SJSS
SPANISH JOURNAL OF SOIL SCIENCE

Soil contribution to CO_2 fluxes in *Chinampa* ecosystems, Mexico

Contribución de los flujos de CO_2 de suelos en ecosistemas de Chinampa, *México*
Contribuição do solo para os fluxos de CO_2 nos ecossistemas Chinampa, *México*

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Received: 29.01.2019 | **Revised:** 13.08.2019 | **Accepted:** 04.05.2020

ABSTRACT

Since soil CO_2 flux is a key component of ecosystem carbon balance, quantifying its contribution to the ecosystem carbon flux and understanding the factors that underlie its temporal variation is crucial for a better comprehension of ecosystem carbon dynamics under climate change and for optimal ecosystem use and management. Our objectives were to quantify the contributions of total soil CO_2 efflux (F_S) to ecosystem respiration (R_E) and heterotrophic soil CO_2 efflux (F_H) to F_S in two *chinampa* ecosystems with different natural grass covers. We also aimed to identify the main environmental drivers of seasonal variability of these contributions. The CO_2 fluxes were measured on each site about every 14 days from September 2008 to August 2009 in the Xochimilco Ecological Park in Mexico City using dark chamber techniques. For two studied sites, R_E, F_S and F_H were estimated on average as 94.1 ± 8.5, 34.7 ± 3.5 and 16.5 ± 1.7 (± S.E.) mg C-CO_2 m^{-2} h^{-1}, respectively. On average over the study period and sites, the annual cumulative R_E, F_S and F_H fluxes were 824 ± 74, 304 ± 31 and 145 ± 15 g C m^{-2} year, respectively. The R_E, F_S and F_H varied between the winter and summer seasons; this variation was explained mostly by seasonal variations of soil temperature, soil water content and shoot plant biomass. Temperature sensitivity of CO_2 fluxes depended on vegetation type and plant growth differences among the sites and decreased in the following order: $R_E > R_s > R_H$. The contribution of F_S to R_E and F_H to F_S for the two studied sites and period averaged about 38% and 50%, respectively regardless of the site vegetation type, but the degree of F_S/R_E and F_H/F_S variability depended on the differences in seasonal dynamics of plant cover. The contribution of F_H to F_S varied from 37% in summer to 73% in winter at the site without a seasonal shift in dominant plant species, but F_H/F_S was close to constant during the year at the site with a seasonal change in dominant plant species. During the cold period, the contribution of F_H to F_S increased following plant growth decrease. The linear regression analysis showed that plant biomass was the dominant factor controlling the seasonal variation of F_H/F_S ratios, whereas the plant biomass dynamic followed the dynamics of soil water content, water table depth, and soil temperature. Our results suggest that seasonal variation of soil contribution to total fluxes from the *chinampa* ecosystem is locally differentiated. These differences were related to differences in seasonal dynamics of cover productivity which has been associated with localization of soil water content. This finding has important implications for assessing the contribution of the *chinampa* ecosystem to the global carbon budget.

RESUMEN

Dado que el flujo de CO_2 del suelo es un componente clave del balance de carbono del ecosistema, la cuantificación de su contribución a las pérdidas de carbono del ecosistema y la comprensión de los factores que subyacen a la variación temporal de la magnitude de los flujos es crucial para una mayor comprensión de la dinámica del carbono del ecosistema conforme a los cambios climáticos y para planificar el uso y la gestión óptima de los ecosistemas. Nuestros objetivos fueron cuantificar la contribución del flujo de CO_2 total del suelo (F_S) a la respiración del ecosistema (R_E) y el flujo de CO_2 heterótrofo del suelo (F_H) con respect a F_S en dos ecosistemas de chinampa *con cobertura de*

DOI: 10.3232/SJSS.2020.V10.N2.04

pastizal de diferente tipo. Además se trataron de identificar los factores principales de la variabilidad estacional de estas contribuciones. Los flujos de CO_2 se midieron en cada sitio cada 14 días desde septiembre de 2008 a agosto de 2009 en el Parque Ecológico de Xochimilco de la Ciudad de México, usando la técnica de cámaras obscuras. En promedio, para los dos sitios estudiados, R_E, F_S y F_H fueron, respectivamente, 94,1 ± 8,5, 34,7 ± 3,5 y 16,5 ± 1,7 (± S.E.) mg C-CO_2 m^{-2} h^{-1}. En promedio, los flujos anuales acumulativos R_E, F_S y F_H durante el periodo de estudio en los dos sitios fueron 824 ± 74, 304 ± 31 y 145 ± 15 g C m^{-2} por año, respectivamente. La variación entre las estaciones de verano e invierno de R_E, F_S y F_H se explicó principalmente por las variaciones estacionales de temperatura del suelo, contenido de agua en el suelo y biomasa de los brotes de las plantas. La sensibilidad a la temperatura de los flujos de CO_2 depende del tipo de vegetación y de las diferencias en el crecimiento de las plantas entre los sitios y disminuye en el orden siguiente: $R_E > R_S > R_H$. La contribución de F_S a R_E y F_H a Fs para los dos sitios estudiados y el periodo promedió cerca de 38% y 50% respectivamente, sin importar el tipo de vegetación del sitio; el grado de variabilidad de F_S/R_E y F_H/F_S dependió de las diferencias en la dinámica estacional de la cobertura de la vegetación. La contribución de F_H a F_S varió de un 37% en verano a un 73% en invierno en el sitio sin cambio estacional de plantas dominantes, pero fue casi constante durante el año para F_H/F_S en el sitio con cambio estacional de especies de plantas dominantes. Durante el period frío la contribución de F_H a F_S aumentó conforme a la disminución del crecimiento de las plantas. El análisis de regresión lineal mostró que la biomasa de las plantas fue el factor dominante que controlaba la variación estacional de las relaciones F_H/F_S, mientras que la dinámica de la biomasa de las plantas siguió la dinámica del contenido de agua en el suelo, la profundidad del manto freático y la temperatura del suelo. Nuestros resultados sugieren que la variación estacional de la contribución del suelo a los flujos totales del ecosistema chinampa *se diferencia localmente. Estas diferencias están relacionadas con las diferencias en la dinámica estacional de la productividad de la vegetación que se asocia con la localización del contenido de agua del suelo. Este hallazgo puede tener implicaciones importantes para evaluar la contribución del ecosistema de* chinampa *al contenido global de carbono.*

