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Soil CO_2 efflux from a mountainous forest-grassland ecosystem in central Taiwan

Wen-Yuan KAO[1,2,]* and Kuo-Wei CHANG[3]

[1]*Department of Life Science, National Taiwan University, Taiwan*
[2]*Institute of Ecology and Evolutionary Biology, National Taiwan University, Taiwan*
[3]*Department of Leisure and Recreation Studies, Aletheia University, Taiwan*

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ABSTRACT. Daytime soil CO_2 efflux from a mountainous forest-grassland ecosystem in central Taiwan was measured approximately monthly from Oct. 2003 to Oct. 2004. The system featured two zones, each dominated by a different vegetation type, one a C_4 grass (*Miscanthus transmorrisonensis*) and the other a hemlock (*Tsuga chinensis* var. *formosana*). The relationship between the soil temperature and soil CO_2 efflux of these two zones was also investigated, and seasonal patterns in these two variables emerged. Soil temperature in the grassland zone ranged from 4 to 16°C, and in the hemlock zone from 2 to 15°C. The magnitude of the daytime soil CO_2 efflux varied from 0.6 to 2.2 μmol m^{-2} s^{-1} and from 0.3 to 1.6 μmol m^{-2} s^{-1} for the grassland and forest zones, respectively. Within the same measuring period, the forest zone had significantly lower soil respiration than the grassland zone. Seasonal changes in the soil CO_2 efflux of both zones correlated strongly with soil temperature. The average Q_{10} values, the factor by which the respiration rate differs for a temperature interval of 10°C, calculated from the exponential relation between soil CO_2 efflux and soil temperature, were 3.5 and 2.8 for the forest and grassland zones, respectively. The result indicates that the soil CO_2 efflux from the forest zone is more sensitive to changes in soil temperature than that from the grassland zone.

Keywords: Hemlock; Grassland; *Miscanthus transmorrisonensis*; Q_{10} value; Soil CO_2 efflux; Soil temperature; *Tsuga chinensis* var. *formosana*; Taiwan.

INTRODUCTION

Soil is the major carbon pool in terrestrial ecosystems (Schlesinger and Andrews, 2000). A small change in the soil carbon may significantly affect the global carbon cycle and climate. The soil respiration rate measured in the field, which reflects the carbon emission from the soil surface, is one of the most important processes affecting the carbon budget of the soil. Thus, measuring soil respiration and evaluating factors affecting the process are important in modeling the global carbon cycle and hence in predicting the future of the environment.

Soil respiration varies with vegetation. It has been reported that respiration rates vary significantly among major biomes (Schlesinger, 1977; Singh and Gupta, 1977; Raich and Schlesinger, 1992; Raich and Tufekcioglu, 2000). Comparisons of adjacent, but different plant communities frequently demonstrate differences in soil respiration rates (Tufekcioglu et al., 2001). Hence, vegetation type is an important determinant of soil respiration.

Soil temperature and moisture, which influence soil biological activity and CO_2 diffusion, are considered the two most common factors affecting the seasonal dynamics of soil CO_2 efflux (Davidson et al., 1998; Kowalenko et al., 1978; Singh and Gupa, 1977). The relationship between soil CO_2 efflux and soil temperature is more often found to be exponential. The Q_{10} value is commonly used to define the temperature sensitivity of respiration and to model the effect of soil temperature on soil CO_2 efflux (Boone et al., 1998; Davidson et al., 1998; Epron et al., 1999; Janssens et al., 2000). The value of Q_{10} is the factor by which the respiration rate differs for a temperature interval of 10°C and is defined as: $Q_{10} = R_{T+10} / R_T$, where R_T and R_{T+10} are respiration rates at temperatures of T and T+10, respectively (Winkler et al., 1996). The range of reported Q_{10} values is large, and the empirical relationships established between field measurements of soil CO_2 efflux and soil temperature reveal that most of these relationships tend to be site specific (Kiefer and Amey, 1992; Oberbauer et al., 1992; Hanson et al., 1993; Howard and Howard, 1993; Raich and Potter, 1995).

