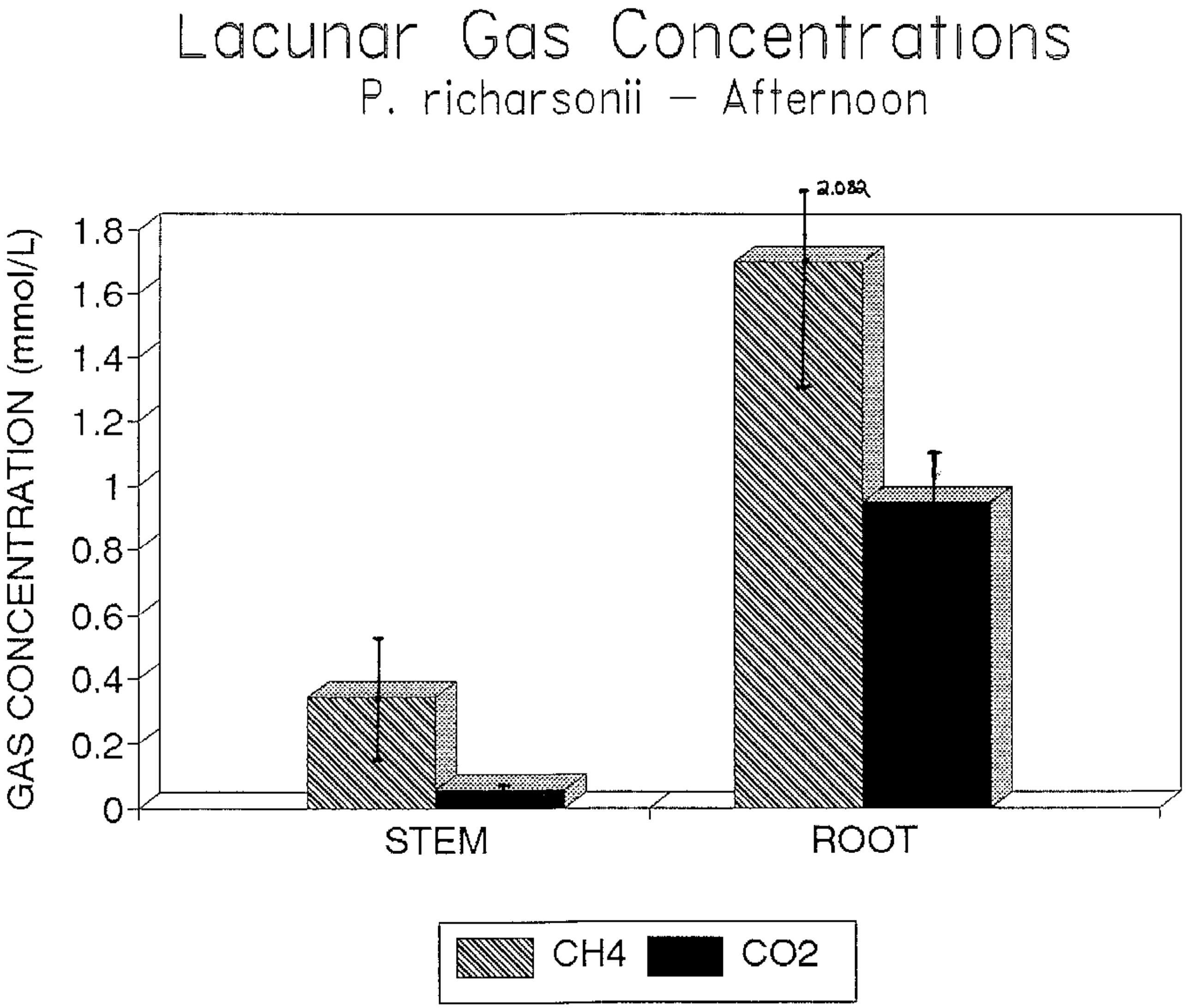

Fig. 10. Afternoon mean lacunar CH_4 and CO_2 concentrations within the stem and root of *Potamogeton richardsonii* (units = mmol/L).