RESUMO

Dado que o fluxo de CO_2 do solo é um componente chave do balanço de carbono nos ecossistemas, a quantificação da sua contribuição para o fluxo de carbono no ecossistema e a compreensão dos fatores subjacentes à sua variação temporal são cruciais para uma melhor compreensão da dinâmica do carbono no ecossistema no âmbito das alterações climáticas e para planear o uso e a mais correta gestão dos ecossistemas. Os nossos objetivos foram quantificar as contribuições do fluxo total de CO_2 do solo (F_S) para a respiração do ecossistema (R_E) e do fluxo heterotrófico de CO_2 do solo (F_H) relativamente a F_S em dois ecossistemas chinampa *com diferentes coberturas naturais de pastagem. Também se pretendeu identificar os principais fatores da variabilidade sazonal dessas contribuições. Os fluxos de CO_2 foram medidos em cada local cada 14 dias de setembro de 2008 a agosto de 2009 no Parque Ecológico Xochimilco na cidade do México usando técnicas de câmara escura. Em média, para os dois sítios estudados, R_E, F_S e F_H foram, respetivamente, 94,1 ± 8,5, 34,7 ± 3,5 e 16,5 ± 1,7 (± S.E.) mg C-CO_2 m^{-2} h^{-1}. Os fluxos anuais cumulativos de R_E, F_S e F_H durante o período de estudo e nos dois sítios foram em média, respetivamente, 824 ± 74, 304 ± 31 e 145 ± 15 g C m^{-2} por ano. A variação entre as estações de verão e inverno de R_E, F_S e F_H explicou-se, principalmente, pelas variações sazonais da temperatura do solo, conteúdo de água no solo e biomassa da parte aérea das plantas. A sensibilidade à temperatura dos fluxos de CO_2 depende do tipo de vegetação e das diferenças no crescimento das plantas entre os sítios e diminuiu de cordo com a ordem seguinte: $R_E > R_S > R_H$. A contribuição de F_S para R_E e F_H para F_S, para os dois sítios e período estudados, foi em média de cerca de 38% e 50%, respetivamente, independentemente da vegetação do sítio; o grau de variabilidade de F_S/R_E e F_H/F_S dependeu das diferenças na dinâmica sazonal da cobertura vegetal. A contribuição de F_H para F_S variou de 37% no verão a 73% no inverno no sítio sem alteração sazonal das espécies de plantas dominantes, tendo sido quase constante durante o ano para F_H/F_S no sítio com alteração sazonal de espécies de plantas dominantes. Durante o período frio a contribuição de F_H para F_S aumentou com a diminuição do crescimento das plantas. A análise de regressão linear mostrou que a biomassa das plantas foi o fator dominante no controlo da variação sazonal das relações F_H/F_S, enquanto a dinâmica da biomassa das plantas seguiu a dinâmica do conteúdo de água no solo, a profundidade do aquífero e a temperatura do solo. Os nossos resultados sugerem que a variação sazonal da contribuição do solo para os fluxos totais do ecossistema* chinampa *se diferencia localmente. Estas diferenças estão relacionadas com as diferenças na dinâmica sazonal da produtividade da vegetação que está associada à localização do conteúdo de água do solo. Este resultado tem implicações importantes para avaliar a contribuição do ecossistema de* chinampa *para o conteúdo global de carbono.*

KEY WORDS
Ecosystem respiration, total soil CO_2 efflux, heterotrophic soil CO_2 efflux.

PALABRAS CLAVE
Respiración del ecosistema, flujo total de CO_2 del suelo, flujo heterotrófo de CO_2 del suelo.

PALAVRAS-CHAVE
Respiração do ecossistema, fluxo total de CO_2 do solo, fluxo heterotrófico de CO_2 do solo.

1. Introduction

Ecosystem respiration (R_E) including aboveground plant respiration and total soil CO_2 flux (F_S) is commonly regarded as the most critical component determining large-scale spatial and temporal variation in ecosystem net carbon balance (Grogan and Jonasson 2005). For characterizing spatial and temporal variability in ecosystem carbon balance and for correct prediction of carbon cycling and sequestration under changing climatic conditions, the controlling factors, component fluxes and their contribution to R_E should be well understood (Kuzyakov and Cheng 2001). The heterotrophic soil CO_2 flux (F_H) (i.e. the decomposition of soil organic matter by the soil microbial community) and autotrophic root respiration are the main contributors to soil CO_2 production and consequently, to F_S (Kuzyakov and Cheng 2001). For grasslands, the contribution of F_H to F_S was reported to range between 40 and 70% (Subke et al. 2006). Considerable variations of the contributions might be connected with large differences among site types and vegetation characteristics (Xavier et al. 2019; Santos et al. 2019). Climate may drive variation of CO_2 fluxes on seasonal and annual time scales (Martin and Bolstad 2005). Since autotrophic and heterotrophic respirations have a differential response to environmental drivers such as temperature, moisture and substrate supply (Hartley et al. 2006; López et al. 2018; Santos et al. 2019) or water table depth (Juszczak et al. 2013), high temporal variability of contributions of each flux component to the ecosystem flux can be expected. Furthermore, root respiration exhibits greater seasonality than heterotrophic respiration (Widén and Majdi 2001) and the seasonal variation of plant biomass could increase temporal variability of the contribution of CO_2 flux components to R_E.

R_E and F_S are widely documented to depend on temperature (Lloyd and Taylor 1994; Alm et al. 1997; Almagro et al. 2009; Mahecha et al. 2010; López et al. 2018; Silva et al. 2019). The temperature sensitivity is expressed as Q_{10}, which is the rate of respiration increase as a consequence of increasing the temperature by 10 °C. The Q_{10} values of autotrophic and heterotrophic respiration varies widely with environmental conditions and terrestrial ecosystem types (Atkin et al. 2005; Ikkonen et al. 2012a). On an annual time scale, the Q_{10} values could be affected by climatic factors such as temperature (Vanhala et al. 2008), soil water content (Ikkonen et al. 2012a), or plant activity (Wang et al. 2010). The differences in temperature sensitivities and their responses to varying external drivers could be partly responsible for temporal variability of the contribution of different components to ecosystem fluxes.

Chinampas are unique anthropogenic wetland ecosystems used for agriculture in the Valley of Mexico since pre-Hispanic times. *Chinampas* were made by hand from the wetland around the lakes in the Valley of Mexico by forming raised fields separated by a system of canals (Jiménez-Osornio and Gómez-Pompa 1987; Blanco-Jarvio et al. 2011). The fields constructed by the accumulation of lacustrine organic loamy sediments were typically characterized by exceptionally high yields (Jiménez-Osornio et al. 1995). In pre-Hispanic times this intensive agricultural system used for growing foodstuffs occupied large areas, but to date, the *chinampa* land area has been greatly reduced due to the expansion of Mexico City. A part of the remaining *chinampas* was reserved in Xochimilco Ecological Park to restore these unique ecosystems without soil cultivation and fertilization but with the development of native vegetation.