Soil CO_2 efflux in forests has been reported to be a significant component in global carbon cycling (Woodwell et al., 1983). Hence, it is important to investigate soil CO_2

*Corresponding author: E-mail: wykao@ntu.edu.tw.

efflux and to understand better the factors that control the process in forest ecosystems. Despite its obvious importance to carbon cycle processes, to our knowledge, there are few studies on the amount of CO_2 efflux from forest soil or on the factors controlling the process of forest soil respiration in Taiwan (Chang et al., 2008). The objectives of this study were to quantify and compare soil CO_2 efflux with two vegetation types, one a grass species and the other by conifer, in a mountainous forest-grassland ecosystem in central Taiwan. We also examined the relationship between soil temperature and soil CO_2 efflux of these two systems. To compare results with other ecosystems, we also calculated the Q_{10} value to indicate the temperature sensitivity of soil respiration.

MATERIALS AND METHODS

Study site

This study was conducted at Tartarchia Anpu (altitude 2,600 m), located in Yushan National Park (23°29' N, 120° 48' E), Nantou County, in central Taiwan. The monthly mean air temperature for the years 1996 to 2000 ranged from 6.5 to 16.7°C, and the mean annual rainfall was ca. 2550 mm (Chen and Wei, 2000). Microclimate data of the study site during the study period are not available. The daily precipitation and mean air temperature—recorded by a nearby weather station (23°30' N, 120°48' E), of the same altitude and approximately 20 km from the study area during the study period—are presented in Figure 1 (Climatological data annual report, Central Weather Bureau, ROC). Compared to mean annual rainfall recorded by this station from 1998 to 2003 (ca. 3,000 mm), the annual precipitation of year 2004 was exceptionally high (ca. 4,000 mm) due to heavy rainfall in July and August.

To examine whether a difference exists in soil CO_2 efflux between different vegetation types, two zones adjacent to each other but dominated by different vegetation types, were selected at the study site. The first zone was dominated by *Miscanthus transmorrisonensis* (a C_4 grass) (Kao, 1997) and the other by *Tsuga chinensis* var. *formosana* (a hemlock). The grassland and the forest zones were separated by approximately 50 m. The soils of the study site are classified as loamy-silty, mixed, mesic, humic, and lithic Dystrudepts (Chen et al., 2001; Owen et al., 2003).

Sampling design

Soil CO_2 efflux of the two vegetation zones were measured approximately monthly from Oct. 2003 to Oct. 2004. Measurements were taken on one day close to the end of each month. August measurements were not available due to equipment failure. During each measuring period, measurements were made twice over two time intervals, morning (between 0830 to 0930 h) and afternoon (between 1430 and 1530 h).

Soil CO_2 efflux can be measured using both static chambers and dynamic methods. The dynamic method has

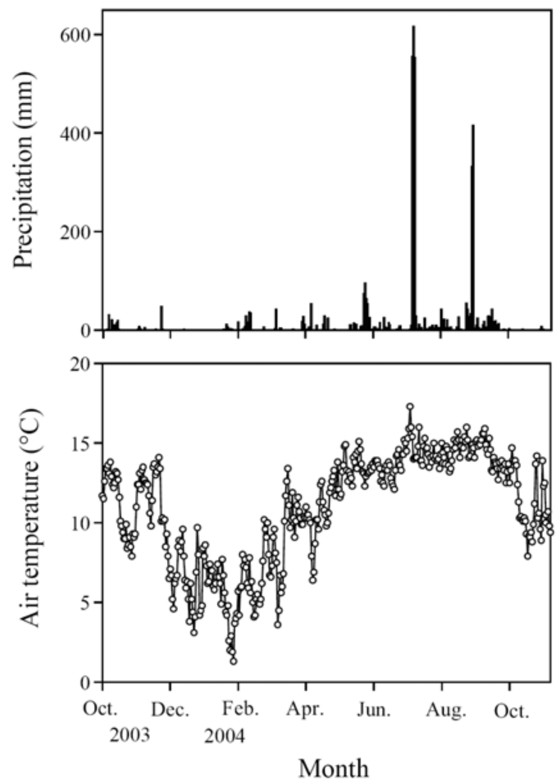

Figure 1. Daily precipitation and mean air temperature during the study period. Data are from Alishan Weather Station, located at the same altitude and approximate 20 km from the study area.