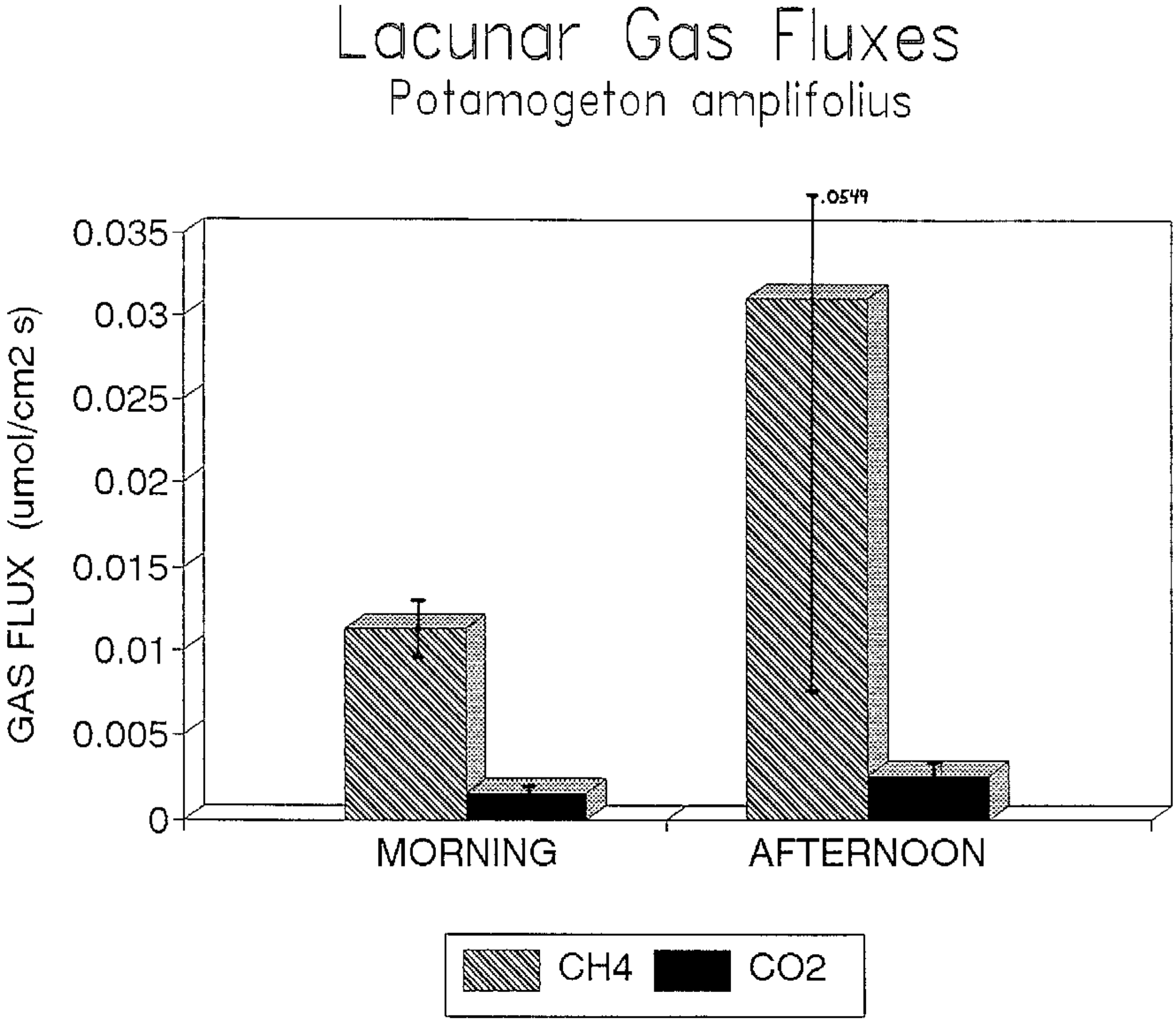

Fig. 8. Daily variation in lacunar CH_4 and CO_2 fluxes in *Potamogeton amplifolius* (units = umol/cm^2/s).

