Methane emissions from different vegetation zones in a Qinghai-Tibetan Plateau wetland

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Abstract

We measured methane (CH_4) emissions in the Luanhaizi wetland, a typical alpine wetland on the Qinghai-Tibetan Plateau, China, during the plant growth season (early July to mid-September) in 2002. Our aim was to quantify the spatial and temporal variation of CH_4 flux and to elucidate key factors in this variation. Static chamber measurements of CH_4 flux were made in four vegetation zones along a gradient of water depth. There were three emergent-plant zones (*Hippuris*-dominated; *Scirpus*-dominated; and *Carex*-dominated) and one submerged-plant zone (*Potamogeton*-dominated). The smallest CH_4 flux (seasonal mean $= 33.1$ mg CH_4 m^{-2} d^{-1}) was observed in the *Potamogeton*-dominated zone, which occupied about 74% of the total area of the wetland. The greatest CH_4 flux (seasonal mean $= 214$ mg CH_4 m^{-2} d^{-1}) was observed in the *Hippuris*-dominated zone, in the second-deepest water area. CH_4 flux from three zones (excluding the *Carex*-dominated zone) showed a marked diurnal change and decreased dramatically under dark conditions. Light intensity had a major influence on the temporal variation in CH_4 flux, at least in three of the zones. Methane fluxes from all zones increased during the growing season with increasing aboveground biomass. CH_4 flux from the *Scirpus*-dominated zone was significantly lower than in the other emergent-plant zones despite the large biomass, because the root and rhizome intake ports for CH_4 transport in the dominant species were distributed in shallower and more oxidative soil than occupied in the other zones. Spatial and temporal variation in CH_4 flux from the alpine wetland was determined by the vegetation zone. Among the dominant species in each zone, there were variations in the density and biomass of shoots, gas-transport system, and root–rhizome architecture. The CH_4 flux from a typical alpine wetland on the Qinghai-Tibetan Plateau was as high as those of other boreal and alpine wetlands.
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1. Introduction

Methane (CH_4) is an important greenhouse gas (Khalil and Rasmussen, 1983). The atmospheric CH_4 concentration has doubled since the industrial revolution (IPCC, 2001) and depends on the balance between sink and source for CH_4. Wetlands account for about 70% of natural CH_4 sources (Khalil, 2000) and roughly 20% of the global CH_4 emission (IPCC, 2001).

Previous studies have quantified CH_4 emissions from various wetlands in the world (Bartlett and Harriss, 1993), and have determined the factors controlling CH_4 flux (Wang et al., 1993; Schimel, 1995; Ding et al., 2003). However, global estimates of CH_4 emission from wetlands are still uncertain, because there is a lack of CH_4 flux data for specific wetlands and flux measurements have not included the spatial variability of CH_4 flux in relation to vegetation, climate, and topography (Schütz et al., 1991; Saarnio et al., 1997). In recent years, vegetation has been recognized as a key factor affecting spatial variation in CH_4 flux (Joabsson et al., 1999; Joabsson and Christensen, 2001).

Vegetation properties, such as density, life form, and species composition, affect three processes—production, consumption, and transport of CH_4—and lead to both enhancement and diminution of CH_4 emission from wetlands. Through litter production and root exudates, plants can provide substrates for methanogenesis (Schütz et al., 1991; Dannenberg and Conrad, 1999). Aquatic plants provide gas conduits, which transport CH_4 from waterlogged soils to the atmosphere (Chanton and Dacey, 1991; Shannon et al., 1996). Previous studies have demonstrated that net CH_4 emissions from wetlands are largely controlled by plant-mediated transport (Kelker and Chanton, 1997). Besides providing a conduit for CH_4 transport, plants inhibit methanogenesis by transporting oxygen from the atmosphere to the soil (Chanton and Dacey, 1991; Epp and Chanton, 1993).

Recent studies of CH_4 sources have focused on high-latitude wetlands, because boreal wetlands store about one-third of the global carbon pool in the soil (Gorham, 1991). Boreal and arctic wetlands are potentially ideal sites for CH_4 production because of the prevalence of waterlogged conditions in seasonally thawed layers (Soegaard and Nordstroem, 1999). Methane emissions from high-altitude wetlands are also of great importance for similar reasons. However, our knowledge of CH_4 emissions in alpine or subalpine wetlands is limited to wetlands on the American continent (West et al., 1999; Wickland et al., 2001). Data on CH_4 flux from other regions, e.g. the Qinghai-Tibetan Plateau, on the Eurasian continent, which has numerous lakes and wetlands (Zhao, 1999), would improve our understanding of the fundamentals of the global CH_4 budget.

The Qinghai-Tibetan Plateau (av. 4000 m a.s.l.) is the largest grassland unit on the Eurasian continent, and its lakes and wetlands occupy a considerable area (ca. 50,000 km^2; Zhao, 1999). Soil organic carbon stored in the plateau represents 2.5% of the global pool of soil carbon. Further, 8% of the soil organic carbon is stored in wetlands of the plateau (Wang et al., 2002). The organic content of the wetlands soil is extremely high because of its low decomposition rate. The unique climate of the region is characterized by cold, long winters and short, cool summers with relatively high precipitation. In summer, the relatively humid climate supports high productivity and induces input of organic carbon to the soil. In winter, the rate of decomposition of organic carbon is low because of the cold. In summer, the rate of decomposition of organic carbon, i.e. the carbon dioxide (CO_2) flux from the plateau, is higher because of the rich organic carbon load in the soil. In wetlands, not only CO_2, but also CH_4, is produced as a result of decomposition of organic carbon. Hence, one would expect CH_4 flux from alpine wetlands to be particularly high in the summer growing season. For precise estimation of CH_4 sources, it is crucial to quantify CH_4 emissions from alpine wetlands on the plateau and to determine the factors, such as vegetation, water depth, and temperature, that influence CH_4 flux from these wetlands.

We therefore aimed: (1) to quantify the spatial and temporal variability of CH_4 flux from a Qinghai-Tibetan Plateau wetland; (2) to determine the key factors controlling the spatial and temporal variation of this flux; and (3) to calculate CH_4 emission from the alpine wetland during the growing season. Details of the alpine wetland will be reported in our other study (Hirota et al. unpublished), in which we recognize four zones: three emergent-plant zones and one submerged-plant zone. We used a static closed-chamber technique to measure CH_4 flux from the four zones during a growing season.

