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Trends in soil respiration on the eastern slope of the Cofre de Perote Volcano (Mexico): Environmental contributions

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ABSTRACT

A soil respiration dataset was examined to determine the importance of environmental factors relating to seasonal variation in soil surface CO_2 flux on the eastern slope of the Cofre de Perote Volcano (Mexico). The results are reported as follows: (1) on the upper section (2500 m asl), average soil respiration varied from 10.3 to 21.5 mg C m^{-2} h^{-1} in coniferous forest, 14.8 to 30.3 mg C m^{-2} h^{-1} in corn field, and 13.4 to 29.9 mg C m^{-2} h^{-1} in abandoned corn field. Soil respiration decreased in spring, when the soil temperature was higher and soil water was lower, while it increased in summer, with non-limiting conditions of soil water. (2) On the lower section (1650 m asl), the average soil respiration varied from 22.5 to 89.6 mg C m^{-2} h^{-1} in tropical montane cloud forest, 17.9 to 128.1 mg C m^{-2} h^{-1} in corn–potato–corn rotation, and 63.0 to 203.2 mg C m^{-2} h^{-1} in grassland. Soil respiration began to rise in late spring, corresponding to the transition from the dry to wet season and reaching its highest value in summer. (3) Soil respiration rates showed a positive exponential correlation with soil temperature ($R^2 = 0.52$; $P < 0.0001$). The model $RS = 0.031e^{0.174T+17.21\theta-16.32\theta^2}$ related soil respiration to soil temperature and soil water, explaining 58% of variation. These results suggest that soil temperature and soil water co-regulate soil respiration. Thus, the dataset suggests that global warming could have a negative effect on soil water availability, resulting in decreasing soil respiration.

1. Introduction

Soil respiration provides the second largest CO_2 flux by which the C fixed by terrestrial vegetation (via photosynthesis) returns to the atmosphere, thus playing a significant role in regulating SOC stocks and C cycling in the terrestrial biosphere (Davidson et al., 2002; Raich and Schlesinger, 1992; Raich et al., 2002; Schlesinger and Andrews, 2000). The carbon dioxide (CO_2) released from soils into the atmosphere is estimated at 68–100 Pg C yr^{-1}, being surpassed only by gross primary productivity (100–120 Pg C yr^{-1}) (IPCC, 2007; Raich and Potter, 1995). Thus, even a relatively small alteration (i.e., increase or decrease) in soil respiration due to land use change or agricultural practices may result in a significant change in the global C cycle (Giardina and Ryan, 2000; Houghton, 2003; Lal, 2004). Soil respiration includes autotrophic respiration by roots and heterotrophic microbial respiration, which is associated with microbial metabolic activities (i.e., mineralization of litter and soil organic matter) (Bernhardt et al., 2006; Deng et al., 2010; Fang and Moncrieff, 1999; Smith et al., 2008). The great temporal and spatial variability of soil respiration is well known; this complicates the interpretation of soil CO_2 flux data (Acosta et al., 2013; Metcalfe et al., 2007). Soil is a complex and spatially heterogeneous mixture of various compounds (e.g. litter, roots, SOM pools) which respond differently to changes in environmental conditions (Rodeghiero et al., 2013; Zimmermann and Bird, 2012). Previous research has shown that soil respiration is especially sensitive to soil temperature and soil water content (e.g. Fang and Moncrieff, 2001; Han et al., 2007), which are environmental factors that interact to affect the mineralization of soil organic matter and therefore influence the temporal variation of soil CO_2 flux (Tang and Baldocchi, 2005; Wiseman and Seiler, 2004; Xu and Qi, 2001). The dependence of soil respiration on soil temperature has been described in several studies (Boone et al., 1998; Cox et al., 2000; Davidson et al., 1998; Fang et al., 2005; Jones et al., 2005; Lloyd and Taylor, 1994). It has been recognized that soil respiration is positively related to soil temperature and is, in fact, characterized as an exponential function (Epron et al., 1999; Lloyd and Taylor, 1994; Mielnick and Dugas, 2000). Soil temperature is often the most important environmental factor for soil respiration because it supplies energy for the respiratory enzymes of both roots and soil microbial biomass (Xu et al., 2011). Thus, soil respiration is highly dependent on soil temperature, and assessment of how SOM responds to climate change becomes vitally important (e.g. Kirschbaum, 2000; Luo et al., 2001; Wan et al., 2007).

Soil water content represents an essential ecological resource controlling plant species composition and productivity (Häring et al., 2013); it therefore determines the supply and quality of substrate in the form of organic litter and root exudates (Rustad et al., 2000). The