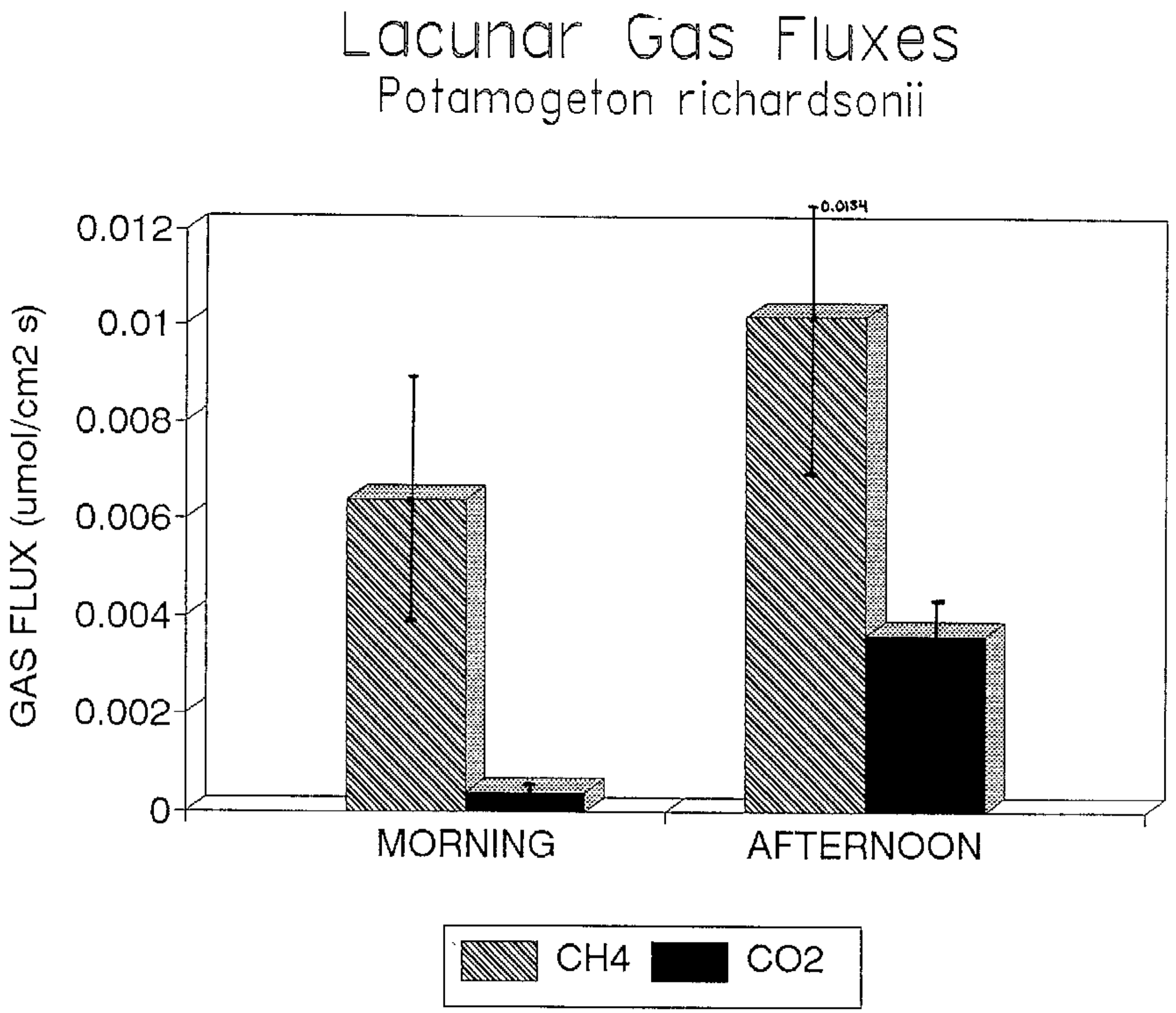

Fig. 11. Daily variation in lacunar CH_4 and CO_2 fluxes in _Potamogeton richardsonii_ (units = *u*mol/cm^2/s).

of methane within the particular plant. In terms of species specific differences, P. amplifolius roots appeared to possess higher CH_4 concentrations than those of P.richardsonii. This could indicate a specific evolved adaptation of P.amplifolius to sediments with higher organic content and reduced conditions favorable to methanogenesis. A more intensive study with direct focus on this issue is required to determine the validity of this supposition.

The data collected on lacunar CO_2 variations over time were more consistent with previous studies. The lacunar system within the macrophyte provides a conduit for diffusion of O_2 down to roots and CO_2 up to the photosynthesizing leaves (Sculthorpe, 1967). Since diffusion of dissolved free CO_2 from lake water can be a limiting factor to aquatic plants, lacunar CO_2 which diffuses up from the roots can augment productivity (Smith & Walker 1980). The majority of the data from the study support this discovery. For P. amplifolius and P. richardsonii, concentrations of CO_2 were much lower in the stem during the afternoon due to photosynthetic consumption. Calculated CO_2 flux rates showed photosynthetically induced increases in the afternoon. Higher concentrations of CO_2 occurred in the roots of both P. amplifolius and P. richardsonii. during the afternoon. This is probably the result of increased root respiration supported by transport of photosynthetically produced oxygen and organic carbon compounds to the roots during the day. Leakage into the surrounding sediments can also augment the respiration of bacteria and invertebrates within the rhizosphere. Bacterial respiration increases CO_2 concentrations in the rhizosphere, creating a larger gradient for CO_2 diffusion into the plant.

Summary

This project's goal was to examine lacunar gas transport in submerged angiosperms. Potamogeton amplifolius and Potamogeton richardsonii were studied to determine the effect of photosynthesis on lacunar gas concentrations and pressures. The pressure experiments involved in the study failed due to equipment difficulties. However, changes in the concentrations and fluxes of methane and carbon dioxide, two important greenhouse gases, were successfully quantified. Methane diffusion from the sediments into the stems appeared to increase with increasing levels of photosynthesis during the afternoon. Lower flows were expected as lacunar transport of photosynthetic oxygen is known to increase studies should examine possible species-specific differences in lacunar gas transport and attempt to quantify methane flux through submersed macrophytes on a larger, lake- wide scale.

Acknowledgements

I would like to thank Dr. Richard G. ("Rick", "the Rickster", "the Rickman", "Rickitickitavi"...) Carlton for his incredible support of this study. Without his investment of time, energy, "know-how", and high-tech wizardry, this project would have never been possible. I would also like to thank my fellow UNDERC students for helping me in my work especially Karin "Who's Marvin?" Young. Kudos go out to Terrance Ehrman for his performance in the role of GC Lord and babysitter this summer. And finally, a special thank-you goes out to all the staff, faculty, and benefactors of the UNDERC program especially the Hank family. UNDERC had a major impact on my life not only academically but personally as well. I will always cherish those ten weeks in the summer of '91.

References Cited

Bolin, B., and Cook, R.B. 1983. The major biogeochemical cycles and their interactions. John Wiley & Sons, 247 pp.

Dacey, J.W.H. 1981. Pressurized ventilation in the yellow waterlily. Ecology 62:1137-1147.

Dale, H.M. 1984. Hydrostatic pressure and aquatic plant growth: a laboratory study. Hydrobiologia 111:193-200.

Kemp, M.W., and Murray, L. 1986. Oxygen release from roots of the submersed macrophyte Potamogeton perfoliatus L.: regulating factors and ecological implications. Aquat. Bot 26:271-283.

Sand-Jensen, K., Prahl, C., and Stokholm, H. 1982. Oxygen release from roots of submerged aquatic macrophytes. Oikos 38:349-354.