Although many studies focused on greenhouse gas production and emission from soil of the Valley of Mexico (Beltrán-Hernández et al. 2007; Silva et al. 2008; Dendooven et al. 2010; Dendooven et al. 2012a, b), little is known about temporal dynamic of CO_2 fluxes from *chinampas* soils (Ortiz-Cornejo et al. 2015) and no information concerning soil contribution to *chinampa* ecosystem fluxes are available. We hypothesized that the magnitude of the F_S contribution to the total *chinampas* flux varies depending on soil water and temperature regime as well as the seasonal dynamic of plant cover. The objective of the study was to evaluate the contribution of F_S to R_E and F_H to F_S, their seasonal variability and dependence on driving factors in *chinampa* ecosystems.

2. Material and Methods

2.1. Study sites

We studied two *chinampas* ecosystems within the Xochimilco municipality of Mexico City, DF, at the geographical coordinates 19°17’45" N and 99°05’34" W and at the altitude of 2240 m above sea level (**Figure 1**). The climate of the study area is temperate subhumid. The area is characterized by an alternation of the dry season from November to March and the rainy season from April to October. The mean annual precipitation for the 1996-2009 period was 686.1 mm, according to the data of the Escuela Nacional Preparatoria meteorological station, Plantel 1 "Gabino Barreda" UNAM (Xochimilco, Mexico City, D.F.) located close to the sampling site. The mean air temperature was 17 °C with a minimum of 13.5 °C in January and a maximum of 19.3 ºC in July as reported by the same meteorological station. The soil of *chinampas* was classified by its origin as Terric Anthrosol (IUSS Working Group WRB 2006) because the surficial layers of the soil were known to be constructed of excavated lacustrine sediments. The soil texture varied from silty loam to clay and the morphology of the soil profile is relatively uniform and the horizons are hardly distinguishable (Ramos-Bello et al. 2011). The morphology of *chinampa*’s soils resembles that of deep organic soils (Histosols), but the organic matter content is lower (García et al. 1994). High salinity and sodicity of groundwater and soils have been reported for the area (Ramos-Bello et al. 2011). The pH of the *chinampas* soils, as was reported by N. Ortiz-Cornejo et al. (2015), is alkaline with total N ranges from 5.9 to 6.2 g kg^{-1} and organic carbon content equals 28.4 t ha^{-1} at the 20-40 cm depth. High organic matter content throughout the topsoil and irregular vertical distribution of organic carbon and bulk density has been reported for the *chinampas* area (Ikkonen et al. 2012b).

Two study sites were located in the Xochimilco Ecological Park in Mexico City (**Figure 1**). The uniqueness of this area is connected with the peculiarity of anthropogenic *chinampas* soils through a specific agricultural practice referred to the Pre-Hispanic period. The distance between the study sites did not exceed 100 m, but they varied in groundwater table depth and dominant plant species composition. The vegetative community of first study site (S1) was dominated by rushes (*Juncus* spp.) and broadleaf cattail (*Typha latifolia* L.). The plant cover of the second site (S2) varied between the seasons: in the dry period the dominant species were bristly oxtongue (*Picris echioides* L.) and greater plantain (*Plantago major* L.), and in the rainy season the vegetation was represented mainly by rushes (*Juncus* spp.) and common reed (*Phragmites australis* (Cav) Trin. ex. Stend.). Single specimens of seashore saltgrass (*Distichlis spicata* L.) were found on both sites. The highest root density was found in the layer of 0-7 cm depth, but it decreased sharply with the depth (Ikkonen et al. 2012a).

Figure 1. Location of the study sites in the Xochimilco Ecological Park in Mexico City, Mexico.

2.2. CO_2 flux measurements

The R_E, F_S and F_H fluxes were measured using static chamber techniques (Alm et al. 1997) every two-three weeks from September 2008 to August 2009. The measurements were performed between 8:00 and 12:00. All chambers were opaque in order to prevent photosynthesis and ensure that only respiration was measured. For ecosystem respiration measurements four stainless steel collars (length × width × height = 40 cm x 30 cm x 10 cm) were inserted into the soil six months prior to the first flux measurement. Locations for collars were selected using the presence of photosynthesizing plants as the main criterion. A steel removable chamber 40 cm x 30 cm x 50 cm (length × width × height) in size was placed and sealed over the collars using water for capsulation of chamber air during each flux campaign. An internal electric fan was used to homogenize air temperature and humidity within the chamber. An aluminum cover was added outside of the chamber to reduce the impact of direct irradiative heating during sampling. The measurement of F_S flux was made with four replicate cylindrical chambers (diameter × height = 10 cm x 15 cm) directly inserted into the soil, about 5 cm below the surface. The locations for the cylindrical chambers were selected between individual plants without their presence inside the chambers. In order to collect the data on F_H, the same cylindrical chambers were inserted into the soil of surface section fenced off by PVC tubes that were inserted 30 cm into the soil six months prior to the measurements. The sections for F_S measurements contained plant litter but did not include photosynthesizing plants and the sections for F_H measurements did not include plant roots.

The headspace gas samples were collected through a sampling port to 20 ml vessels (Corning System, USA) using a double-sided needle every 10 min from 0 to 30 min. The vessels were vacuum sealed with a rubber stopper and metal cap. All air samples were transported to a laboratory and analyzed within 24 h following gas collection. The CO_2 molar fraction were recorded by HP Agilent 6890 GC System gas chromatographer (GMI, USA) with a Poropac-Q column (35 ºC of column's temperature and 300 ºC of detector's temperature; argon was used as carrier gas). The flux was calculated by estimating the slope of the increase in CO_2 molar fraction in the chamber, adjusted for air temperature and pressure.

2.3. Environmental measurements and shoot plant biomass

Air temperatures, air pressure and water table depth (WTD) were recorded on each sampling occasion immediately after the flux measurements. The ambient air temperature, atmospheric pressure and humidity were simultaneously registered with a weather station (Crosse Technology, USA). Soil temperatures at 5-cm depth in the organic soil layer were recorded using a portable temperature probe (WIKA, USA) immediately after the flux measurements at both S1 and S2 sites and at 30-min intervals using a 5TM sensor with an E50-series data logger (Decagon, USA) at the S1 site from September 2008 to August 2009. The soil water content at 5-10 cm depth was determined gravimetrically in four replicates by oven drying the samples at 105 ºC for 24 h. WTD was measured in soil profile pits.