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relationship between soil respiration and soil water is very complex, evolving numerous mechanisms (e.g. gas and solute diffusion, enzyme activities) and depends on site-specific environmental factors such as frequency and duration of rainfall (Luo and Zhou, 2006; Thomas, 2012). The effect of soil water content on soil respiration has been explained empirically by absolute or relative measures of volumetric water content (Reichstein and Janssens, 2009). Studies show that the optimum for soil respiration is normally found at intermediate water contents (e.g. field capacity), where macropore spaces are generally air-filled, thus aiding oxygen diffusion, and micropore spaces are usually water-filled, thereby facilitating diffusion of soluble organic carbon (Allison and Treseder, 2008; Davidson et al., 2000; Liu et al., 2009; Smith et al., 2003). The general assumption is that both very low and very high water contents reduce soil respiration due to the direct inhibition of biological activity (Davidson et al., 2000; Reichstein and Janssens, 2009). Linn and Doran (1984) interpreted this phenomenon mechanistically for microbial respiration as limitation of oxygen diffusion via pore spaces in very wet soils and restraint of soluble organic carbon in water films in very dry soils. Rewetting phenomena frequently increase soil respiration by mineralization of dead biomass or by desorption processes, which make the labile substrate available to soil microbial biomass (Orchard and Cook, 1983). Soil respiration also depends on vegetation type (Raich and Tufekcioglu, 2000; Rustad et al., 2000), which influences the carbon substrate availability and quality supplied to soil (Zhang et al., 2003). In fact, as soil respiration increases along with temperature, organic substrates are consumed, resulting in decreasing substrate availability (Tucker et al., 2013). However, SOM is composed of several substrate pools that exhibit different temperature sensitivities (Conant et al., 2011; Hartley and Ineson, 2008; Knorr et al., 2005). Additionally, human actions related to conversion of natural to agricultural ecosystems have the potential of modifying soil respiration by altering environmental conditions (e.g. soil temperature, water content), including soil carbon input (Li et al., 2007; Raich and Tufekcioglu, 2000). Altitudinal gradients offer an excellent opportunity for studying soil respiration in a wide range of environmental conditions (e.g. climate, soil type, natural system, agricultural landscape). In Mexico, extensive land use changes have taken place on the eastern slope of the Cofre de Perote Volcano. Specifically, many areas of coniferous and tropical montane cloud forests experience various disturbances (e.g. conversion of forest to agricultural land) that can affect soil organic carbon pools at different magnitudes. Thus, soil respiration due to local soil conditions must be quantified to permit an understanding of the response of terrestrial ecosystems to environmental variations relating to anthropogenic disturbance. I hypothesize that the conversion of natural vegetation to agricultural ecosystems increases soil respiration by altering environmental conditions (e.g. raising soil temperature) and that this stimulates microbial activity. To test this hypothesis, I examine a soil respiration dataset collected monthly from August 1999 to June 2000 from the upper section of the study area (2500 m asl) and from May 2003 to June 2004 from the lower section (1650 m asl), on the eastern slope of the Cofre de Perote Volcano (Mexico). The objectives of the present research were as follows: (1) to investigate the seasonal response of soil respiration changing in environmental factors (e.g. soil temperature, soil water content), and (2) to quantify the effects of land use on soil respiration.

2. Materials and methods

2.1. Sites conditions

This study was conducted on two altitudinal sections of the Cofre de Perote Volcano's eastern slope. The upper section, situated at 2500 m asl (19° 26′ 24″ N, 97° 07′ 17″ W), has a topography consisting of steep slopes and deep gullies. The climate is moist, cold temperate with frequent fog; the annual precipitation is 1670 mm. The mean temperature is 9.4 °C, with January the coldest month (6.9 °C) and May the hottest (11.6 °C). The average monthly air temperature and cumulative precipitation during the research (1999–2000) appear in Fig. 1. The native vegetation composition is dominated by coniferous forest (*Pinus patula* Schltdl. & Cham., *Pinus pseudostrobus* Lindl., *Pinus ayacahuite* C. Ehrenb. ex Schltdl.). Here, deforestation is common and forest is often converted to corn (*Zea mays* L.) plots. It is also common to observe abandoned agricultural plots, permitting the establishment of secondary shrub vegetation dominated by *Baccharis conferta* Kunth. At this altitude, the estimated soil organic carbon stored was 426 Mg C ha^{-1} at a depth of 1 m (Campos, 2002. unpublished doctoral thesis, Colegio de Postgraduados, Chapingo, Mexico). The soil was classified as Hydric Pachic Melanudand (Soil Survey Staff, 1999), which has developed from the weathering of volcanic ash. The following land use types were assessed: coniferous forest, corn field, corn field abandoned two years earlier, and corn field abandoned ten years earlier. Corn seeding begins in mid-March and harvesting

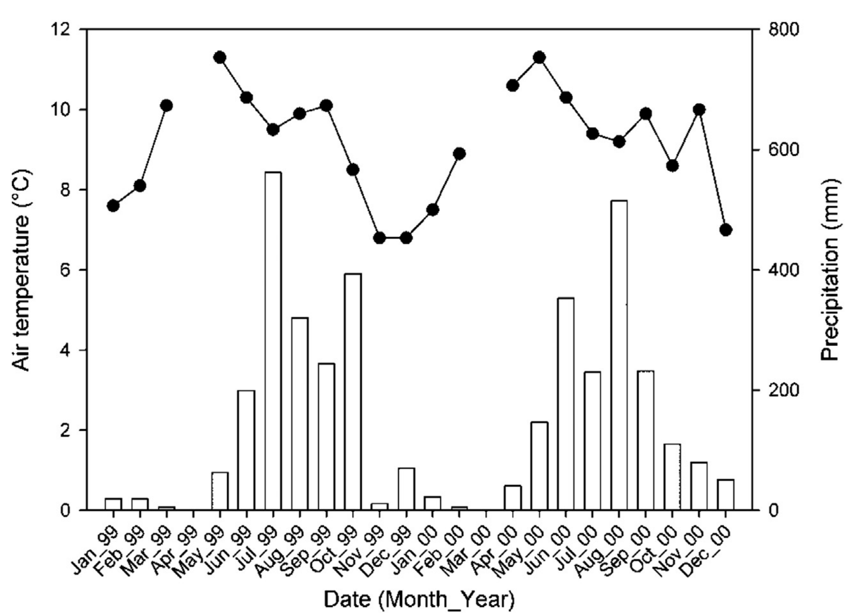

Fig. 1. Monthly mean air temperature (solid circle) and precipitation (bar) from January 1999 to December 2000 for the upper section (data were obtained at the Tembladeras Meteorological Station, Veracruz, Mexico).