Schuette, J.L. 1990. Structural adaptations of submersed vascular plants to gas exchange and oxygen transport. Ph.D. Dissertation, Michigan State University, 142 pp.

Sculthorpe, C.D. 1967. The biology of aquatic vascular plants. New York, St. Martin's Press, 610 pp.

Smith, F.A. and Walker, N.A. 1980. Photosynthesis by aquatic plants: effects of unstirred layers in relation to assimilation of CO_2 and HCO_3^- and to carbon isotopic discrimination. New Phytologist 86:245-259.

Wetzel, R.G. 1983. Limnology. Chicago, Saunders College Publishing, 767 pp.

Wium-Andersen, S., and Andersen, J.M. 1972. The influence of vegetation on the redox profile of the sediment of Grane Langso, a Danish Lobelia lake. Limnol.Oceanogr.17:948-952.

Appendix

This section includes overall data from which calculations for gas concentrations and fluxes were made. The diffusion coefficients $(D_s)_2$ used for CH_4 and CO_2 flux calculations were .26 cm^2/s and .139 cm^2/s respectively.
The section also includes figures, which though relevant to the paper, were considered distracting to the reader or secondary in importance to experiment data figures for inclusion within the body of the paper itself.

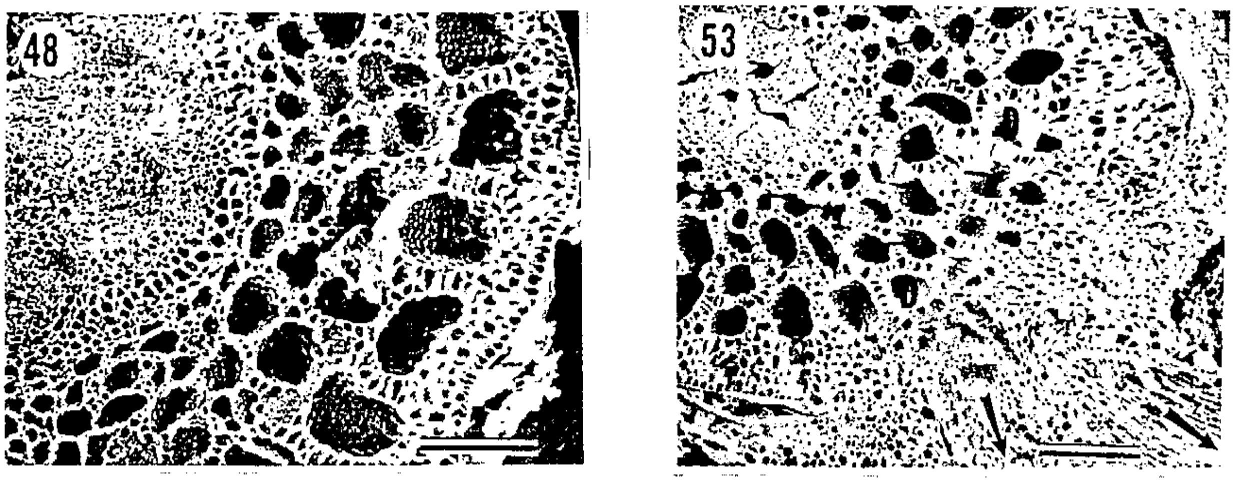

Fig. 1. #48 - Cross-section through node of *Potamogeton* stem; #53 - Cross-section of *Potamogeton* rhizome. bar in each = 0.25 mm. (Micrographs courtesy of Schuette, 1990.)