2. Materials and methods

2.1. Site description

The study site was located in the Luanhaizi wetland, approximately 4 km from the Haibei Alpine Meadow Ecosystem Research Station (lat 37° 29'N, long 101°12'E, 3250 m a.s.l.) of the Chinese Academy of Sciences (CAS), in the northeast part of the Qinghai-Tibetan Plateau (Fig. 1). The catchment was flooded at an average water depth of 30 cm over the growing season. The annual mean temperature is -2 °C, and the annual precipitation is 500 mm (Klein et al., 2001). The Luanhaizi wetland is surrounded by small hills on all sides, from which an inflowing stream comes down to the catchment (Fig. 1). Vegetation was composed of four major species dominating in zones at different distances from the flood line.

There were three emergent-plant zones, dominated by *Carex allivescers* V. Krez. (ZCar), *Scirpus distigmaticus* L. (ZSci), or *Hippuris vulgaris* L. (ZHip), and one submerged-plant zone dominated by *Potamogeton pectinatus* L. (ZPot) along a gentle gradient of shallow to deep water (Fig. 2). ZCar made up 3.4% of the study area; ZSci 20.5%; ZHip 2.6%, and ZPot 73.5% (Hirota et al., unpublished). Vegetation distribution was assessed by a *V*-value (m^3), calculated by multiplying mean plant height from the soil surface (cm) by coverage area (cm^2) of individual plant species. On 14 July 2002, plant height and coverage were measured in 50×50 cm^2 plots at intervals of 2.5 m along a line transect from the flood line to the point at which vegetation was dominated only by *P. pectinatus*. Detailed information on the vegetation zones in which CH_4 flux was measured is given in Table 1.

A pilot study was conducted to check gas-transport mechanisms of emergent plants, molecular diffusion or convective gas flow, in summer 2001, because we needed to select an appropriate method for measuring CH_4 flux via emergent plants according to the gas-transport mechanism. A chamber method should not be applied to the plants that show convective gas flow (Hirota and Tsuchiya, 2003).
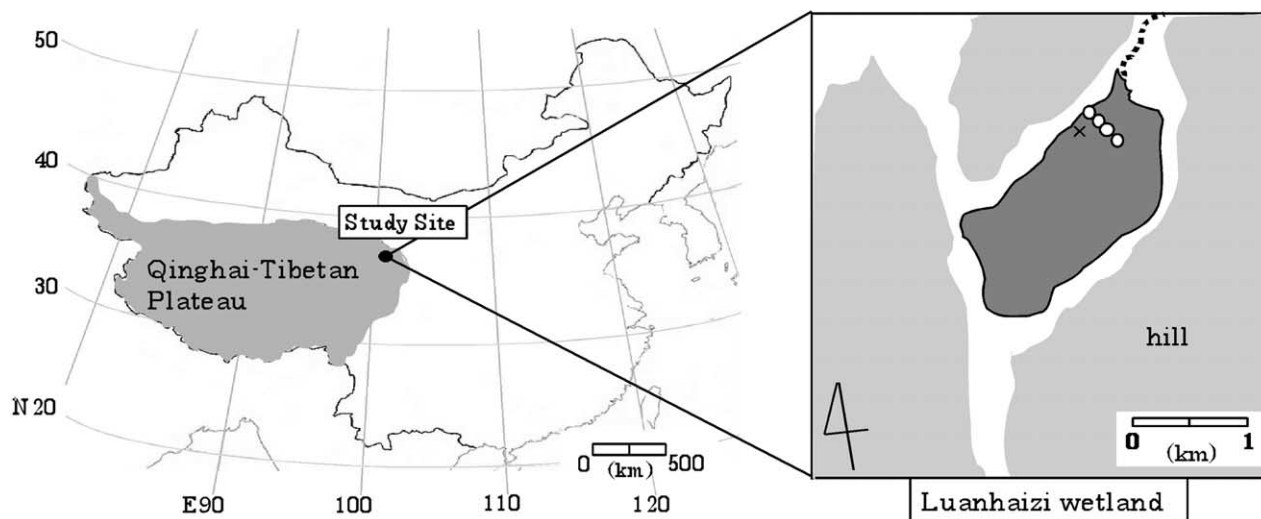
Fig. 1. Location of the study site, Luanhaizi wetland. The cross represents the meteorological tower and the open circles represent CH_4 flux measurement sites. Dashed line represents a stream.

Gas-transport mechanism of all the emergent plants was mainly molecular diffusion because no internal pressurization was observed during the daytime. Hence, a chamber method was adapted to measure CH_4 flux in this study.

2.2. Environmental factors

A meteorological tower equipped with sensors and a data logger (Thermic 2300A, Eto Denki Ltd, Tokyo) was placed between *ZHip* and *ZSci* at the northwestern edge of

the wetland (Fig. 1). The tower was used to monitor temporal changes in air temperature, water temperature at 10 cm depth, soil temperature at 5 cm depth, photosynthetic photon flux density (PPFD) above and below the water surface, and soil oxidation–reduction potential (ORP) at 0, 2.5, 5, 7.5, 10, 20, and 30 cm depth, with permanently installed instruments (air temperature, MT-060, Eko Instruments, Tokyo; water and soil temperature, TidbiT TBI32-20 + 50, StowAway, Bourne, MA; PPFD, ML-020P, Eko Instruments, Tokyo; ORP, RM-20P, TOA Electric Co., Tokyo). Meteorological
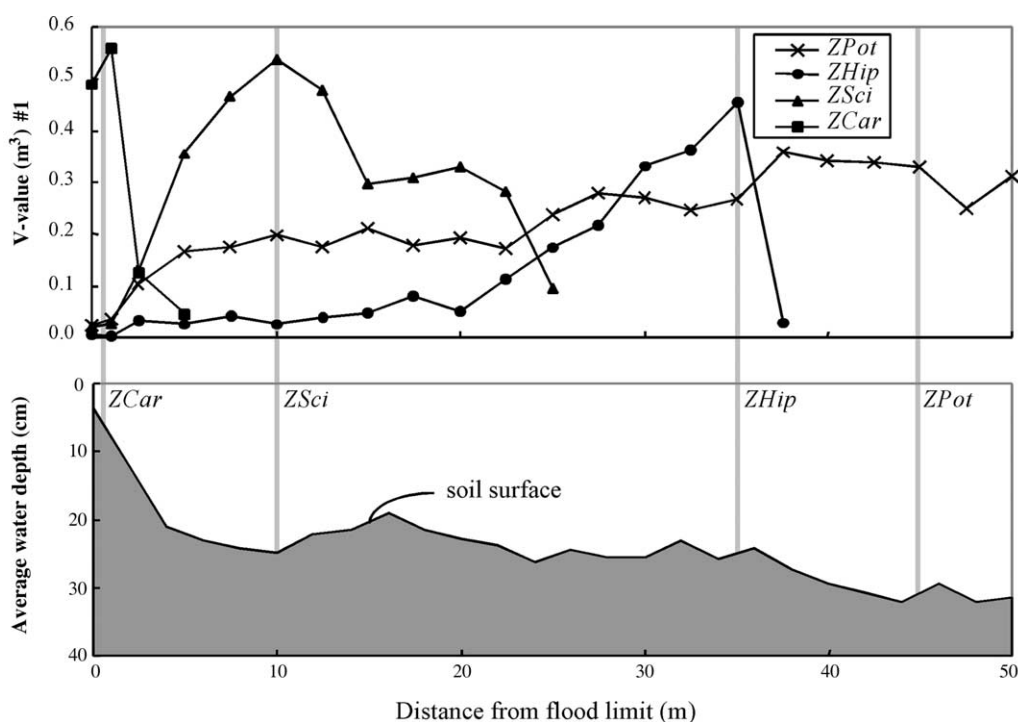