in December. The corn crops receive annual applications of approximately 3.0 Mg ha^{-1} year^{-1} of sheep and goat manure during seeding. Inorganic fertilizers are generally applied over the growing season, averaging 155 kg N ha^{-1} year^{-1} and 20.5 kg P ha^{-1} year^{-1}.

The lower section, located at 1650 m asl (19° 30′ 09″ N, 96° 59′ 10″ W), has a topography dominated by high hills. The climate is humid subtropical with frequent fog, mainly during autumn and winter; the annual precipitation is 2080 mm. The mean temperature is 19.3 °C, with January the coldest month (15.8 °C) and May the hottest (22.2 °C). Average monthly air temperature and cumulative precipitation during the research period (2003–2004) appear in Fig. 3. Here, native vegetation is represented by tropical montane cloud forest, the most species-rich ecosystem in Mexico because it occurs across less than 1% of the territory but harbors 2500 plant species that grow preferentially or exclusively in this type of forest (Rzedowski, 1996). The floristic composition (Castillo-Campos, 1991) of tropical montane cloud forest is dominated by *Liquidambar macrophylla* Oerst., *Carpinus caroliniana* Walter, *Ulmus mexicana* (Liebm.) Planch., *Platanus mexicana* Moric., *Clethra macrophylla* M. Martens & Galeotti, *Quercus xalapensis* Bonpl., and *Quercus germana* Schltdl. The three most common tree fern species are *Alsophila firma* (Baker) D. S. Conant, *Lophosoria quadripinnata* (J. F. Gmel.) C. Chr., and *Sphaeropteris horrida* (Liebm.) R. M. Tryon (Bernabe et al., 1999). Here, vast areas of tropical montane cloud forest have been replaced, primarily by grasslands but also by corn plots. Grasslands are grazed mixed-grass prairies dominated by *Paspalum notatum* Flüggé, *Pennisetum clandestinum* Hochst. ex Chiov., and *Cynodon dactylon* (L.) Pers. (Hoffmann, 1993). Cattle are maintained throughout the year, with a stocking rate of 1.0 animal unit per hectare (Hoffmann, 1993). At this altitude, the estimated soil organic carbon stored was 248 Mg C ha^{-1} at the first 1 m depth (Campos, 2002. unpublished doctoral thesis, Colegio de Postgraduados, Chapingo, Mexico). The soil was classified as Typic Hapludand (Soil Survey Staff, 1999) that has developed from volcanic parent material. The following land use types were assessed: tropical montane cloud forest, grassland, and corn (*Z. mays* L.)–potato (*Solanum tuberosum* L.)–corn rotation. Here, the corn (April to November)–potato (December to March)–corn (April to November) rotation is a common crop sequence. Corn seeding begins in mid-May and harvesting in November, while potato seeding begins in December and harvesting in April. Approximately 3.0 Mg ha^{-1} of poultry manure is applied during corn seeding. Corn crops are generally fertilized with 155 kg N ha^{-1} year^{-1} and 20.5 kg P ha^{-1} year^{-1}. Inorganic fertilizer is not applied to grassland.

2.2. Topsoil sampling and analytical procedures

Five replicate soil samples were collected randomly from each land use type. These surveys all include topsoil samples, which are of particular interest from an agricultural perspective. Soil samples were air-dried and sieved through a 2 mm screen. Chemical variables included organic carbon determined by the Walkley–Black method (Nelson and Sommers, 1996), total nitrogen by Kjeldahl digestion (Bremner, 1996), pH (1:2.5 H_2O) (Thomas, 1996), and exchangeable bases (Ca^{2+}, Mg^{2+}, K^+, Na^+) extracted with 1 M NH4OAc (pH 7). Nutrient levels in the extracts were determined by atomic absorption spectrometry (Ca^{2+}, Mg^{2+}) and flame emission (K^+, Na^+).

2.3. Soil respiration determinations

On the upper section, soil respiration measurements were carried out over an 11-month period with 8 observations from August 1999 to June 2000. On the lower section, soil respiration measurements were made over a 14-month period from May 2003 to June 2004. Soil respiration was measured using the static chamber method (Aslam et al., 2000; Conant et al., 2000; Kabwe et al., 2002). This technique is based on CO_2 absorption and uses alkali traps placed inside the static chamber. These were constructed using 110 mm diameter, 98 mm high PVC cylinders, with one end sealed air-tight with a stopper and silicon. At each mid-month measurement period, six static chambers were placed randomly in each land use type, including one blank as a control. The static chambers were inserted in the soil to a depth of 3.5 cm. Vials containing 1 M NaOH were placed inside each. Blanks were subjected to the same procedure, but rather than inserting them into the soil, I sealed them with five layers of polyethylene foil layers and an aluminum cover. After exposure for 24 h, the vials were collected and CO_2 absorbed in NaOH traps was quantified by titrating with HCL after precipitating the carbonate with 10 mL $BaCl_2$ (10%) and using phenolphthalein as a visual indicator. Vials had a base area equal to 13% of the static chamber surface. In grassland, the surface plant cover inside the chamber was cut before measurement.