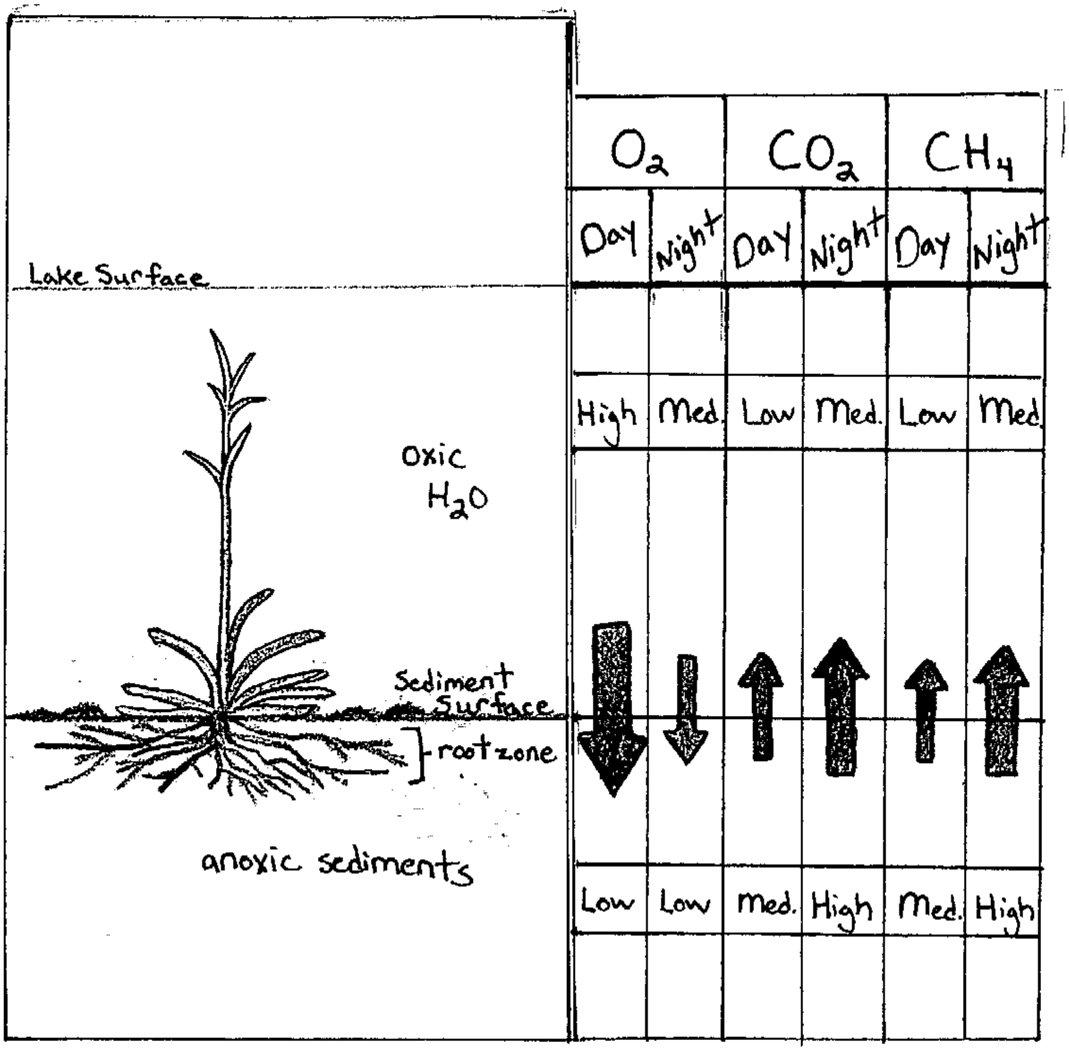

Fig. 2. Predicted relative gas concentrations and flux vectors for O_2, CO_2, CH_4 under day vs. night conditions in a submersed angiosperm. (sizes of arrows indicate relative fluxes.)