Fig. 2. 'V-value' vegetation distribution of dominant species (top) and schematic cross-section from flood limit (bottom). Gray lines represent CH_4 flux measurement point of each zone; *ZPot* (×), *ZHip* (●), *ZSci* (▲) and *ZCar* (■).

Table 1
Species component (relative biomass, %), total biomass, and water depth (with range) in four vegetation zones, Luanhaizi wetland

Zone	Vegetation	Relative biomass[a] (%)	Total biomass[a] (g DW m^{-2})	Water depth (cm)
Zpot	*P. pectinatus* L.	100	120	27 (14–38)[b]
	H. vulgaris L.	0		
	S. distigmaticus L.	0		
	C. allivescers V. Krez	0		
ZHip	*H. vulgaris* L.	85	393	24 (13–33)
	P. pectinatus L.	15		
	S. distigmaticus L.	0		
	C. allivescers V. Krez	0		
ZSci	*S. distigmaticus* L.	80	412	19 (9–25)
	H. vulgaris L.	13		
	P. pectinatus L.	7		
	C. allivescers V. Krez	0		
ZCar	*C. allivescers* V. Krez	88	384	12 (1–20)
	H. vulgaris L.	5		
	S. distigmaticus L.	4		
	P. pectinatus L.	3		

Dominant species in each zone is denoted by the asterisk ([*]).
[a] Mean value during the measurement period, early July to mid-September 2002.
[b] Range of water depth indicates minimum and maximum values at the same points during the measurement period.

measurements were made every 10 min from July 2002 to mid-September 2002. The water depth was measured next to the tower everyday. Precipitation data were obtained from the CAS station located about 4 km northwest of the wetland site.

2.3. Estimation of plant biomass during growing season

We estimated the temporal changes in aboveground biomass of plants growing in a chamber installed in each zone for measuring CH$_4$ flux. Three zones (other than *ZPot*) had mixed vegetation of a few species. Aboveground biomass in these three zones was expressed as the sum of biomass of all species in the chamber. The biomass of each species was calculated by multiplying the number of shoots in the chamber at the time of CH$_4$ flux measurement by the biomass per shoot. After the final flux measurement, we harvested the aboveground parts of the surviving plants in the chamber and measured the depth of the root zone of one dominant plant.

2.4. Methane flux measurement

Methane flux was measured by the static chamber method of Whalen and Reeburgh (1988) every 2 weeks

from early July to mid-September 2002. Daily CH$_4$ flux from each zone was measured at 13:00, 15:00, 17:00, 19:00, 22:00, 1:00, 4:00, 7:00, 9:00, 11:00 and 13:00 (Beijing time) on 4–5 July, 19–20 July, 25–26 July, 12–13 August, 26–27 August and 14–14 September. In order to minimize disturbance of the measurement sites during gas sampling, the measurement was made on a stool, which was set so that measurement point were not shaded and the vegetation and soil near the measurement sites remained intact. A chamber used in this study is the same as used by Koizumi et al. (2001). One acrylic frame (collar, 0.35 m^2) per zone was set 2 days before the flux measurement to reduce the influence of vegetation and soil disturbance on CH$_4$ flux. An upper cylindrical chamber (21 cm in diameter) with a water jacket was placed on the frame. The chamber was made of transparent Plexiglas that transmits approximately 88% of PPFD. We replaced water inside the chamber with cool water before measurement started. We succeeded in controlling within a rise of 2 °C in air temperature inside the chamber during the measurement time. Different heights (25, 40, 65 cm) of chamber were used, depending on the vegetation height. The closed chamber was equipped with a fan to ensure complete mixing of the inside air during measurements. Gas samples were withdrawn from the headspace of the closed chamber through an injection port with a needle directly into a 5 ml evacuated vial 1, 3, 6, 9, and 12 min after the system was closed. These samples were analyzed by a gas chromatograph equipped with a Porapak Q column (80/120 mesh) and a flame ionization detector (GL 390B, GL Science, Tokyo). Injection, detection, and column-oven temperatures were 120, 150 and 50 °C, respectively, and pure helium (He) was used as a carrier gas. The samples were injected into the gas chromatograph directly by gas-tight syringe (A-2 Type Gas Syringes, Valco Instruments, Texas). Analytical error on duplicate samples was less than 1%. Gas standards were run every 10 duplicate vials. The gas chromatograph had a detection limit of 0.02 ppmv. Increase rate of CH$_4$ concentrations in the chamber was determined by a linear regression. The methane flux was calculated by multiplying slope of the linear regression by the chamber height. The minimum detectable CH$_4$ flux was estimated to be 0.02 mg CH$_4$ m^{-2} h^{-1}. Ebullition often occurred during the flux measurement and CH$_4$ concentration of the ebullition gas sampled on daytime in August 2001 was high (1–2%). Hence, when ebullition from the soil surface was observed during measurements, we stopped the gas sampling and restarted it after a few minutes. The correlation coefficient of the regression had to be higher than $R^2 = 0.90$, otherwise the sample was rejected. This resulted in the rejection of 9.3% of all the flux measurements. Gas samples in the vials were stored in China for 2 months, and then transported by air from China to Japan. We checked for gas leakage during storing and air transport by testing gas standards stored in

the same type of vial. We did not detect any changes in gas concentration.