The amount of CO_2–C was calculated from the following formula (Anderson, 1982): $CO_2\text{–C (mg)} = (B - V)\,NE$, where B is the volume (mL) of acid used to titrate the NaOH solution from the blanks, V the volume (mL) of acid used to titrate the NaOH solution in the vials exposed to the soil atmosphere, N the normality of titrating acid, and E the equivalent weight (6 for C). Data are expressed as milligrams of CO_2–C per square meter per hour.

On each measurement date, I determined soil water content and soil temperature from areas adjacent to the static chambers. Soil temperature was measured between the hours of 12:00 and 13:00 with a thermometer placed at a depth of 10 cm. The gravimetric water content at a depth of 0–10 cm was determined by drying the soil at 105 °C. Data were converted to volumetric water content using bulk density.

2.4. Data analyses

The effect of sampling dates and land uses, as well as their interactive effects on soil respiration, soil temperature and soil water content, were determined by repeated measures GLM (general linear model) with

Table 1
Chemical properties of topsoil from the study sites.

Landscape position/land use type	C	N	C/N	Ca^{2+}	Mg^{2+}	K^+	Na^+	pH
	%			cmol$_c$ kg^{-1}		cmol$_c$ kg^{-1}		
Upper section (2500 m asl)								
Coniferous forest	22.6 ± 3.80	0.86 ± 0.05	27.1 ± 5.34	2.1 ± 0.47	0.29 ± 0.05	0.30 ± 0.01	0.14 ± 0.00	3.6 ± 0.07
Corn field	16.7 ± 0.57	0.85 ± 0.07	20.2 ± 1.73	2.4 ± 0.33	0.24 ± 0.05	0.28 ± 0.05	0.15 ± 0.00	4.8 ± 0.10
Corn field abandoned two years	11.1 ± 0.31	0.62 ± 0.01	17.8 ± 0.45	3.1 ± 0.17	0.48 ± 0.09	0.47 ± 0.04	nd	4.7 ± 0.05
Corn field abandoned ten years	18.9 ± 4.67	0.70 ± 0.04	26.3 ± 5.05	0.6 ± 0.13	0.20 ± 0.04	0.24 ± 0.02	0.18 ± 0.01	3.7 ± 0.06
Lower section (1650 m asl)								
Tropical cloud forest	16.4 ± 2.11	1.07 ± 0.08	14.9 ± 0.82	8.3 ± 0.96	2.40 ± 0.66	0.44 ± 0.10	0.16 ± 0.01	4.3 ± 0.30
Grassland	13.8 ± 0.56	0.92 ± 0.02	14.9 ± 0.58	1.8 ± 0.22	0.58 ± 0.12	0.19 ± 0.01	0.14 ± 0.00	4.3 ± 0.11
Corn–potato–corn rotation	6.06 ± 0.25	0.45 ± 0.06	14.9 ± 3.06	3.1 ± 0.26	1.11 ± 0.07	1.14 ± 0.29	0.14 ± 0.00	4.4 ± 0.05

nd = not detected.

sampling dates as a repeated measure and replication as a random effect. These were considered to be significantly different if $P \leq 0.05$. All statistical analyses were done using SAS software (SAS Institute Inc., 2000).

Regression analysis was performed to determine the relationships among soil respiration rate, soil temperature, and soil water content. I assessed the sensitivity of mean soil respiration rate to soil temperature by fitting the following exponential function to the data:

$$RS = y_0 + a * \exp(bT)$$

where RS is the mean soil respiration rate (mg C m^{-2} h^{-1}), T is the soil temperature (°C), and y_0, a and b are the constants fitted by the least-square technique.

3. Results and discussion

3.1. Topsoil properties

Descriptions of the chemical topsoil properties for sites are given in Table 1. The concentration of soil organic carbon decreased with altitude from 226 g kg^{-1} on the upper section (coniferous forest) to 60 g kg^{-1} on the lower section (corn–potato–corn rotation). The pH values were strongly acid, ranging from 3.5 to 4.8. Tropical montane cloud forest and grassland topsoil on the lower section had higher N concentrations than coniferous forest and corn field on the upper section. Additionally, the C/N ratio was higher on the upper than lower section. Generally, the labile pool of soil organic matter is an important substrate for soil respiration (Zheng et al., 2009); here, topsoil with soil organic matter that is higher in quality tends to have a greater potential for soil CO_2 flux. Exchangeable bases (Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}) were characterized by their low concentrations. The higher values for Mg^{2+} and K^{+} on the lower section may be due to farming practices, such as the application of poultry manure.