Shoot biomass was measured four times during the flux measuring period in 2008-2009: September 18, November 18, January 27, and April 13 for Site 1 and September 4, November 18, January 27, and April 13 for Site 2. We quantified shoot plant biomass by clipping green vegetation and litter within four randomly located 20 x 20 cm plots outside permanently designated locations for CO_2 flux measurement. The clipped material was separated into plant species and total litter, dried at 105 ºC and weighed after drying.

2.4. Statistical analysis

The C-CO_2 flux results are presented as means ± SE. We defined the proportion of soil respiration (F_S) in the total ecosystem respiration (R_E) as a percentage F_S/R_E and the proportion of heterotrophic respiration (F_H) in total soil respiration as a percentage F_H/F_S. Data were tested for normality and homogeneity of variance using the Chi-Square test and Levene's test in Statistica (v.8.0.550.0, StatSoft, Inc). Differences of means between the two studied sites were tested with one-way ANOVA followed the least significance difference (LSD) test. The correlation coefficients were calculated to examine the relationships between R_E, F_S, F_H, F_S/R_E, F_H/F_S, soil temperature, soil water content, water table depth and shoot biomass. The statistical significance was judged at the 5% probability level and the statistical analyses were performed using Statistica (v.8.0.550.0, StatSoft, Inc). The sensitivities of CO_2 fluxes to variations in soil temperature were calculated in the form of Q_{10} values according to Meyer et al. (2018). Annual cumulative C-CO_2 fluxes were defined using mean flux values for the measuring period.

3. Results

3.1. Environmental variables and shoot plant biomass

According to the data of the “Gabino Barreda" meteorological station, the total precipitation from September 2008 to August 2009 was close to 450 mm, which was lower than the mean annual value for the same period (**Figure 2A**). During the dry season (from October to April) the area received only 10% of the total precipitation. At both sites WTD followed precipitation pattern, but the temporal variations in WTD were much higher at S2 than at S1 (**Figure 2B, Table 1**). WTD at S1 remained only a few cms below the surface throughout the measuring period. WTD was nearly 10 cm deeper at S2 compared with S1 for the August-February period and more than 30 cm deeper at the end of the dry season (February-April). From May to August, WTD trends showed only small differences between the study sites. Following the patterns of precipitation, soil water content was high from May to September and low from October to April at both sites, but the values were 1.5-2.5 times higher at S1 (**Figure 2C**). The lowest soil water content values were recorded from November to April and the highest ones immediately after the beginning of the May to August rainy season. Mean soil temperature at 5 cm depth did not differ significantly between S1 and S2 sites (**Table 1**). During the study period, the mean annual soil temperature was about 15.0 °C (**Figure 2D**).

Table 1. Mean ± standard error of measured values at the S1 and S2 sites of *chinampa* ecosystem for the study period

Parameter	S1	S2
Soil water content, %	322 ± 24^{a}	145 ± 22^{b}
WTD, cm	17.7 ± 1.9^{b}	27.4 ± 3.4^{a}
Soil temperature, °C	14.8 ± 0.6^{a}	16.1 ± 0.5^{a}
Total shoot biomass, g m^{-2}	406 ± 151^{b}	706 ± 107^{a}
R_E, mg C-CO_2 m^{-2} h^{-1}	78.0 ± 13.1^{a}	108.1 ± 10.3^{a}
F_S, mg C-CO_2 m^{-2} h^{-1}	28.0 ± 5.4^{a}	40.5 ± 4.3^{a}
F_H, mg C-CO_2 m^{-2} h^{-1}	13.0 ± 2.9^{b}	19.6 ± 1.8^{a}
F_S/R_E, %	36.7 ± 3.0^{a}	39.4 ± 3.2^{a}
F_H/F_S, %	50.0 ± 5.6^{a}	50.1 ± 1.7^{a}
Winter season		
F_S/R_E, %	42.9 ± 3.6^{a}	36.1 ± 3.4^{a}
F_H/F_S, %	72.6 ± 4.6^{a}	50.7 ± 1.6^{b}
Summer season		
F_S/R_E, %	32.2 ± 1.6^{a}	36.1 ± 3.4^{a}
F_H/F_S, %	36.8 ± 2.6^{b}	49.8 ± 1.8^{a}

WTD – water table depth, R_E – ecosystem respiration, F_S – total soil CO_2 flux, F_H – heterotrophic soil CO_2 flux, F_S/R_E – contribution of F_S to R_E, F_H/F_S – contribution of F_H to F_S. Means followed by different letters in the same line are significantly different (LSD test). N = 76 and 85 (Soil temperature, R_E, R_s, R_H) 19 and 22 (Soil water content, WTD, F_S/R_E, F_H/F_S), 16 and 16 (Total shoot biomass) for S1 and S2, respectively.