We also examined whether or not CH$_4$ flux occurred via the stomata of plants. After the final gas sampling during daytime (Beijing time 13:00–13:30), the chambers were covered with a few sheets of aluminum foil for a light–dark experiment. Flux measurements were made in the dark following 30 min of dark acclimation.

We measured the environmental factors at the flux measurement point: PPFD in the chamber, ambient air temperature, air temperature in the chamber, water temperature at 5 cm depth, soil temperature at 5 cm depth, and ORP at 5 and 30 cm soil depths.

Factors controlling daily and seasonal variations in CH$_4$ flux, were tested by multivariate analysis based on partial correlations (StatView-J5.0, HULINKS).

3. Results

3.1. PPFD, temperature, precipitation, water depth, ORP

Daily mean PPFD in air and water, air temperature, soil temperature at 5 cm depth, water depth in the four zones, and daily precipitation at the CAS station are shown in Fig. 3. Daily mean PPFD in air and water fluctuated from 72 to 885 μmol m^{-2} s^{-1} and from 26 to 295 μmol m^{-2} s^{-1}, respectively. Submerged plants therefore received about one-third the light intensity received by emergent plants during the growing season. Daily mean air temperature gradually decreased during the growing season (15.5– 4.9 °C). Rainfall events occurred over the growing season (maximum, 20.6 mm d^{-1}). Daily mean soil temperature at 5 cm depth varied among the four zones: *ZPot*(12.2– 19.2 °C) > *ZHip*(12.0–18.4 °C) > *ZSci*(11.9–16.8 °C) > *ZCar*(10.0–15.5 °C). The difference in daily mean soil temperature between *ZPot* and *ZCar* was about 3 °C during the growing season. Water depth decreased gradually, reached a minimum in each zone (*ZPot*: 13.5 cm, *ZHip*: 12.9 cm, *ZSci*: 9.1 cm, *ZCar*: 1.3 cm) on 2nd August, and was then restored by rainfall and leveled off to show only small, changes for the rest of the growing season. Water depth was greatest in the order of *ZPot*(13.5–37.6 cm) > *ZHip*(12.9–32.7 cm) > *ZSci*(9.1–24.9 cm) > *ZCar*(1.3– 19.8 cm).

Values of ORP in soil of a mixed vegetation of *P. pectinatus*, *H. vulgaris*, and *S. distigmaticus* close to the meteorological tower were consistently less than −200 mV in the deeper soils of 5–30 cm. Slightly higher ORP occurred at 0 and 2.5 cm. The mean ORP at 5 and 30 cm depth near the chambers had similar values over three zones (*ZPot*, *ZHip* and *ZCar*), −135 mV at 5 cm and −182 mV at 30 cm, respectively, with the exception of *ZSci*, (−68 mV at 5 cm and −101 mV at 30 cm; Fig. 4A). In addition, the mean ORP measured near the chamber in all zones was lower at 30 cm soil depth than at 5 cm depth (Fig. 4A). Root zone depth

showed a species-specific distribution between 0 and 10 cm ($P < 0.001$). The shallowest root zone was found for *ZSci* (at 1.3 cm soil depth; Fig. 4B).

3.2. Temporal and zonal variations in plant biomass

The total plant biomass increased during the early growing season, and the time to peak biomass varied among the zones. Peak biomass of the submerged plant, *P. pectinatus*, was lower (173 g DW m^{-2}) than that of the emergent plants, *H. vulgaris*, *S. distigmaticus* and *C. allivescers*, (415, 525, and 511 g DW m^{-2}, respectively). There were only *P. pectinatus* inside the chamber in *ZPot*, whereas *ZHip*, *ZSci*, and *ZCar* had mixed vegetation with individual dominant species of *H. vulgaris*, *S. distigmaticus*, and *C. allivescers*, respectively. Species other than the dominant species contributed 39–5.9% of the total biomass; this contribution tended to decrease gradually later in the growing season. The biomasses of *ZPot* and *ZCar* showed no decrease in mid-September, but those of *ZHip* and *ZSci* decreased.

3.3. Methane flux

3.3.1. Daily variation in methane flux

Methane flux from *ZPot*, *ZHip*, and *ZSci* showed a clear diurnal variation, increasing early in the morning, reaching a peak at noon, and decreasing in the afternoon. The daily variation became more marked as plants grew. The daily pattern of CH$_4$ flux coincided with that of PPFD. The effects of dark conditions on CH$_4$ flux were different among zones (Table 2). Methane fluxes from the three zones showing marked daily variations were reduced under dark conditions, by about 80% of that under light conditions for *ZPot* and *ZHip* and by about 50% for *ZSci*. The *ZCar* values showed only slight differences between light and dark conditions.

Methane flux in *ZPot* and *ZHip* was correlated positively with PPFD, especially late in the growing season (partial correlation coefficient = 0.75 and 0.59; Table 3). Methane flux in *ZSci* showed a slightly positive correlation with PPFD over the entire season (partial correlation coefficient = 0.44) and a slightly negative correlation with soil temperature over the entire period (partial correlation coefficient = −0.51). Diurnal CH$_4$ flux in *ZCar* had no significant correlation with any environmental factor.