3.2. Soil respiration rates and environmental factors

3.2.1. Upper section (2500 m asl)

Seasonal precipitation and air temperature patterns during the study period (1999–2000) appear in Fig. 1. The climate is moist, cold temperate with frequent fog and the mean temperature is 9.4 °C. December is the coldest month (6.9 °C) and May the hottest (11.6 °C). Total annual rainfall is 1670 mm. Strong rainstorms occur frequently in summer (June–September). Winter is dry, and this trend continues until mid-spring.

Seasonal variations in soil respiration, temperature, and water content are shown in Fig. 2. Soil temperature at a 10 cm depth was higher in spring and summer, with maximum values in September and May, and lower in winter, with the lowest values in January at each site. The seasonal pattern was similar at all sites, but soil temperature was slightly lower in coniferous forest throughout the study period. Soil temperature gradually decreased from September, reaching its lowest value in January; after March, it rose steadily, reaching its maximum level in May. Regarding soil water content, the seasonal pattern was relatively different among sites. For example, soil water content in coniferous forest and corn field abandoned ten years earlier was higher in summer and early autumn and then decreased progressively from mid-autumn until mid-spring, with the lowest values in May. These two sites had lower soil water content than those of the other two sites. Soil water content in the corn field and corn field abandoned two years earlier followed a heterogeneous seasonal pattern during the study period, possibly due to tillage practices. Repeated measures ANOVA showed a significant land use-by-sampling date interaction for separate analyses of soil temperature and soil water content (Table 2). A significant interaction between land use and sampling date means that the effect of sampling date on soil temperature and soil water content depends on land use type.

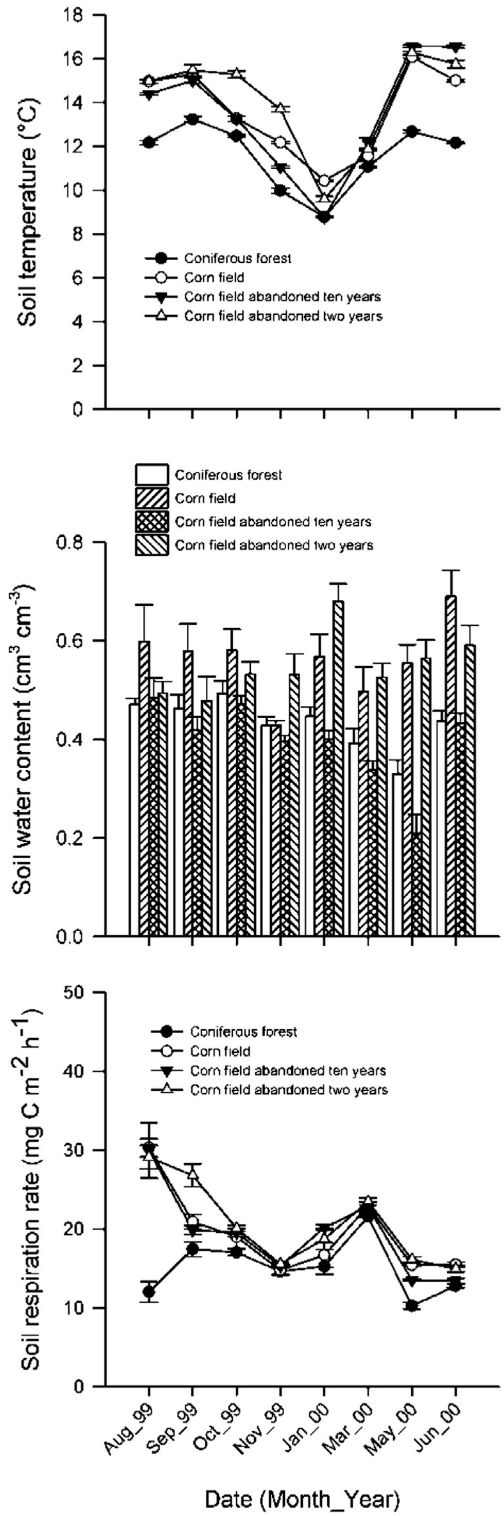

Fig. 2. Seasonal variations in soil temperature, soil water content, and soil respiration rate, measured in the upper section of the eastern slope of the Cofre de Perote Volcano. The error bars indicate standard error.

Soil respiration rates were slightly higher in croplands than in coniferous forest (Fig. 2). Raich and Tufekcioglu (2000) indicate that land use change has the potential to modify soil respiration rates by influencing soil microclimate and organic substrate input to the soil. In this study, the seasonal dynamics of soil respiration in croplands exhibited the highest ratio in mid-summer, with a peak in August followed by a decrease starting at the end of summer and continuing until November.

Table 2
Results of the ANOVA with repeated measures for the effect of land use and sampling date, and the interaction between them on soil respiration, soil temperature and soil water content, in upper section.