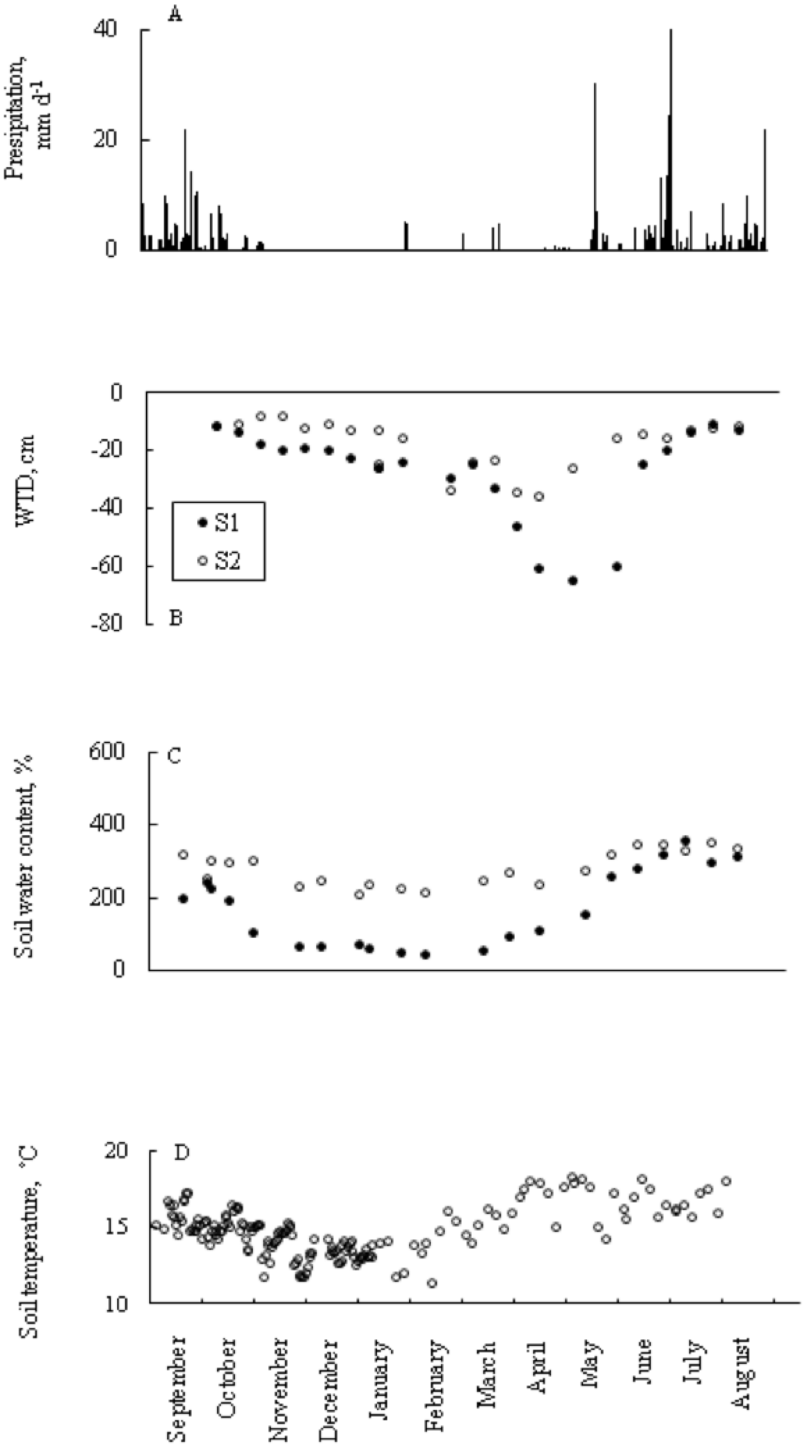

Figure 2. Precipitation (A), water table depth (WTD) (B), soil water content within 5-10 cm depth (C) and daily mean soil temperature at 5-cm depth (D) during the study period at the S1 and S2 sites.

The shoot plant biomass differed between the study sites (**Figure 3, Table 1**). The site S2, where the water table was lower during winter, had higher total plant biomass and litter than S1. In the rainy summer season, the S2 vegetation was dominated by rushes and common reed, and in winter it was replaced mainly by bristly oxtongue and seashore saltgrass. This replacement was connected with the lowering of WTD. For the S1 site, the seasonal change of dominant plant species was not observed. The decreases of shoot plant biomass started in November at both sites, but at the S2 site it quickly recovered due to active growth of the winter period vegetation (‘dry season type’). Unlike the S1 site, litter mass of S2 was high during the winter and close to zero during the summer. The decomposition rate of S1 litter was slow probably because WTD remained only a few cm below the surface during the measurement period. The results indicated significant positive relations between total shoot biomass and soil water content and a negative relation between biomass and WTD in S1. For the S2 site, shoot plant biomass was positively related to soil water content and temperature (**Table 2**).

3.2. Seasonal variation in CO_2 fluxes

The mean C-CO_2 fluxes for the measuring period are shown in **Table 1**. Although R_E, F_S and F_H were

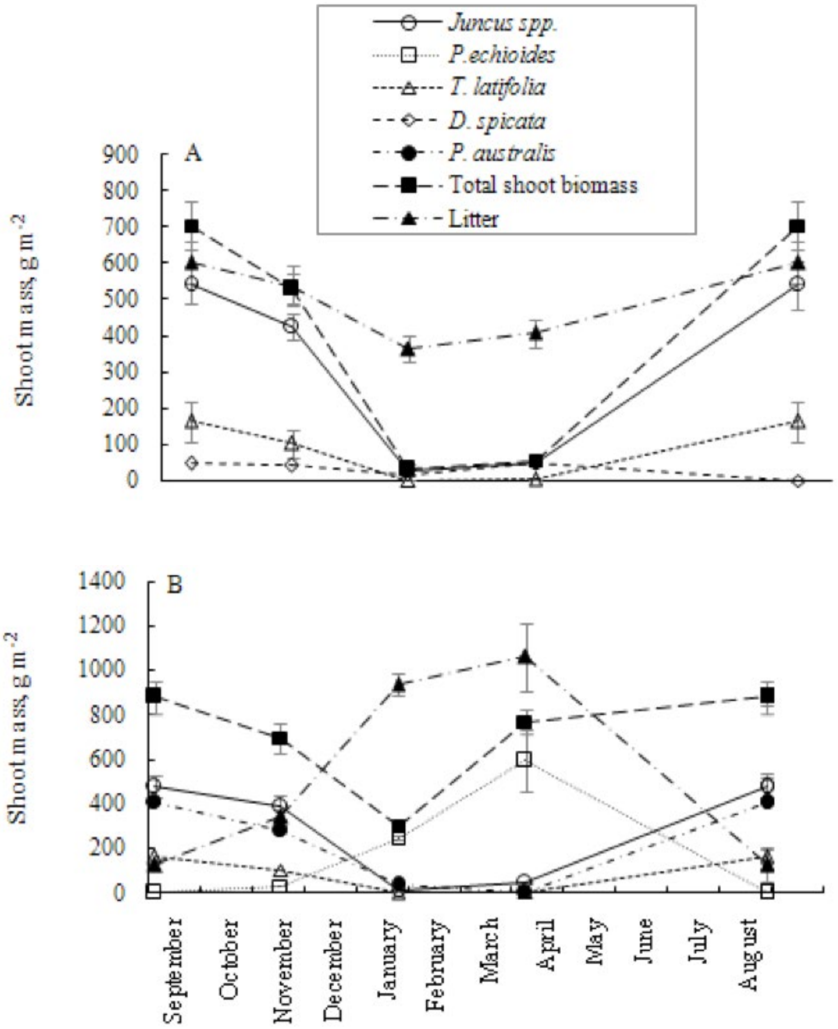

Figure 3. The dynamics of shoot plant biomass for the S1 (A) and S2 (B) sites during the study period.