3.3.2. Seasonal variation in methane flux

The variation in seasonal methane flux (mg CH$_4$ m^{-2} d^{-1}) is shown in Fig. 5. The smallest CH$_4$ flux was 10.9– 65.5 mg CH$_4$ m^{-2} d^{-1} in *ZPot*. The highest was 104.8– 296.2 mg CH$_4$ m^{-2} d^{-1} in *ZHip*. *ZSci* and *ZCar* showed intermediate ranges: 25.4–156 mg CH$_4$ m^{-2} d^{-1} and 45.9– 253.8 mg CH$_4$ m^{-2} d^{-1}, respectively. The magnitude and pattern of CH$_4$ flux varied among the zones. Higher CH$_4$ flux was observed in *ZHip* and *ZCar* than in *ZPot* and *ZSci*. *ZHip*
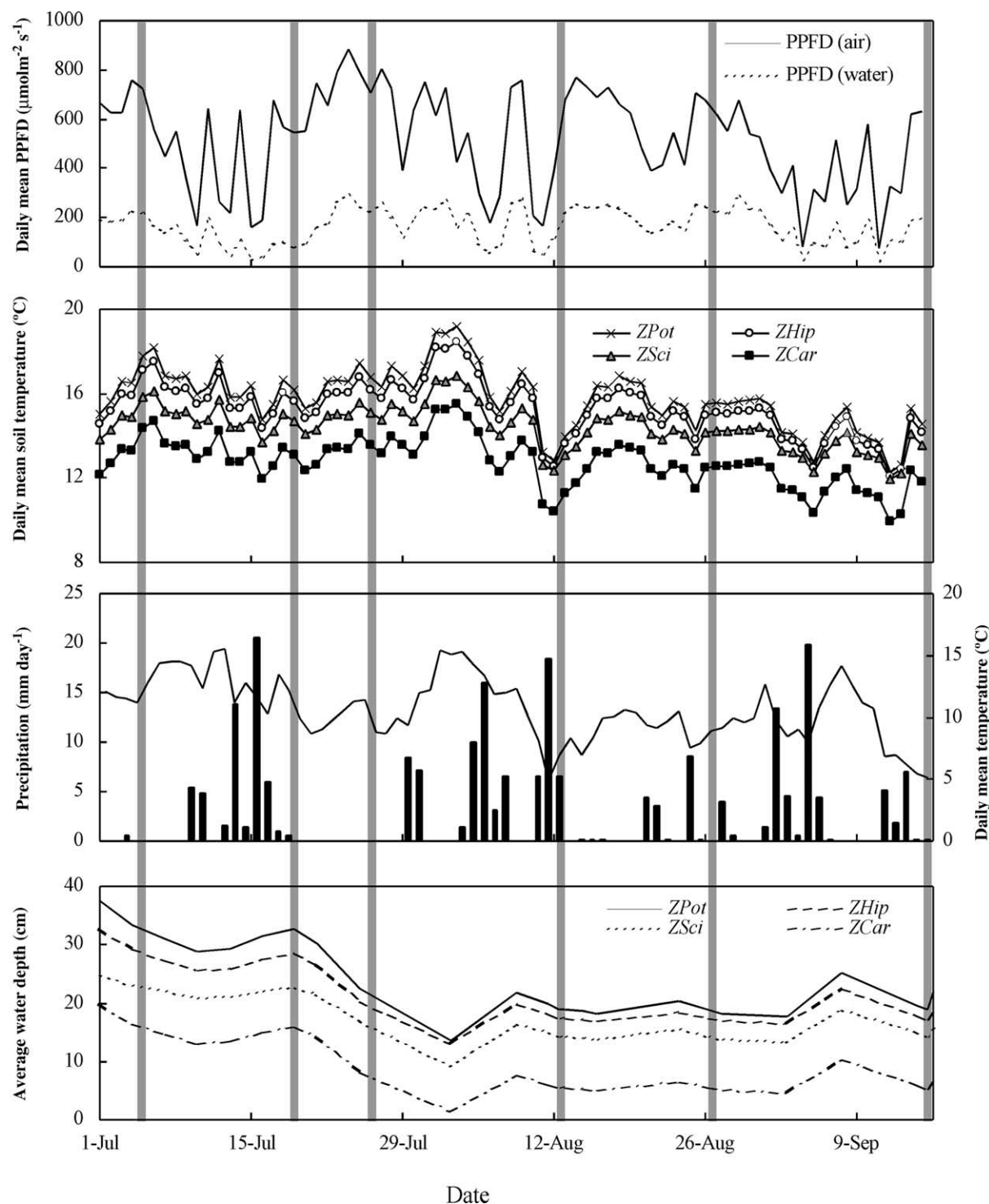
Fig. 3. Temporal variations in environmental factors—PPFD (in air and water), soil temperature at 5 cm depth, air temperature, precipitation, and water depth—from 1st July to 15th September 2002. Gray lines show dates of CH$_4$ flux measurement (4–5th July, 19–20th July, 25–26th July, 12–13th August, 26–27th August, and 14–15th September).

and ZCar revealed rapid increases in CH$_4$ flux early in the growing season and no change between August and September, the CH$_4$ flux in ZPot slowly increased and decreased in September, whereas ZSci slowly increased until late in the growing season (Fig. 5).

In all the zones, the daily summed CH$_4$ flux was correlated positively with estimated total aboveground biomass inside chamber and plant length (Table 4), but the daily summed CH$_4$ flux was correlated negatively with water depth, air temperature, soil temperature, and PPFD
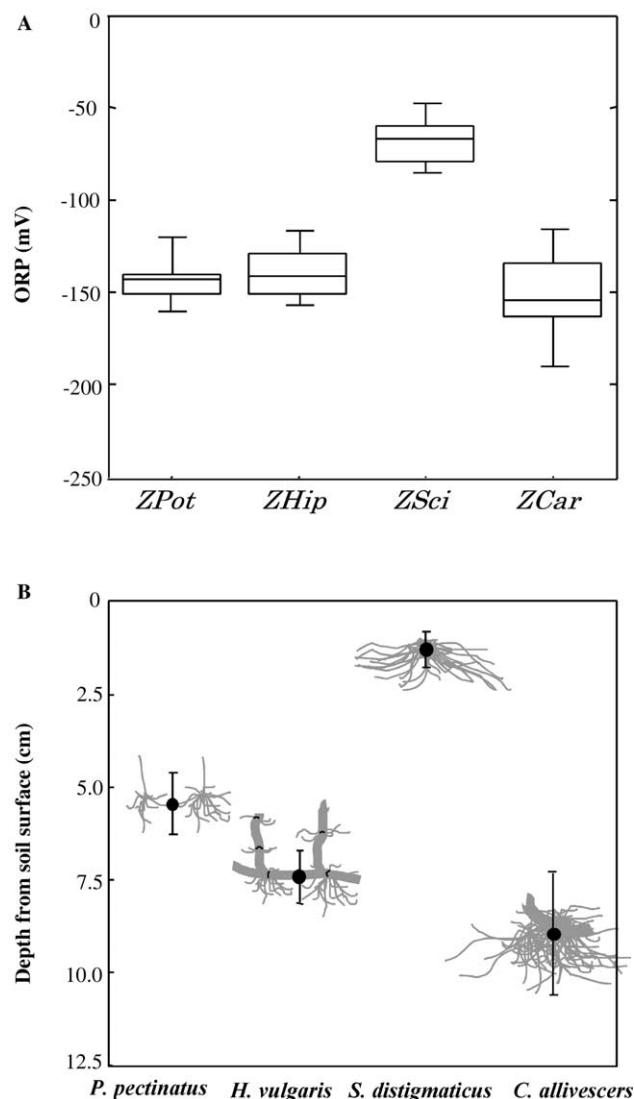
Fig. 4. (A) ORP values at depths of 5 cm (open box plots) and 30 cm (shaded box plots). Each box and whisker plot was drawn from ORP values measured between 19th July and 15th September 2002 ($n = 52$). (B) Mean depth and SD (vertical bars, $n = 6$) of root zone of each species.