been shown to be more accurate and less biased for a wide range of flux rates (Jensen et al., 1996). Accordingly, in this study we used the dynamic method to estimate the soil CO_2 efflux. In each of the study stands, a transect across the vegetation community was established. Twelve PVC rings, 10 cm tall and 25 cm diameter, were inserted about 1 cm into the soil along the transect. Once inserted, rings were left in place in the field throughout the measurement period. Soil CO_2 efflux was measured with a LI-COR 6200 (Licor, Lincoln, NE) coupled to a LI-COR 6000-09 chamber. Measurements were made by drawing down the CO_2 concentration and measuring the flux rate for six consecutive 5-s observations. Soil temperatures were automatically logged during CO_2 efflux measurements with a chromel-constantan thermocouple penetration probe wired directly to the LI-6200 sensor housing attached to the forest floor gas exchange chamber. Because both the fine root biomass in each stand and microbial activity were reported previously to be concentrated above a depth of 20 cm (Yang et al., 1998), the temperature probe was inserted into the soil adjacent to each PVC chamber ring to a depth of 10 cm at the time of the flux measurement.

In each stand, twelve soil samples, 10 cm in diameter, each adjacent to the PVC chamber ring were collected from a soil depth of 0-10 cm (O horizon, according to Chen et al., 2001). Soil samples were sealed and kept in a cooler until they were returned to the laboratory for the measurement of pH value, moisture, and C and N contents. The pH value of the soil was determined using a pH meter (Suntex TS-2, Taiwan) by mixing soil with distilled water in a proportion of 1 to 10. Gravimetric soil moisture content was determined by drying the collected soil samples at 60°C to constant weight (W_{dry}) after the wet soil sample was weighted (W_{wet}). Soil water content (SWC) (percent dry weight) was then calculated as follows: SWC (%) = $[(W_{wet} - W_{dry})/ W_{dry}] \times 100$. Total carbon and nitrogen contents were analyzed using an elemental analyzer (NA 1500, Fison, Italy).

Statistical analyses

Difference in the selected properties—pH value, moisture, and C and N contents—of the two vegetation types was tested using a Student's-t test. Significant levels are reported as $P < 0.05$.

An exponential equation was used to describe the relationship between soil CO_2 efflux (Rs) and soil temperature (Ts) as follows:

$$Rs = R_{10} \times Q_{10}^{(Ts-10)/10}$$

where R_{10} is a parameter. Q_{10} values were log transformed and compared by Duncan's test (SigmaStat, Systat Software).

RESULTS

Selected soil properties of the soil samples

Significant difference was found in water and in C and N contents between the grassland and the forest zone soil (Table 1). Soil in the grassland had significantly lower water but higher C and N contents than the hemlock forest zone (Table 1). Soils of both zones had similar pH values.

Soil temperature and soil CO_2 efflux

Seasonal variation in soil temperature at a depth of 10 cm was found in both zones with the highest temperatures in July and August and the lowest in January. In the grassland zone, they ranged from 4 to 16°C (Figure 2A), and in the hemlock zone the range was from 2 to 15°C (Figure 2B).

The magnitude of the daytime soil CO_2 efflux varied from 0.6 to 2.2 µmol m^{-2} s^{-1} and from 0.3 to 1.6 µmol m^{-2} s^{-1} for the grassland and forest zones, respectively (Figure 2C, D). Within both zones, a seasonal pattern of CO_2 efflux from soil was also found (Figure 2C, D), which increased from winter to summer and decreased from summer to fall. In the same measuring period, the grassland zone had significantly higher soil CO_2 efflux than the forest zone.