Table 2. Statistical data (*P* value, R^2) indicating relationships between measured CO$_2$ fluxes, F_S/R_E, F_H/F_S and environmental variables at the S1 and S2 sites of *chinampa* ecosystem

	S1		**S2**	
Variable	*P* value	R^2	*P* value	R^2
R_E				
Soil water content	< 0.001	0.63	< 0.001	0.41
WTD	0.028	-0.09	0.285	0.02
Soil temperature	< 0.001	0.59	0.112	0.04
Total shoot biomass	0.002	0.18	< 0.001	0.18
F_S				
Soil water content	< 0.001	0.49	0.002	0.21
WTD	0.440	-0.01	< 0.001	0.36
Soil temperature	< 0.001	0.49	0.001	0.17
Total shoot biomass	0.616	0.00	< 0.001	0.30
F_H				
Soil water content	0.239	0.04	< 0.001	0.34
WTD	0.470	0.01	0.680	0.00
Soil temperature	< 0.001	0.46	0.020	0.09
Total shoot biomass	0.206	-0.03	< 0.001	0.30
F_S/R_E				
Soil water content	< 0.001	-0.26	0.030	-0.10
WTD	0.002	0.17	0.224	0.02
Soil temperature	0.704	-0.00	0.006	0.12
Total shoot biomass	< 0.001	-0.41	0.154	0.03
F_H/F_S				
Soil water content	< 0.001	-0.48	< 0.001	0.28
WTD	< 0.001	0.56	0.003	-0.13
Soil temperature	0.031	-0.09	0.081	-0.05
Total shoot biomass	< 0.001	-0.85	0.917	0.00
Total shoot biomass				
Soil water content	< 0.001	0.65	< 0.001	0.69
WTD	< 0.001	-0.53	0.019	0.09
Soil temperature	0.04	0.08	< 0.001	0.36

WTD – water table depth, R_E – ecosystem respiration, F_S – total soil CO$_2$ flux, F_H – heterotrophic soil CO$_2$ flux, F_S/R_E – contribution of F_S to R_E, F_H/F_S – contribution of F_H to F_S. N = 76 (S1) and 85 (S2).

higher at the S2 than at the S1 site, no significant differences in mean seasonal fluxes were found among the sites ($P > 0.05$). Regardless of the flux and vegetation type, all the CO$_2$ fluxes exhibited a pronounced seasonal variation with the lowest values during the cold period from November to February and the highest values during the warm period (**Figure 4**), indicating the strong positive correlation of the flux with the temperature (**Table 2**). After the winter period, when the R_E values were minimal, an increase of R_E was recorded at the S2 earlier than at the S1. The results did not indicate a significant relationship between F_S or F_H and soil water content or WTD ($P > 0.05$) especially at the S1 site characterized by low seasonal variability of WTD. The annual cumulative R_E, F_S and F_H fluxes were higher by about 30% at the S2 than at the S1 (**Table 2**). For the site S1, the annual cumulative R_E, F_S and F_H fluxes were 683 ± 109, 246 ± 47 and 114 ± 25 C m^{-2} year, respectively, and for the S2 site, these parameters were 947 ± 85, 355 ± 36 and 172 ± 15 C m^{-2} year, respectively.

3.3. Seasonal variation in the contribution of F_S to R_E and F_H to F_S

The contribution of F_S to R_E or F_H to F_S did not differ significantly between the study sites ($P > 0.05$), however, the F_S/R_E and F_H/F_S values of the S1 site, in contrast to the S2, showed a

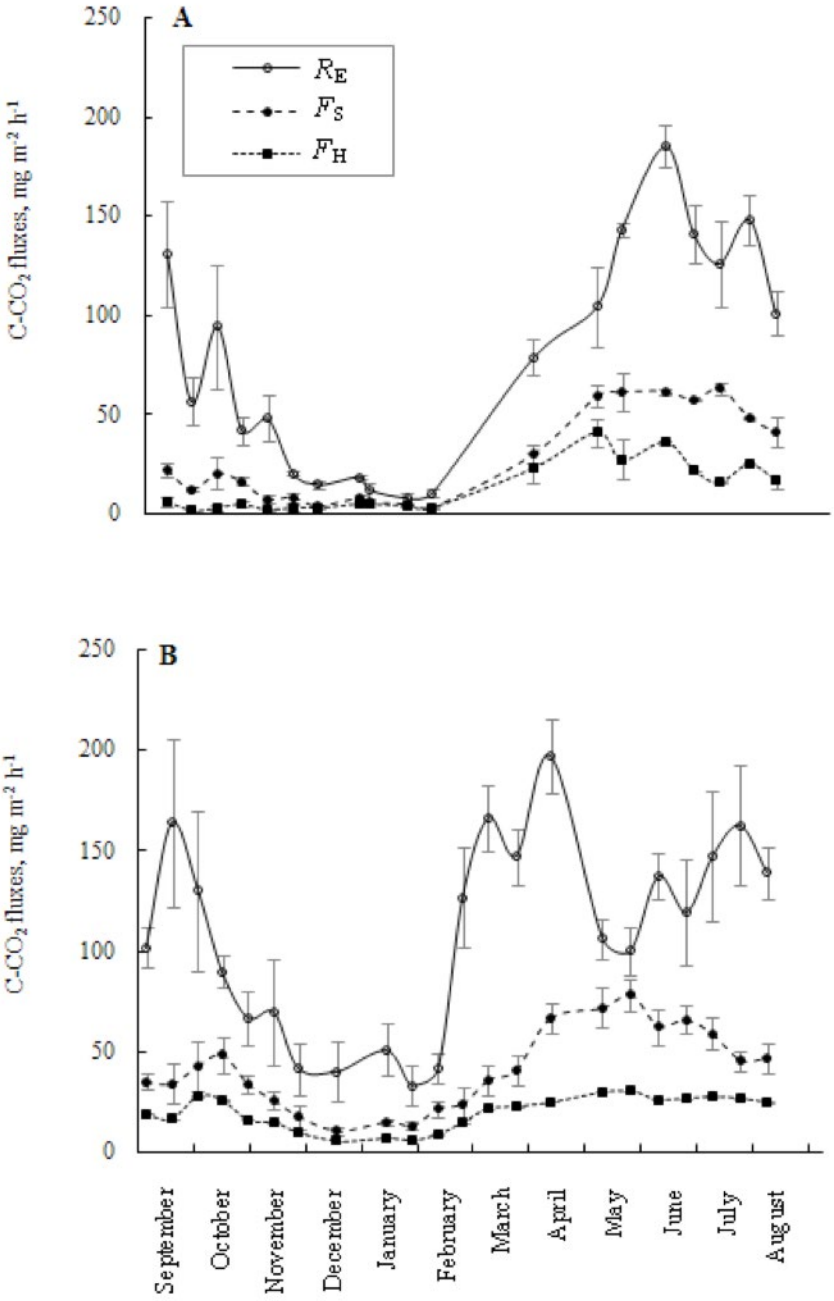

Figure 4. Mean ± standard error of observed values of the ecosystem respiration (R_E) rate, total soil CO_2 flux (F_S) and heterotrophic soil CO_2 flux (F_H) for the S1 (A) and S2 (B) sites.

trend that varied between seasons (**Figure 5**). While the daily F_S/R_E and F_H/F_S values in the S2 were close to the means for the measuring period, they were lower than the mean values during the warm season and higher than ones during the cold season in the S1 (**Table 1**).