Table 2
Methane flux measured under light and dark conditions

Date	Methane flux under light/dark condition (mg CH_4 m^{-2} h^{-1})			
	ZPot	ZHip	ZSci	ZCar
5-Jul.	1.4/0.4 (0.29)	6.9/1.2 (0.17)	3.9/2.7 (0.69)	4.0/3.7 (0.93)
20-Jul.	2.5/0.6 (0.24)	7.0/1.0 (0.14)	3.0/2.5 (0.83)	7.5/7.0 (0.93)
26-Jul.	1.0/0.3 (0.30)	14.4/1.5 (0.10)	5.2/2.4 (0.46)	11.1/10.5 (0.95)
13-Aug.	3.6/0.6 (0.17)	19.9/2.2 (0.11)	6.5/3.0 (0.47)	8.6/7.6 (0.88)
27-Aug.	3.9/0.7 (0.18)	7.9/2.6 (0.33)	6.9/4.3 (0.63)	9.0/8.0 (0.89)
15-Sep.	1.8/0.4 (0.22)	16.0/4.1 (0.26)	9.2/3.5 (0.38)	14.1/12.4 (0.88)
Average	2.4/0.5 (0.21)	12.1/2.1 (0.27)	5.8/3.1 (0.53)	9.0/8.2 (0.91)

Measurements under artificial darkness taken after the last daytime measurement of CH_4 flux. Values in parentheses show ratio of CH_4 flux under dark/light conditions.

(Table 4). Other environmental factors, such as water temperature and ORP, had no significant correlation with the fluxes during the growing season. The estimated total aboveground biomass inside the chamber was the best predictor of the CH_4 flux in each zone (partial correlation coefficient $= 0.88$ for *ZPot*, 0.90 for *ZHip*, 0.87 for *ZSci* and 0.85 for *ZCar*). The slope of linear regression of *ZSci* (slope $= 0.28$, $P < 0.01$) was significantly lower than those of *ZPot*, *ZHi* and *ZCar* (slopes $= 0.61$, 0.63, and 0.44, respectively, $P < 0.01$).

4. Discussion

4.1. Spatial and temporal variation in methane emission

The Luanhaizi wetland was flooded at a shallow depth, three emergent plants and one submerged plant formed the zonal vegetation along the water-depth gradient. A plant community dominated by *C. allivescers* V. Krez. existed in the shallowest water zone, and coexisting communities of *S. distigmaticus* L, *H. vulgaris* L. and *P. pectinatus* L. appeared with increasing water depth (Fig. 2 and Table 1). *P. pectinatus*, a submerged plant, mainly occupied the deepest water zone where no other plant was able to exist. Such vegetational zones are found in worldwide wetlands (Mitsch and Gosselink, 2000). The zonal distribution reflects interspecific differences in ability to adapt to water depth.

Many studies have attempted to explain the spatial variation of CH_4 emissions within wetlands in relation to changes in environmental factors, i.e. temperature, water depth, topography (Moore et al., 1990; Waddington et al., 1996; Heyer et al., 2002). Most attempts, however, have failed to relate spatial variation in abiotic factors to that in CH_4 emission. The same result applies to the present study. However, the relationships between temporal changes in CH_4 fluxes and abiotic factors occurred and varied among the vegetational zones. Clear diurnal changes in CH_4 flux in *ZPot*, *ZHip*, and *ZSci* were significantly correlated with PPFD especially in the late season, whereas CH_4 flux in *ZCar* showed no clear correlation (Table 3). The results of our light–dark experiments suggest the presence of stomatal control of CH_4 flux in *ZPot*, *ZHip*, and *ZSci*, as do the results of other several studies (Thomas et al., 1996). Therefore, CH_4 flux from the dominant species in *ZPot*, *ZHip*, and *ZSci* is mainly controlled by stomatal opening and closure. In contrast, no evidence for stomatal control was found in *ZCar*. It is known that the emission of CH_4 is not always associated with stomatal control. Nouchi et al. (1990) found that, in rice plants, CH_4 was emitted not from stomata, but from micropores located on the abaxial epidermis of the leaf sheath.

Soil temperature is an important factor limiting CH_4 flux (Daulat and Clymo, 1998). Whiting and Chanton (1992)

Table 3
Partial correlation coefficient between diurnal CH_4 flux and environmental factors: diurnal changes in PPFD, air temperature, water temperature, soil temperature, and ORP

		Partial correlation coefficient				
		PPFD	AT	WT	ST5	ORP5
ZPot	Early[a] ($n = 24$)	0.25*	− 0.25	− 0.16	0.17	0.25
	Late[b] ($n = 27$)	0.75***	− 0.34*	0.19	0.28	− 0.71*
	Entire[c] ($n = 51$)	0.37***	− 0.09*	− 0.06	− 0.36**	0.06
ZHip	Early ($n = 27$)	0.35	0.24	− 0.41	0.28	0.23
	Late ($n = 29$)	0.59***	− 0.00	0.02	− 0.08*	0.00
	Entire ($n = 56$)	0.48***	0.12	− 0.19	− 0.09*	0.34*
ZSci	Early ($n = 25$)	0.29*	0.15	− 0.69	− 0.15**	0.15
	Late ($n = 28$)	0.52**	− 0.28*	0.54*	0.10	0.50
	Entire ($n = 53$)	0.44**	− 0.01	0.15	− 0.51***	0.36**
ZCar	Early ($n = 29$)	− 0.10	− 0.05	0.00	− 0.30	− 0.44*
	Late ($n = 28$)	0.07	0.00	0.13	− 0.11	0.36
	Entire ($n = 57$)	− 0.02	− 0.12	− 0.15**	− 0.28*	− 0.19

AT: air temperature, WT: water temperature, ST5: soil temperature at 5 cm depth, ORP5: ORP at 5 cm depth. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.
[a] From 4th July to 26th July (three time measurements).
[b] From 12th August to 15th September (three time measurements).
[c] From 4th July to 15th September (six time measurements).

found that diurnal variation in CH_4 flux in a *Carex*-dominated wetland was related to soil temperature variation. In this study, not only the *Carex*-dominated zone (*ZCar*), but also the other zones showed no clear relationship between daily CH_4 flux and the soil temperature (Tables 3 and 4). A possible explanation is the existence of methanotrophic bacteria (Van der Nat and Middelburg, 1998) and other bacteria, such as sulfate-reducing bacteria, which compete with methanogens (Blodau and Moore, 2003). Further, understanding of the effects of these bacteria on the methanogens is needed to elucidate variations in CH_4 flux.