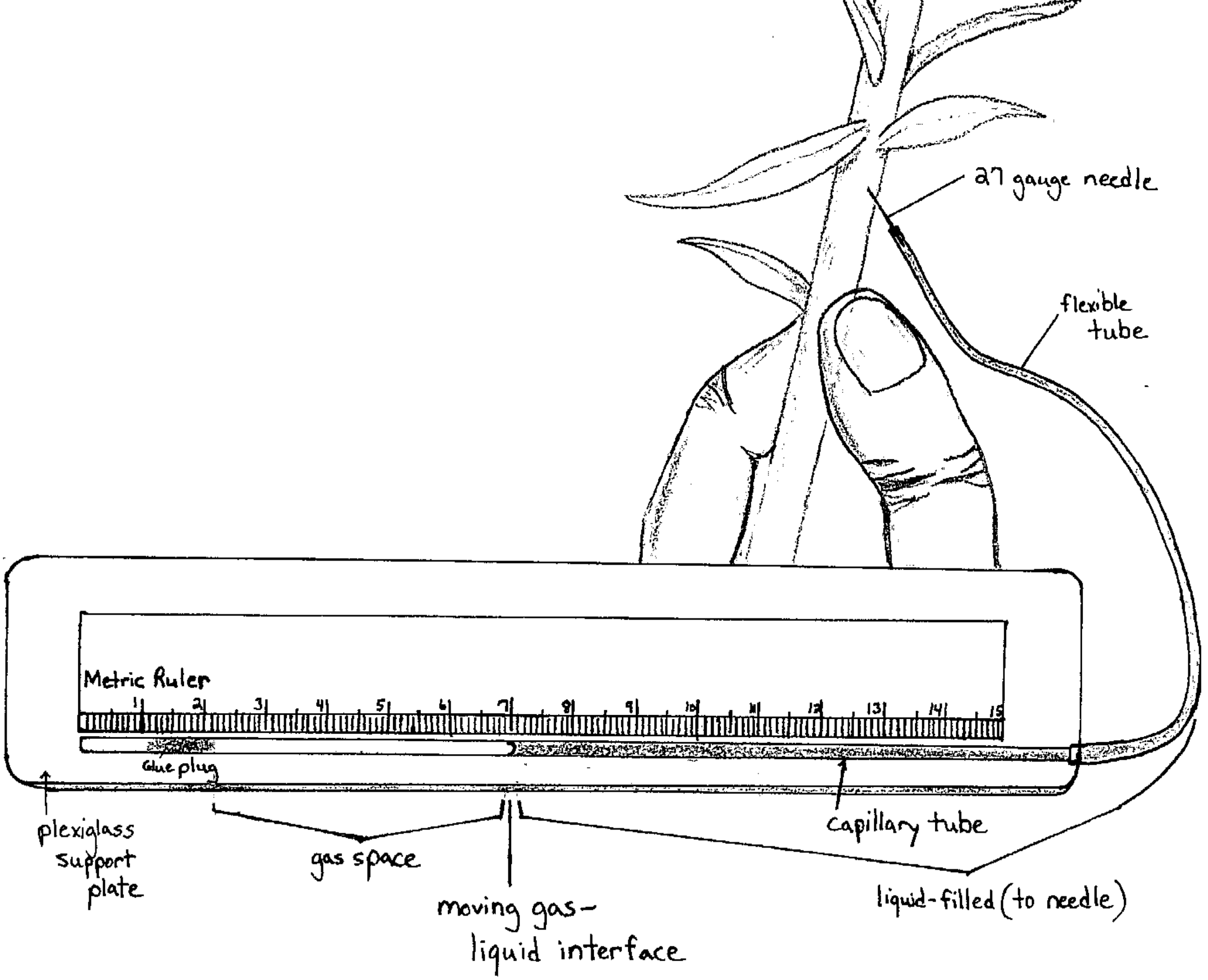

Fig. 3. Manometer for measuring lacunal gas pressures in situ. A leftward deflection indicates greater lacunal pressure relative to ambient hydrostatic. (drawing approximately to scale)

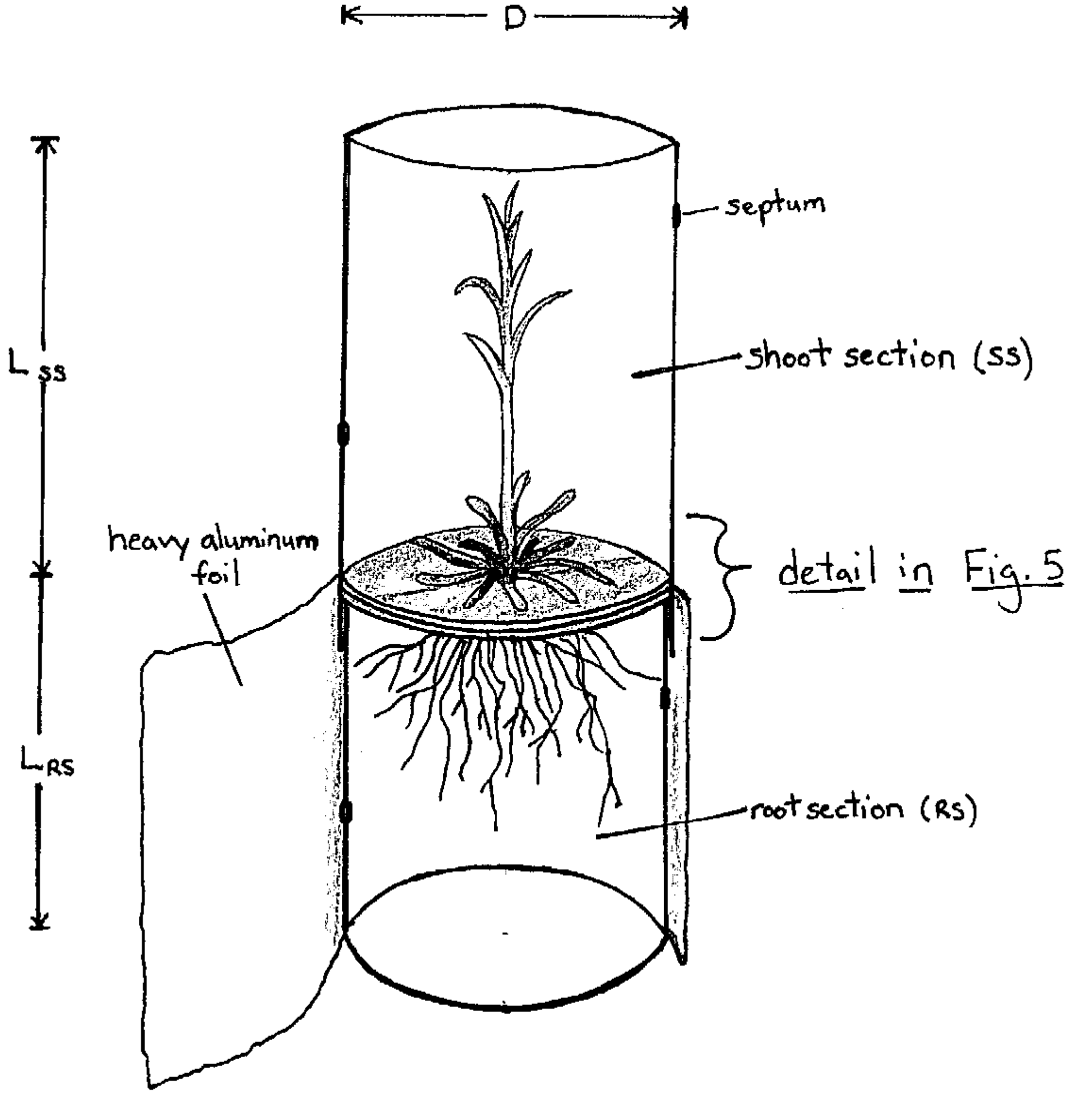

Fig. 4. Divided Cylinder System used for evaluating internal gas fluxes under controlled conditions.