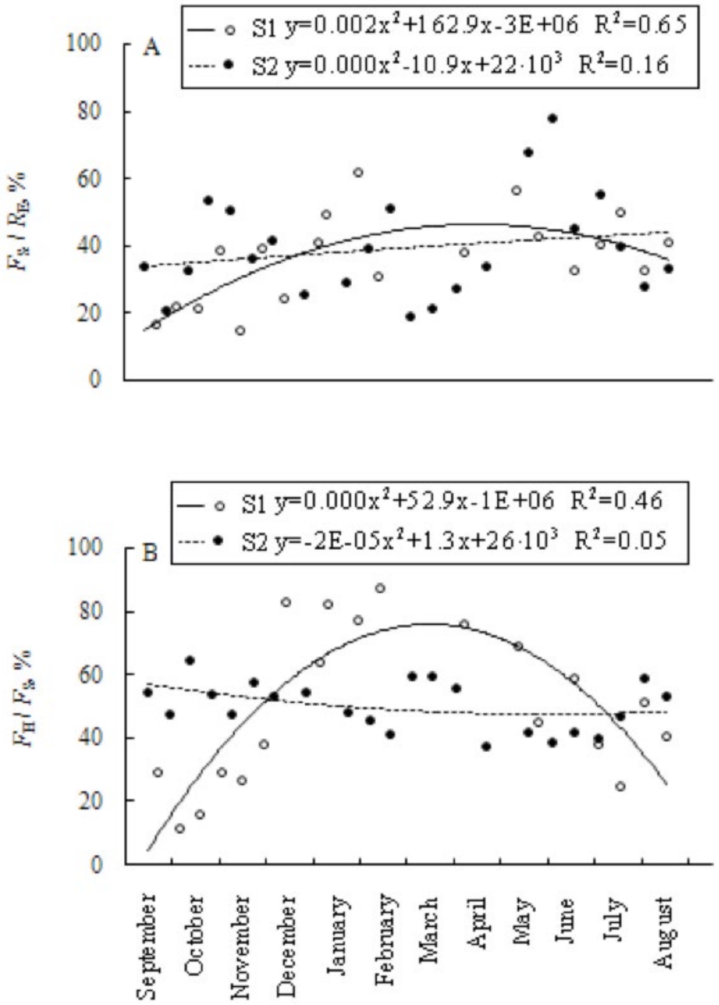

Figure 5. The contribution of F_S to R_E (F_S/R_E, A) and F_H to F_S (F_H/F_S, B) for the S1 and S2 sites during the study period.

3.4. Environmental factors controlling CO_2 fluxes

The variations in CO_2 fluxes in the *chinampas* area were clearly associated with the variations of all measured independent parameters: soil water content and temperature, WTD, and plant biomass (**Table 2**). However, the degree of influence of environmental variables and biomass on the CO_2 fluxes differed depending on flux and vegetation type. The regression analysis of the results of the S1 site indicated that R_E was significantly positively correlated with soil water content and soil temperature, whereas at the S2 site the variation in R_E was explained by the dependence on soil water content alone. A positive correlation of R_E with total shoot biomass was found for both study sites. Whereas soil respiration at the S1 could be explained by the relationships with soil water content and temperature, for the S2 the F_S flux was mostly affected by WTD and plant biomass. The F_H variation was explained by soil temperature alone at the S1 and by the combined influence of soil water content, soil temperature and shoot biomass at the S2. Total shoot biomass had the strongest negative effect on F_S/R_E and F_H/F_S at the S1, but not at the S2. Soil water content was negatively related with F_H/F_S at the S1 and positively related with F_H/F_S at the S2. A combined effect of soil water content, WTD and soil temperature on total shoot biomass was found for both study sites.

4. Discussion

This study was carried out to partition the components of ecosystem respiration and their individual responses to environmental factors, such as temperature, soil water content, and vegetation type in the *chinampa* ecosystem. The mean and annual cumulative CO_2 flux observed in this study (**Table 1**) were lower than respective values shown for a broad range of grassland ecosystems (Wang and Fang 2009; Hu et al. 2016). Low soil CO_2 fluxes can be explained by a high salt content in soils in the Valley of Mexico (Dendooven et al. 2010), where the *chinampas* area is located. The bottom sediments of the former lake Texcoco located in the center of the Valley of Mexico were enriched with pyroclastic deposits. Weathering of the volcanic ash resulted in the release of sodium, and, consequently, in the sodicity of the lake and soils formed later in the exposed lacustrine sediments when the lake Texcoco was drained in the 17th century (Luna-Guido et al. 2000). In the soils of the former lake of Texcoco the pH values can range from 9.8 to 11.7 and electrolytic conductivities in saturation extracts vary from 22 to 150 dS m^{-2} (Beltrán-Hernández et al. 2007). Excessive amounts of salts result in poor soil structure and inhibit biological processes (Dendooven et al. 2010). The production of CO_2 decreases with increased electrolytic conductivity (Beltrán-Hernández et al. 2007), which depends on salt concentration and thus high salinity and sodicity of soils reported for the *chinampas* area (Ramos-Bello et al. 2011) might be one of the reasons for the low soil CO_2 fluxes observed in this study. Moreover, high soil water content especially can be at least partly responsible for the depressed CO_2 fluxes in the *chinampas* area due to the limitation of O_2 diffusion into the soil and, thus, aerobic decomposition of organic carbon (Alm et al. 1997). In our study a significant positive soil water content effect was generally observed for all sites (**Table 2**). The soil water content explained about 40-60% of the variability of R_E and 20-50% of the variability of F_S, with the effect especially well marked at the S1 site. It should be noted that WTD had less impact on CO_2 fluxes than soil water content, but in general, the CO_2 fluxes decreased with increased WTD at the S1 and increased with decreased WTD at the S2.