In recent years, biotic factors, such as vegetation, are currently considered to control CH_4 emissions from wetlands, because aquatic plants affect the production, consumption, and transport of CH_4 (Whiting and Chanton, 1992; Joabsson and Christensen, 2001). In the Luanhaizi wetland, spatial variation of CH_4 flux was characterized by the dominant plants that varied in life form, density and biomass of shoots, gas-transporting mechanism, and root–rhizome architecture.

Especially, life form, emergent or submerged, is of significant importance, since it leads to substantial difference in the way to emit CH_4 from plants: the emergent plant can directly transport CH_4 from the waterlogged soil to the atmosphere, whereas the submerged plants release CH_4 from the soil, not to the atmosphere, but to the water.

Plant-mediated CH_4 fluxes in both emergent and submerged plants are controlled directly and indirectly by gas-transport via plants, by the provision of organic matter from roots for methanogenesis, and by release of O_2 from roots for methanotrophs. Two gas-transport mechanisms, molecular diffusion and convective gas flow, are well

documented in some plants (Brix et al., 1992; Nouchi and Mariko, 1993). There are considerable differences in gas flow rates between the two mechanisms (Sorrell et al., 1997). Several studies have reported that the spatial variation in CH_4 flux from wetlands is attributable to the spatial distribution of aquatic plants with different gas-transport mechanisms (Whiting and Chanton, 1996; Van der Nat et al., 1998). Our previous investigation showed that the three dominant emergent plants in the Luanhaizi wetland used molecular diffusion gas-transport mechanism. Hence, differences in gas-transport mechanisms among the emergent-plant zones cannot be related to spatial variations in CH_4 flux. Instead, differences in CH_4 fluxes among the emergent-plant zones can be explained in part by differences
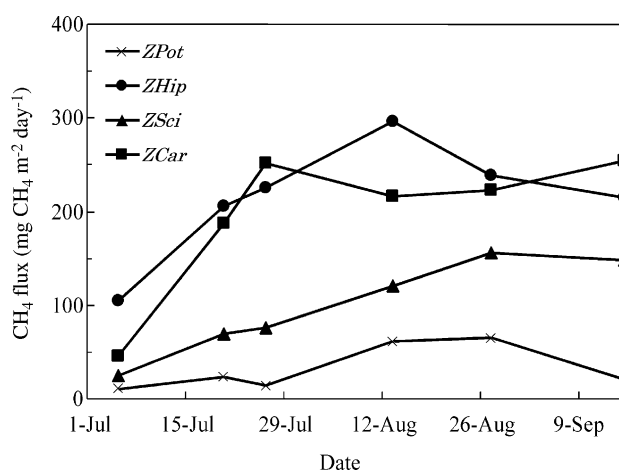

Fig. 5. Seasonal variation of CH_4 flux in *ZPot* (✕), *ZHip* (●), *ZSci* (▲), and *ZCar* (■). Daily CH_4 flux was calculated by summing up hourly measured CH_4 fluxes.

Table 4
Partial correlation coefficient between daily summed CH_4 flux and control factors for all the zones during the growing season ($n = 6$)

	Partial correlation coefficient							
	PPFD	AT	WT	ST5	ORP5	WD	PL	AGB
ZPot	−0.58*	−0.25	−0.16	−0.65*	0.18	−0.59**	0.69**	0.88***
ZHip	−0.75*	−0.58	−0.11	−0.71*	0.34	−0.78**	0.71**	0.90***
ZSci	−0.41*	−0.76	−0.05	−0.65**	0.80	−0.98*	0.92**	0.87***
ZCar	−0.38	−0.69	0.02	−0.40**	−0.13	−0.77**	0.70**	0.85**

AT: air temperature, WT: water temperature, ST5: soil temperature at 5 cm depth, ORP5: ORP at 5 cm depth, WD: water depth, PL: Plant length above water surface for emerged plants and above soil surface for submerged plant, AGB: above ground biomass inside chamber *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

in the detailed growth forms. The lowest CH_4 flux found in *ZSci* is probably related to the distribution of the underground parts of the dominant plant in shallower and more oxidative soil (Figs. 4 and 5). In contrast, the dominant plants in *ZHip* and *ZCar* extended their root systems into deeper and more anaerobic soil and transported CH_4-rich gas to the atmosphere.

In submerged plants zone, CH_4 flux are likely controlled by ebullition and diffusion from plants and soil surface (Sorrell and Dromgoole, 1987). Heilman and Carlton (2001a) demonstrated that CH_4 transport of other *Potamogeton* species were caused by ebullition from floral spikes and molecular diffusion. In *P. pectinatus*, ebullitive release of lacunar gas from leaf sheath was observed on sunny days. In addition, the pilot study in 2001 showed that the ebullitive gas contained not only oxygen, but also a lot of CH_4 (ca. 1%). The results reveal that the submerged plant uses the lacunar CH_4 transport. Although this study does not identify what mechanism controls lacunar CH_4 transport during the daytime, Heilman and Carlton (2001a) pointed out the possibility of convective flow in a few *Potamogeton* species. Some researchers have pointed out that CH_4 emitted to the water phase may be oxidized by communities of epiphytic methanotrophs (Sweerts et al., 1991; Heilman and Carlton, 2001b). In fact, CH_4 flux from the submerged-plant zone (*ZPot*) was significantly lower than that from the emergent-plant zones (Fig. 5). Moreover, it is possible that low CH_4 flux in *ZPot* results from low diffusion of CH_4 to the atmosphere. The possibility would favor accumulation of CH_4 in the soil and enhance ebullitive CH_4 emission from the soil surface.