Landscape position and factor	df	Soil respiration		Soil temperature		Soil water	
		F	*P*	*F*	*P*	*F*	*P*
Upper section (2500 m asl)							
Land use	3	60.3	<0.001	149.5	<0.001	144.7	<0.001
Sampling date	7	68.5	<0.001	421.9	<0.001	5.2	<0.001
Land use × sampling date	21	11.4	<0.001	14.2	<0.001	3.1	<0.001

There was then a gradual increase starting in early winter and peaking in March, when soil temperature began to rise and soil water content was relatively high. As soil wets out, organic substrate diffusion becomes unlimited and thus promotes microbial activity (Moyano et al., 2013). This mechanism may explain the increase in soil respiration in late winter. Together, soil temperature and water content play a critical role in regulating the seasonal variations of soil respiration at a given site (Davidson et al., 1998; Fang and Moncrieff, 2001; Joffre et al., 2003; Lloyd and Taylor, 1994). For example, soil respiration is not sensitive to temperature under low water content but is under high water content (Harper et al., 2005). From the results of the present study, it appears that the increase in soil respiration at the end of winter occurred because there was more water in the soil and soil temperature conditions were already appropriate for microbial activity. In contrast, soil respiration decreased in spring, when soil temperature was the highest and soil water content was the lowest, especially in coniferous forest and corn field abandoned ten years earlier. This can be explained by the fact that, during dry periods, the moisture content of soil decreases and solute diffusion slows, limiting the supply of organic substrate for microorganisms (Moyano et al., 2013). Previous studies (e.g. Howard and Howard, 1993; Mo et al., 2005) demonstrated that soil respiration tends to decrease during periods of drought at high temperatures. Therefore, in summer, under non-limiting soil water conditions and soil temperature elevation, soil respiration increased at most study sites. Several studies (e.g. Raich and Schlesinger, 1992; Zheng et al., 2005) have reported that soil temperature is a good predictor of soil respiration when water availability is adequate and is not a limiting factor. A low temperature is the main limiting factor for root growth and soil microbial activity of ecosystems in cloudy regions (Zheng et al., 2009). At this altitude, the rainy season begins in June, which explains why soil water in most of the monitored land use types tended to increase and soil temperature to drop compared to the previous month. The repeated measures ANOVA showed that land use, sampling date, and the interaction between the two affected soil respiration (Table 2). This means that on different sampling dates, the soil respiration response generally differed depending on land use.

3.2.2. Lower section (1650 m asl)

Fig. 3 shows the meteorological parameters for the research period from January 2003 to December 2004. The climate is humid subtropical with frequent fog, mainly during autumn and winter, and the mean temperature is 19.3 °C. January is the coldest month (15.8 °C) and May the hottest (26.1 °C). The mean annual rainfall is 2081 mm. During the study period, intense rainstorms occurred frequently from late spring to early autumn, while less rainfall occurred in late autumn and winter.

Soil respiration, temperature, and water content showed seasonal variations during the study period (Fig. 4). Soil temperature displayed clear seasonal variation and peaked in summer (May, June) and then decreased gradually at all sites, reaching its lowest values in winter (February), while in early spring it began to increase. Tropical montane cloud forest tended to have the lowest soil temperature of the three sites at any given time. Generally, soil water content was highest in grassland and lowest in tropical montane cloud forest. At all sites, soil water content began to increase around mid-spring (early May), reaching its highest level in June (corn–potato–corn rotation) and September (tropical montane cloud forest, grassland). As represented in Fig. 4, soil water content in grassland remained practically stable from September to April. In tropical montane cloud forest and corn–potato–corn rotation, soil water content tended to decrease from mid-autumn (October) to late winter (February) and then increased. Repeated measures ANOVA (Table 3) showed a significant interaction between land use and sampling date, revealing that the effect of sampling date on soil temperature and soil water content depends on land use type.

In this study, soil respiration rates were lowest in tropical montane cloud forest than in croplands. In terms of seasonal variation, soil

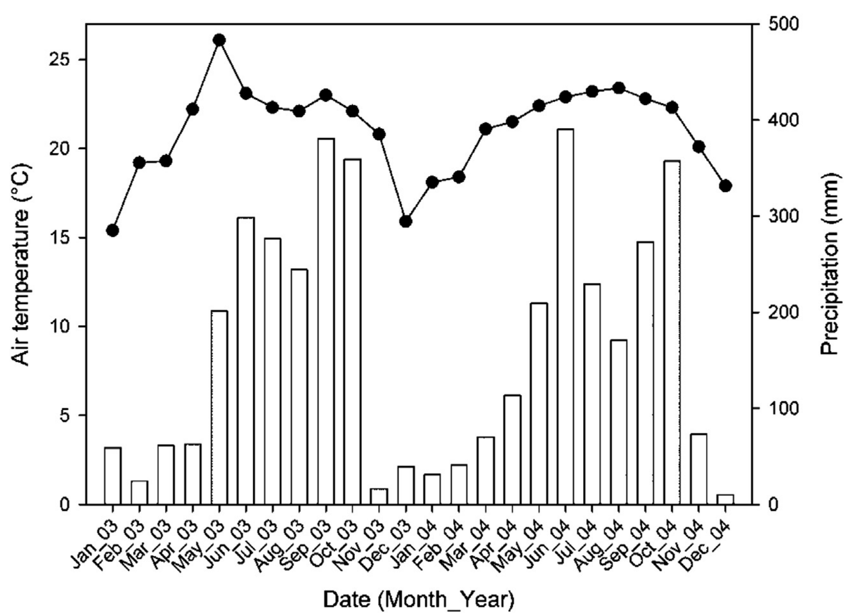

Fig. 3. Monthly mean air temperature (solid circle) and precipitation (bar) from January 2003 to December 2004 for the lower section (data were obtained at the Teocelo Meteorological Station, Veracruz, Mexico).