Temporal variation in soil CO_2 efflux was found in the grassland but not in the forest zone (Figure 2C, D). Within the forest zone, a similar rate of soil CO_2 efflux was measured at 0830 and 1430 h on the same day of measurement (Figure 2D). Two patterns were found in the grassland zone: during Nov., Dec., Jan., Feb., March, and May, CO_2 efflux measured at 1430 h was higher than that measured at 0830 h (Figure 2C). However, during June, July, and September, CO_2 efflux measured at 0830 was higher than that measured at 1430 h.

Table 1. Selected soil properties of the grassland and the hemlock zone (mean ± S.E., n = 12). Values within the same raw followed by different superscripts represent significant difference at P = 0.05.

	Grassland	Hemlock forest
pH	4.4 ± 0.1^a	4.3 ± 0.1^a
H_2O content (%)	40.0 ± 2.2^a	62.4 ± 3.3^b
C content (%)	9.4 ± 0.7^a	7.2 ± 0.8^b
N content (%)	0.62 ± 0.20^a	0.44 ± 0.20^b

Relationship between soil CO_2 efflux and soil temperature

When data from soil CO_2 efflux measurements within a single year were pooled and regressed against temperature, the soil CO_2 efflux was strongly correlated with soil temperature. The exponential equation describes the relationship best for both zones (Figure 3). In the forest zone, no significant difference was found in the relationship between the soil CO_2 efflux and soil temperature measured at 0830 h ($Rs = 0.78 \times 3.45^{(Ts-10)/10}$, $r^2 = 0.87$) and 1430 h ($Rs = 0.77 \times 3.57^{(Ts-10)/10}$, $r^2 = 0.87$). In contrast, for the grassland zone significant difference was found in the Q_{10} values of the relationship measured at 0830 h ($Rs = 0.92 \times 3.64^{(Ts-10)/10}$, $r^2 = 0.72$) and 1430 h ($Rs = 0.91 \times 2.00^{(Ts-10)/10}$,

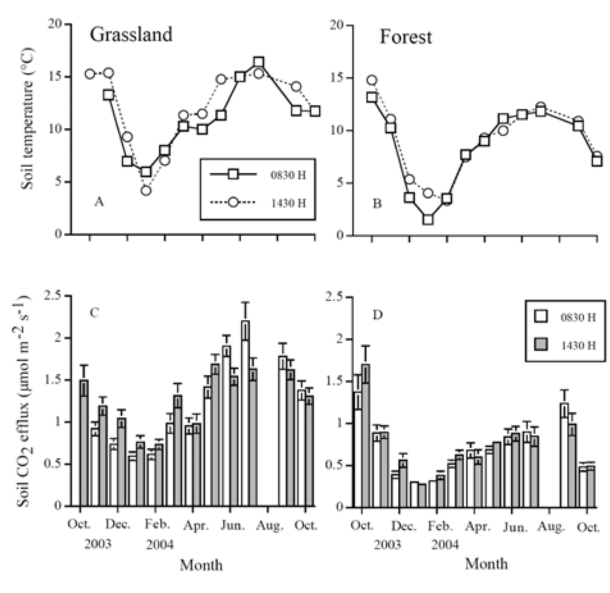

Figure 2. Patterns of soil temperature at 10 cm depth measured at 0830 h (square) and 1430 h (circle) (A, B), and soil CO_2 efflux measured at 0830 (open bar) and 1430 h (solid bar) (C, D) for the grassland and hemlock forest zone. Standard error of the mean are plotted as error bars.