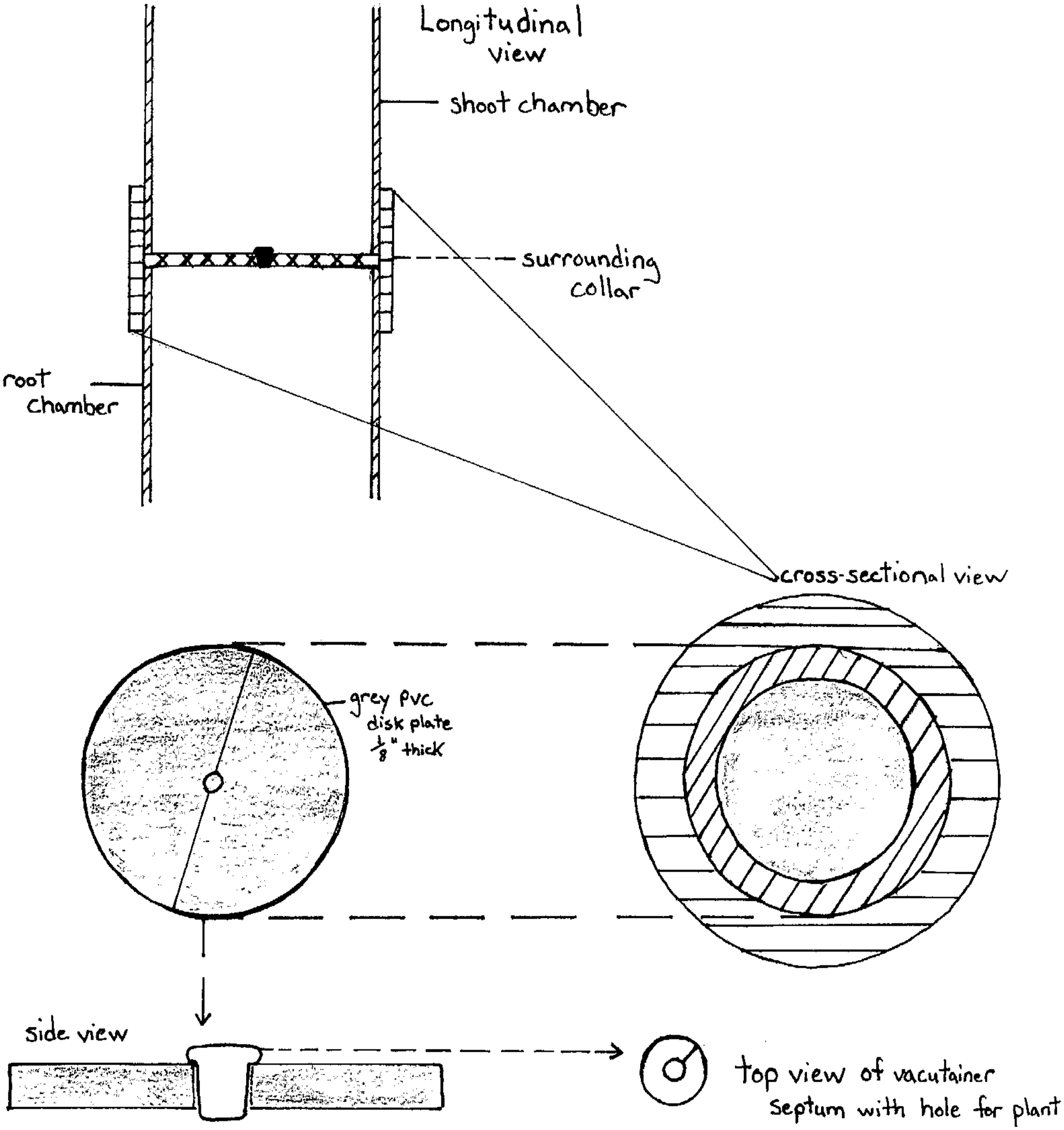

Fig. 5. Blow-up of Divider System separating two chambers.

Table 3. Lacunar methane concentrations and fluxes in Potamogeton amplifolius.

Morning 8am

Samp#	Sample site	CH4 ratio	[CH4] mmol/L	dx cm	CH4 dC/dx umol/cm4		CH4 J umol/cm2s
25	stem	0.45	0.201	45	0.0469		0.0122
32	stem	0.06	0.027	40	0.0357		0.0093
33	stem	0.20	0.089	45	0.0476		0.0124
35	stem	0.08	0.036				
26	root	5.18	2.313		Flux	mean>	0.0113
28	root	4.69	2.094		Calc.	std>	0.0014
30	root	15.14	6.759				
31	root	3.26	1.455				
34	root	5.00	2.232				

Concentration Calc.		CH4			CH4
stem	mean>	0.088	root	mean>	2.971
	std>	0.069		std>	1.918

Afternoon 3pm

Samp#	Sample site	CH4 ratio	[CH4] mmol/L	dx cm	CH4 dC/dx umol/cm4		CH4 J umol/cm2s
1	stem	1.02	0.455	50	0.0055		0.0014
3	stem	0.04	0.018	40	0.0397		0.0103
7	stem	1.75	0.781	43	0.1262		0.0328
9	stem	0.20	0.089	40	0.3008		0.0782
11	stem	0.44	0.196	40	0.1260		0.0328
2	root	1.64	0.732				
4	root	3.60	1.607		Flux	mean>	0.0311
6	root	15.80	7.054		Calc	std>	0.0266
8	root	13.91	6.210				
10	root	27.15	12.121				
12	root	11.73	5.237				

Concentration Calc.		CH4			CH4
stem	mean>	0.308	root	mean>	5.493
	std>	0.279		std>	3.757

Table 4. Lacunar carbon dioxide concentrations and fluxes in Potamogeton amplifolius.