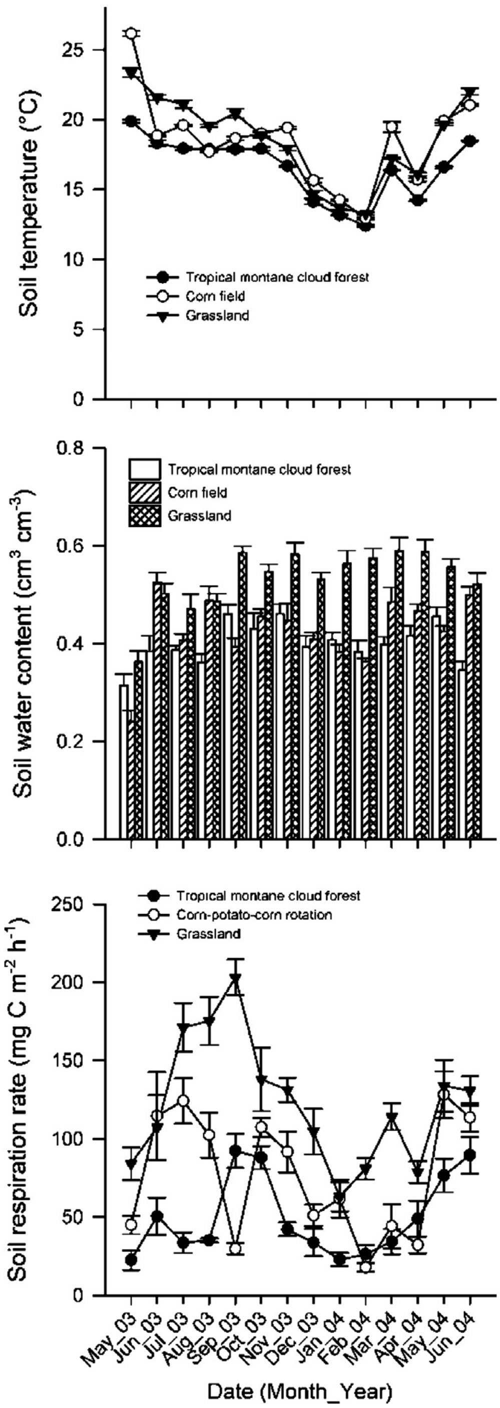

Fig. 4. Seasonal variations in soil temperature, soil water content, and soil respiration rate, measured on the lower section of the eastern slope of the Cofre de Perote Volcano. The error bars indicate standard error.

respiration began to rise in late spring, between May and June of 2003 and April and May of 2004, corresponding to the transition from dry to wet seasons, when soil water content increases. This is partly caused by the fact that when soils are relatively dry, metabolic activity increases strongly once water becomes available (Reichstein et al., 2003; Smith et al., 2003). This means that soil respiration in the study area will be increased by warming only in years with sufficient soil water. Previous studies (e.g. Inoue and Koizumi, 2012; Moyano et al., 2013) have reported that soil water serves as an agent for solubilizing and increasing the availability of organic substrates, whereas during dry periods, soil water content decreases and water in soil pores becomes increasingly disconnected, limiting substrate supply to microbial communities. Soil respiration is recognized to reflect the availability of organic carbon for microbial nutrition. In this research, the highest soil respiration was observed in summer, with peaks in September for tropical montane cloud forest and grassland sites and in July 2003 and May 2004 for the corn–potato–corn rotation site. These results suggest that the seasonality of soil respiration is strongly affected by summer rain patterns, which can increase soil water content to the point that it is no longer a limiting factor. Soil wetting, especially during the summer, can enhance microbial activities, leading to soil organic matter decomposition and resulting in a quick increase in the soil respiration rate. This suggests that soil water plays a more important role in the soil respiration rate during the transition from dry to wet seasons. Previous studies (e.g. Davidson et al., 1998; Reichstein and Beer, 2008) reported a decrease in soil respiration during dry periods. Wu and Brookes (2005) pointed out that natural drying–rewetting cycles cause fluctuating soil water contents that produce a rapid flush of CO_2 evolution. Likewise, during periods of drought, soil moisture can reduce soil respiration by limiting microbial contact with available organic substrates at low soil water contents (Orchard and Cook, 1983). In this study, soil respiration began to slow in autumn, with the lowest level in winter, when the soil temperature was relatively cooler. In all cases, across sites and dates, soil respiration diminished as soil temperature dropped. These results suggest that soil respiration may be especially influenced by soil temperature in winter seasons, when the soil is at its lowest temperature. However, the low soil respiration level recorded in May of 2003 was probably linked to the dry, warm soil conditions present prior to the rainy season. It has well been documented that soil temperature, water content, and organic substrate are the major factors controlling soil respiration (e.g. Davidson et al., 1998; Lloyd and Taylor, 1994; Moyano et al., 2013; Raich and Tufekcioglu, 2000). In this research, the repeated measures ANOVA showed that both sampling date, land use, and their interaction affected soil respiration significantly (Table 3). This means that on different sampling dates, soil respiration responses generally differed depending on land use.

Table 3
Results of the ANOVA with repeated measures for the effect of land use and sampling date, and the interaction between them on soil respiration, soil temperature and soil water content, in lower section.