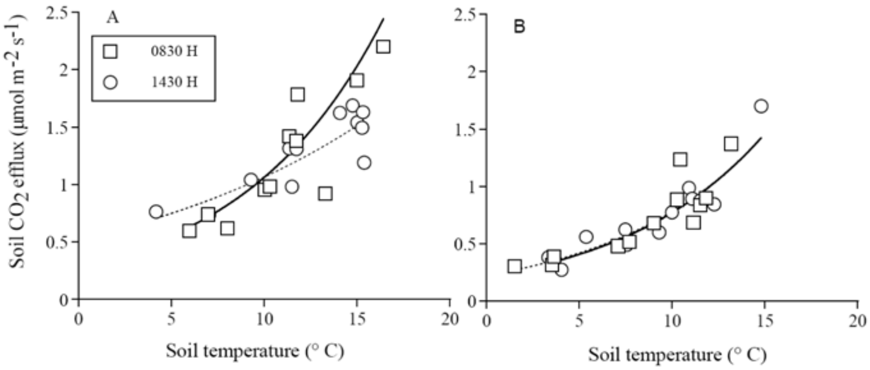

Figure 3. The relationship between soil CO_2 efflux, measured at 0830 h (square) and 1430 h (circle), and soil temperature for the grassland (A) and the forest zone (B). The exponential fits are presented by solid and dashed lines for measurement taken at 0830 h and 1430 h, respectively.

$r^2 = 0.68$). Values collected in the morning were significantly higher than those taken in the afternoon.

DISCUSSION

Soil CO_2 efflux often exhibits seasonal variability. Because temperature is the primary factor controlling the rates of all metabolic reactions, variations in temperature can be expected to have temporal effects on the soil CO_2 flux. Monthly measurements from this study also reveal that soil temperature is a good predictor of soil respiration rate seasonally, i.e. rates tended to increase from the beginning to the middle of the growing season along with seasonal temperatures (Figure 2C, D). As a result, rate of soil CO_2 efflux from both zones is strongly related to soil temperature (Figure 3). Results from this study also support the general hypothesis that soil temperature is one of the best statistical predictors of soil respiration.

The relationship, however, seems to be ecosystem-specific. For example, Raich and Schlesinger (1992) reviewed global data from *in situ* measurements and summarized Q_{10} values for total soil respiration, which varies from 1.3 to 3.3 with a median value of 2.4 for a range of ecosystems, most of which were forests. In contrast, higher Q_{10} values were reported for six different sites, from 3.4 to 5.6, in a temperate forest in the USA (Davidson et al., 1998). A greater range of Q_{10} values, between 2 and 6, has been reported for a number of European forest ecosystems studied within the EUROFLUX project (Janssens et al., 2000). Accordingly, the Q_{10} calculated for the hemlock and the grassland in this study are within the ranges of what has been reported.

The main components of soil CO_2 efflux are root respiration and soil microbial activity. Autotrophic respiration is thought to comprise 40 to 90% of total soil CO_2 efflux (Kucera and Kirkham, 1971; Norman et al., 1992; Hanson et al., 1993; Dugas et al., 1999). The variation in Q_{10} values and temporal variation in soil CO_2 efflux in grassland and some daily measurements showed opposite trends, with higher soil respiration rates at lower soil temperature. This might be related to diel patterns in root respiration that are linked to above ground metabolism. For example, Craine et al. (1999) found that variation in factors that affect carbon availability to roots were important determinants of soil CO_2 efflux in a Minnesota grassland. The climate conditions at high altitude are generally quite variable and might affect the photosynthetic performance of the C_4 grass. Decreased light supply, for example, would reduce the photosynthesis of this species (Kao et al., 1997). Tight links between photosynthesis and carbohydrate supply to roots and between carbohydrate supply and root respiration have been demonstrated (Szaniawski and Kielkiewicz, 1982; Amthor, 1994; Lambers et al., 1996). These results suggest that studies that measure or model soil CO_2 flux should consider whether short-term variation in CO_2 efflux is significant.