Morning 8am

Samp#	Sample site	CO2 ratio	[CO2] mmol/L	dx cm	CO2 dC/dx umol/cm4		CO2 J umol/cm2s
25	stem	0.12	0.080	45	0.0171		0.0024
32	stem	0.37	0.248	40	0.0102		0.0014
33	stem	0.43	0.288	45	0.0058		0.0008
35	stem	0.34	0.228				
26	root	1.27	0.850		Flux	mean>	0.0015
28	root	0.83	0.556		Calc.	std>	0.0006
30	root	0.79	0.529				
31	root	0.98	0.656				
34	root	0.82	0.549				

Concentration Calc.		CO2			CO2
stem	mean>	0.211	root	mean>	0.628
	std>	0.078		std>	0.120

Afternoon 3pm

Samp#	Sample site	CO2 ratio	[CO2] mmol/L	dx cm	CO2 dC/dx umol/cm4		CO2 J umol/cm2s
1	stem	0.09	0.060	50	0.0208		0.0029
3	stem	0.11	0.074	40	0.0075		0.0010
7	stem	0.12	0.080	43	0.0232		0.0032
9	stem	0.14	0.094	40	0.0126		0.0017
11	stem	0.10	0.067	40	0.0293		0.0041
2	root	1.64	1.098				
4	root	0.56	0.375		Flux	mean>	0.0026
6	root	*	*		Calc	stdv>	0.0011
8	root	1.61	1.078				
10	root	0.89	0.596				
12	root	1.85	1.239				

* anomolous CO2 reading (ratio=6.11)

Concentration Calc.		CO2			CO2
stem	mean>	0.075	root	mean>	0.877
	std>	0.012		std>	0.332

Table 5. Lacunar methane concentrations and fluxes in Potamogeton richardsonii.

Morning 8am

Sample #	Sample site	CH4 ratio	[CH4] mM	dx	CH4 dC/dx umol/cm4		CH4 J umol/cm2/s
37	stem	0.13	0.058	50	0.0204		0.0053
39	stem	1.22	0.545	38	0.0182		0.0047
41	stem	0.43	0.192	30	0.0390		0.0101
43	stem	0.29	0.129	35	0.0378		0.0098
45	stem	0.52	0.232				
47	stem	0.2	0.089	45	0.0077		0.0020
38	root	2.42	1.080				
40	root	2.77	1.237		Flux	mean>	0.0064
42	root	3.05	1.362		Calc.	std>	0.0031
44	root	3.25	1.451				
48	root	5.05	2.254				
50	root	0.98	0.438				

Concentration Calc.			CH4			CH4
	stem	mean>	0.208	root	mean>	1.304
		std>	0.162		std>	0.538

Afternoon 3pm

Sample #	Sample site	CH4 ratio	[CH4] mM	dx	CH4 dC/dx umol/cm4		CH4 J umol/cm2/s
13	stem	1.55	0.692	35	0.0313		0.0081
15	stem	0.42	0.188	35	0.0540		0.0140
17	stem	0.54	0.241	35	0.0235		0.0061
21	stem	0.62	0.277	33	0.0484		0.0126
14	root	4	1.786				
16	root	4.65	2.076		Flux	mean>	0.0102
18	root	2.38	1.063		Calc.	std>	0.0032
22	root	4.2	1.875				

Concentration Calc.			CH4			CH4
	stem	mean>	0.349	root	mean>	1.700
		std>	0.200		std>	0.383

Table 6. Lacunar carbon dioxide concentrations and fluxes in Potamogeton richardsonii.

Morning 8am

Sample #	Sample site	CO2 ratio	[CO2] mM	dx	CO2 dC/dx umol/cm4		CO2 J umol/cm2/s
37	stem	1.29	0.864	50			
39	stem	0.52	0.348	38	0.0016		0.0002
41	stem	0.45	0.301	30	0.0047		0.0007
43	stem	0.23	0.154	35	0.0031		0.0004
45	stem	0.77	0.516				
47	stem	1.01	0.676	45	0.0012		0.0002
38	root						
40	root	0.61	0.408		Flux	mean>	0.0004
42	root	0.66	0.442		Calc.	std>	0.0002
44	root	0.39	0.261				
48	root	0.72	0.482				
50	root	1.09	0.730				

Concentration Calc.		CO2			CO2
stem	mean>	0.477	root	mean>	0.465
	std>	0.239		std>	0.152

Afternoon 3pm

Sample #	Sample site	CO2 ratio	[CO2] mM	dx	CO2 dC/dx umol/cm4		CO2 J umol/cm2/s
13	stem	0.08	0.054	35	0.0182		0.0025
15	stem	0.08	0.054	35	0.0260		0.0036
17	stem	0.1	0.067	35	0.0253		0.0035
21	stem	0.07	0.047	33	0.0347		0.0048
14	root	1.03	0.690				
16	root	1.44	0.964		Flux	mean>	0.0036
18	root	1.42	0.951		Calc.	std>	0.0008
22	root	1.78	1.192				

Concentration Calc.		CO2			CO2
stem	mean>	0.055	root	mean>	0.949
	std>	0.007		std>	0.178