Temperature is commonly shown to be the major driver of ecosystem or soil CO_2 fluxes, as temperature rise can stimulate biological activity resulting in increased gas fluxes (Silvola et al. 1996). In agreement with a number of previous reports (Silvola et al. 1996; Hu et al. 2016) we also found that CO_2 fluxes in the *chinampa* ecosystem show a positive relationship with soil temperature explaining about 50-60% of flux variations at the S1 site, but much less at the S2 (**Table 2**). For the *chinampa* ecosystem, the temperature sensitivity of all types of CO_2 fluxes, especially for R_E, were higher at the S1 site than at the S2 site (**Table 3**), which can be due to the differences in the seasonal dynamics of plant cover. The vegetation cover of the S2, in contrast to the S1, varies between seasons (**Figure 3**), changing from 'wet season type' to 'dry season type' in November. During the dry period, while the green shoot biomass of the S1 is close to zero, bristly oxtongue and greater plantain plants actively grow at the S2 thereby increasing not only R_E, but also F_S via root and rhizosphere respiration and F_H via the rhizosphere priming effect (Kuzyakov and Cheng 2001). The dry and cold periods are closely related to each other in the study area, thus the development of new vegetation cover under low temperature could modify temperature sensitivity of CO_2 fluxes and cause a decline in annual Q_{10} values at the S2 (**Table 3**). This is consistent with the statement of Song et al. (2014) that temperature sensitivity of R_E reflects the ecosystem's structure and related biotic and abiotic factors that can closely interact with each other. Temperature sensitivity of soil CO_2 fluxes can be modulated by soil water content (Almagro et al. 2009). In our case, soil water content influenced the temperature sensitivity of CO_2 fluxes via the shift of dominant plants during the year. Thus, seasonal vegetation trend effects on the temperature response of R_E, F_S and F_H should not be ignored for a correct prediction of CO_2 fluxes under climatic changes.

The mean values of the contributions of F_S to R_E for the studied *chinampa* sites are significantly lower than those reported in the literature (Zobitz et al. 2008). Due to low values of F_S, presumably caused by high salts content in soils and consequent low microbiological activity, F_S was not the main contributor to R_E at both sites of *chinampa* ecosystem. Recent studies demonstrated that the F_S contribution to R_E and F_H contribution to F_S can vary between seasons with a large proportion of soil microbial respiration during the winter period (Zobitz et al. 2008). The component contribution variability could be due to seasonal variation in microbial community composition and plant physiological and growth processes (Grogan and Jonasson 2005). Moreover, above- and belowground vegetation parts or microbial biomass could differ in their respiration response to changes in environmental factors (Hartley et al. 2006), causing variability in the contribution of components to soil and ecosystem CO_2 fluxes. The two studied sites of *chinampa* ecosystem were different in their seasonal trend of the F_S/R_E and F_H/F_S ratios (**Figure 5**). In contrast to the S1 site, at the S2 site, the mean contribution of F_S to R_E and F_H to F_S did not vary significantly between the winter and summer seasons (**Table 1**) despite the correlation with the soil water content or temperature (**Table 2**). We assume that the seasonal shift in the abundance of dominant species and active plant growth during the winter period caused an increase in the contribution of autotrophic respiration to winter CO_2 fluxes and a decrease in variability of the F_S/R_E and F_H/F_S ratios at the S2. At the S1, where plant growth was depressed during the cold season, the contribution of F_S to R_E and R_H to F_S was higher in winter and lower in summer (**Table 1**). This confirms the fact that changes in the relative contributions of individual component fluxes to R_E are regulated by a shift in plant internal allocation of recently fixed plant-associated carbon in an ecosystem (Grogan and Jonasson 2005). The linear regression results showed that plant biomass was the dominant factor controlling the seasonal variation of F_H/F_S ratios at the S1 (**Table 2**), wherein plant biomass dynamics followed the dynamics of soil water content, WTD and soil temperature. During the winter period with low soil temperature and soil water content, the contribution of heterotrophic respiration to soil respiration increased following plant growth depression at the S1. In addition, the winter increase in the F_H/F_S ratios at the S1 appeared to be the result of lower temperature sensitivity of heterotrophic compared to autotrophic respiration (**Table 3**).

Table 3. Q_{10} values of measured CO_2 fluxes at the S1 and S2 sites of *chinampa* ecosystem

CO_2 flux	S1	S2
R_E	3.0	0.9
F_S	2.4	1.6
F_H	1.8	1.4

R_E – ecosystem respiration, F_S – total soil CO_2 flux, F_H – heterotrophic soil CO_2 flux. N = 76 (S1) and 85 (S2).

5. Conclusions

The studied *chinampa* ecosystem sites with different vegetation characteristics demonstrated that R_E, F_S and F_H were lower than those reported for most grasslands. This presumably could be caused by the high salinity and sodicity of *chinampa* soils. Despite their low values, R_E, F_S and F_H showed seasonal variations followed by variations in shoot biomass, soil water content and temperature, whereas temperature sensitivity of CO_2 fluxes reflected the vegetation-type and plant growth differences among the sites. The seasonal variation of soil contribution to total CO_2 fluxes was locally differentiated for the *chinampa* ecosystem. These differences were related to differences in seasonal dynamics of cover productivity which has been associated with localization of soil water content. The variability of the contributions of F_S to R_E and F_H to F_S was clearly expressed at the site without a seasonal change of plant dominant species, while the component contribution did not vary between the seasons at the site where the plant dominants of ‘dry season type’ and ‘wet season type’ changed. This confirms the fact that soil contribution to CO_2 fluxes may depend on the vegetation type and seasonal dynamics of the plant cover. Further studies are needed to improve management of the *chinampas* area in Mexico in order to reduce their carbon losses. These ecosystems contain huge amounts of organic carbon, which may be released to the atmosphere in the case of their improper use. In this respect, the research should be focused on the balance of carbon in the *chinampas* under different land uses and management practices, and on the response of these ecosystems to the global climatic change.

6. Acknowledgements

The research was was supported by the projects of the Ministry of Science and Higher Education of the Russian Federation no. 0218-2019-0074 and 0218-2019-0079. The authors express their gratitude to Dr. A. Martínez-Arroyo and Mr. J. M. Hernández-Solís (Centro de Ciencias de la Atmósfera, UNAM, México) for the contribution to the laboratory analyses. We thank the Escuela Nacional Preparatoria, Plantel 1 "Gabino Barreda" UNAM (Xochimilco, Mexico City, D.F) for the meteorological information.

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