Soil CO_2 efflux has been shown to be ecosystem-specific in magnitude. Vegetation may affect soil respiration by influencing soil microclimate and structure, the quantity of detritus supplied to the soil, the quality of that detritus, and the overall rate of root respiration. In a comparison of the effect of vegetation type on the soil CO_2-C flux, Raich and Tufekcioglu (2000) also found that coniferous forests had about 10% lower rates of soil respiration than did adjacent broad-leaved forests growing on the same soil type, and grassland had on average about 20% higher soil respiration rates than did comparable forest stands. Our measurement also shows that the grassland zone had about 60% higher soil CO_2 efflux than the hemlock zone during the daytime period. Many factors might contribute to the difference. For example, higher soil temperatures in the grass zone might contribute to the higher soil CO_2 efflux relative to the forest zone (Figure 2). Tufekcioglu and Kucuk (2004) reported that grasslands have higher fine root biomass compared to adjacent forests, which might contribute to a higher soil respiration of grassland. In addition, soil water content was found to affect soil respiration rate (Davidson et al., 1998). The difference in soil CO_2 efflux of both zones might also due to their difference in soil water content. It has been found that high soil water content might inhibit bacterial activity and hamper the CO_2 diffusion from the soil. Across major biomes, a direct relationship between soil respiration and net primary productivity was found (Raich and Schlesinger, 1992). Thus, differences in net primary productivity of the grassland and hemlock forest could also contribute to the different soil CO_2 efflux of both zones. Further studies are needed to understand the mechanisms causing the difference in the soil CO_2 efflux of these two zones.

Soil respiration is one of the major fluxes in the global carbon cycle. This study and others have shown that the efflux of soil carbon is highly sensitive to changes in temperature, and the magnitude of the effect of temperature on the soil CO_2 efflux is ecosystem and vegetation type specific. This suggests that accurate prediction of climate effects on C cycles depends on more measurements of soil CO_2 efflux in different ecosystems. In addition, increased soil respiration with global warming is likely to provide a positive feedback to the greenhouse effect. Research on the role of soil processes and a much better understanding of the rate functions are crucial to modeling and predicting the potential effect of soil on changes in climate.

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台灣中部高山森林-草原生態系土壤二氧化碳釋放率

高文媛[1,2] 章國威[3]

[1] 國立臺灣大學 生命科學系

[2] 國立臺灣大學 生態學與演化生物學研究所

[3] 真理大學 休閒遊憩事業學系

本文比較台灣中部一高山生態系內芒草 (*Miscanthus transmorrisonensis*) 覆蓋的草原區，以及主要為鐵杉 (*Tsuga chinensis* var. *formosana*) 覆蓋的森林區白天之土壤呼吸率。從 2003 年 10 月起到 2004 年 10 月每個月在原地測量其土壤二氧化碳釋放率和土壤溫度。結果發現土壤二氧化碳釋放率和土壤溫度有季節性變化 ： 草原區土壤溫度變化從 4 to 16°C, 而森林區則從 2 to 15°C；白天草原區土壤二氧化碳釋放率從 0.6 到 2.2 µmol m^{-2} s^{-1}，森林區則從 0.3 到 1.6 µmol m^{-2} s^{-1}；在同一測量時段森林區土壤二氧化碳釋放率皆低於草原區土壤。兩區的土壤二氧化碳釋放率都跟土壤溫度成指數正相關。從土壤二氧化碳釋放率跟土壤溫度迴歸相關推算森林區平均 Q_{10} 值 (當溫度改變 10°C 時，土壤呼吸率的變化倍數) 為 3.5 高於草原區的 2.8；此結果顯示 ： 森林區土壤二氧化碳釋放率對土壤溫度變化的敏感度高於草原區的土壤。

關鍵詞 ： 鐵杉 ； 草原 ；*Miscanthus transmorrisonensis*；Q_{10} 值 ； 土壤二氧化碳釋放率 ； 土壤溫度 ； *Tsuga chinensis var. formosana*； 台灣。