Landscape position and factor	df	Soil respiration		Soil temperature		Soil water	
		F	*P*	*F*	*P*	*F*	*P*
Lower section (1650 m asl)							
Land use	2	268.3	<0.001	814.9	<0.001	88.4	<0.001
Sampling date	13	16.5	<0.001	933.1	<0.001	13.4	<0.001
Land use × sampling date	26	6.0	<0.001	46.3	<0.001	5.0	<0.001

3.3. Dependence of soil respiration on environmental factors

In soil, temperature and water content are considered to be two of the most important environmental factors controlling temporal variations in soil respiration (Lloyd and Taylor, 1994; Davidson et al., 1998; Fang and Moncrieff, 2001). In the present study, there was a positive exponential correlation (Fig. 5) between soil temperature and soil respiration rate, accounting for 52% of the variations in soil respiration ($P < 0.0001$). Previous studies have indicated the strong dependence of temperature on soil respiration (Deng et al., 2010; Lee et al., 2010; Lou et al., 2003; Sheng et al., 2010; Tang et al., 2006; Zheng et al., 2009). The main reasons for this dependence are that environmental conditions exist which influence the seasonal availability of carbon substrate (e.g., total organic carbon and labile organic carbon) (Campbell and Law, 2005). According to Liu et al. (2009), respiratory substrate availability plays a crucial role in the response of soil respiration to soil temperature. The

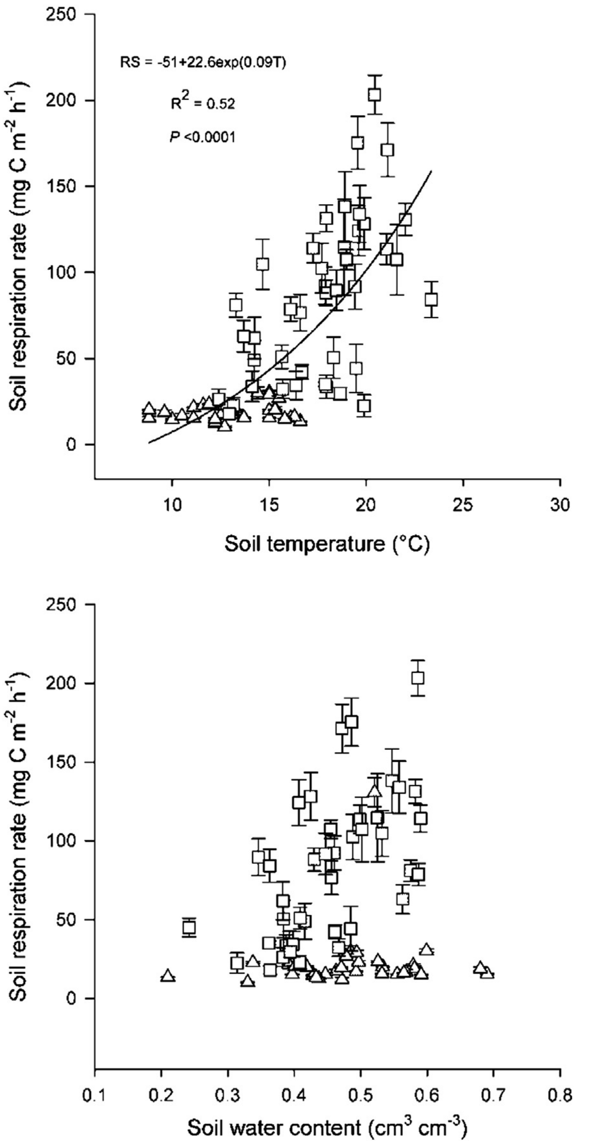

Fig. 5. Dependence of soil respiration (mg C m^{-2} h^{-1}) on soil temperature (°C) and soil water content (cm^3 cm^{-3}). Triangles and squares represent the upper and lower sections, respectively. Vertical bars indicate standard errors of the mean.

relationship between soil water content and the soil respiration rate is illustrated in Fig. 5. In this study, soil respiration rates were not significantly correlated with soil water contents. In contrast, Tang et al. (2006) reported that soil respiration was correlated with both soil respiration and soil moisture. Davidson et al. (1998) reported that soil temperature and soil water content influenced soil respiration as independent or confounded factors. Positive linear relationships between soil respiration and soil water content have been found in subtropical forests (Deng et al., 2010). This relationship is very complex, involves numerous mechanisms, and varies with site-specific environmental conditions (Luo and Zhou, 2006). In this study, soil respiration was best controlled by the combined effects of soil temperature and soil water content ($RS = 0.031e^{0.174T+17.21\theta-16.32\theta^2}$), which together explain 58% of the variation.

4. Conclusion

The research showed that there was substantial variation in soil respiration within and between sites and seasons. The magnitude of soil respiration responded to site-specific environmental conditions. Soil respiration in natural vegetation was substantially lowest than that in agricultural fields, surely due to differences in soil temperature and soil water content. The soil respiration rate increased exponentially with increasing soil temperature. In spring, soil respiration was limited due to a reduction in water availability, whereas in summer responded to soil temperature as soil water availability increased. These results revealed that soil respiration is less sensitive to soil water content at lowest soil temperatures but becomes more sensitive at highest soil temperatures when soil water is not a limiting factor. Thus, the results reveal that soil respiration in the study area could be increased by global warming only if it is accompanied by sufficient soil water availability.

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