The indirect regulation of CH_4 flux by plants includes processes that both enhance and attenuate CH_4 production in soil. Enhancement processes provide substrates for methanogens through production of root exudates, senescence and decay (Schütz et al., 1991; Whiting and Chanton, 1992). The amount of organic matter released from plants into the soil is related to plant productivity and biomass. In this study, growth of aboveground biomass increased CH_4 flux in all the zones (Table 4). Similar results have been demonstrated in other wetlands dominated by emergent plants, such as boreal and arctic wetlands (Whiting and Chanton, 1993; Joabsson et al., 1999). Therefore, plant

biomass is one of the best predictors of spatial and temporal variations in CH_4 flux. However, plants may attenuate CH_4 emission by providing oxygen to methanotrophic bacteria in the rhizosphere. Some studies have suggested that rhizospheric CH_4 oxidation consumes 10–90% of the CH_4 produced (Epp and Chanton, 1993; Denier van der Gon and Neue, 1996).

In many boreal and arctic wetlands, water table drops during summer below the soil surface, suppressing methanogenesis, stimulating methane oxidation and favoring aerobic mineralization (Saarnio et al., 1997; Juutinen et al., 2003). Hence, the water table is important as one of main factors in the spatial and temporal variation of CH_4 flux (Waddington et al., 1996; Ding et al., 2003). However, we observed a negative strong partial correlation between CH_4 flux and water depth during the growing season in all the zones (Table 4) because the Luanhaizi wetland was allowed to maintain some standing water at a certain depth during the growing season. Hence, effect of variation in water table on CH_4 flux in the Luanhaizi wetland, may be different from that of boreal and arctic wetlands. In the Luanhaizi wetland, water depth is presumably effective at controlling the plant length of the aerial parts from which CH_4 is emitted to the atmosphere.

Further, we would like to emphasize the importance of the presence of submerged plants that can exist in shallow-to-deep water (Fig. 2). The relationship between CH_4 flux and biomass in the submerged-plant zone (*ZPot*) was similar to that in two of the emergent-plant zones (*ZHip* and *ZCar*). Hence, not only the biomass of emergent plants, but also that of submerged plants should be taken into account in calculations of CH_4 flux from plant biomass.

4.2. Characteristics of methane emission in alpine wetland

On the basis of the point-measured CH_4 flux and the area occupied by each zone, we roughly estimated the mean CH_4 emission from the Luanhaizi wetland to be 57.0 mg CH_4 $m^{-2} d^{-1}$ over the plant-growing season, July –September 2002 (Table 5). Methane emission from the emergent-plant zones in the Luanhaizi wetland was as high as that from boreal, arctic and other alpine wetlands (Table 5). This is because the plant productivity biomass of the alpine

Table 5
Comparison of mean CH_4 flux in various northern wetlands during the growing season

	Vegetation	CH_4 flux		Biomass (g DW m^{-2})	Study period	Reference
		(mg CH$_4$ m^{-2} h^{-1})	(mg CH$_4$ m^{-2} d^{-1})			
Alpine wetland ecosystems						
Alpine wetland in Qinghai-Tibetan Plateau (a.s.l. 3250 m)	Entire	2.46	57.7	282	4-Jul.−15-Sep. 2002	This study
	ZPot	1.38	33.1	171		This study
	ZHip	8.92	214	471		This study
	ZSci	4.57	99.5	614		This study
	ZCar	8.19	196	544		This study
Alpine wetland in tundra, Colorado Front Range, USA (a.s.l. 3500 m)	*Carex* meadow	ND	8.45 (1.30−26.4)	ND	Jun.−Sep. 1992 and 1993	West et al. (1999)
Alpine wetland at southern rocky mountains, USA (a.s.l. 3200 m)	*Carex* and *Eleocharis*	ND	251	127	Jun.−Sep. 1998	Wickland et al. (2001)
Boreal and Arctic wetland ecosystems						
Minerotrophic peatlands in the northern boreal wetland, Finland	ND	ND	8.10−250 (dry), 15.0−330 (wet)	ND	Jun.−Sep. 1994 and 1995	Huttunen et al. (2003)
Carex-dominated fen in Quebec, USA	*Carex*	3.25	ND	68.4	28-Jul.−4-Aug. 1990	Whiting and Chanton (1992)
Ombrotrophic peatland, UK	*Sphagnum*	3.17	ND	ND	1−2-Oct. 1997	Greenup et al. (2000)
Glacial lake Agassiz peatland in Minnesota, USA	*Carex* (fen), Sphagnum (bog)	ND	187 (fen), 86.1 (bog)	ND	Jun.−Sep. 1997	Chasar et al. (2000)
Arctic wet tundra in Alaska, USA	Wet sedge meadow	ND	10.5−150	ND	Jul. 1991; Jun.−Jul. 1992; Jul. and Aug. 1993	Schimel (1995)
Peatland in Minnesota, USA	Bog lake	2.50−5.50	ND	ND	Growing season 1991 and 1992	Shurpali and Verma (1998)

ND indicates no data available in each paper.

wetlands is large, and a large quantity of organic carbon derived from plant material enters the soil; the soil of alpine wetlands on the plateau is extremely rich in organic matter (Wang et al., 2002). Because there are numerous wetlands on the plateau (Zhao, 1999) and a large CH_4 emission rate, the Qinghai-Tibetan Plateau is considered to play an important role as a global CH_4 source.

The distribution and biomass of different aquatic plants regulated CH_4 emission from the alpine wetland (Table 5). Plant productivity in alpine ecosystems is considered to be low because of the short growing season and severe climate (e.g. cool temperatures and low precipitation; Körner, 1999). Plant productivity, as determined by photosynthesis and respiration, depends heavily on temperature (Aber and Melillo, 2001). Hence, small variations in climate will lead to extensive changes in plant productivity and biomass. Therefore, global climate change will influence CH_4 emission from the Qinghai-Tibetan Plateau wetlands.

About 74% of the total area of the Luanhaizi wetland is dominated by the submerged plant *P. pectinatus*. Recently, dryness in wetlands and lakes on the Qinghai-Tibetan Plateau has been increasing year by year (Xu and Sudo, 1994) and thus hydrarch succession in the Luanhaizi wetland may extend the emergent-plant zone distributed in wet soils or slightly flooded soils and degrade the submerged-plant zone. In our study, the emergent-plant zones *ZHip*, *ZSci*, and *ZCar* emitted large quantities of CH_4 produced in the soil (214, 99.5, 196 mg CH_4 m^{-2} d^{-1}, respectively), and the submerged-plant zone *ZPot* emitted 33 mg CH_4 m^{-2} d^{-1}. Therefore, a change in vegetation zones from submerged-plant to emergent-plant as a result of a rapid decrease in water depth might increase CH_4 flux from the alpine wetland in the future. To accurately predict this scenario, long-term studies of CH_4 flux in alpine wetlands and vegetation change with climate change are needed.

Acknowledgements

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