

Contribution of Heterotrophic Respiration to Total Soil Respiration in a Wheat Field

Chompunut Chayawat^{1*}, Chuckree Senthong¹ and Monique Y. Leclerc²

¹Department of Plant Science and Natural Resources, Division of Agronomy, Faculty of Agriculture, Chiang Mai University, Chiang Mai 50200, Thailand

²Lab for Environmental Physics, The University of Georgia, Griffin, Georgia 30223, USA

*Corresponding author. E-mail: chompunut7@hotmail.com

ABSTRACT

The contribution of soil respiration needs to be understood to evaluate the implications of environmental change on soil carbon cycling and sequestration. The response of soil respiration to varying environmental factors was studied in a wheat field. The continuous soil gradient method combined with the trench method was used to (1) determine the temporal variation of total soil respiration (R_s) and heterotrophic respiration (R_h) and (2) investigate the relative effect of soil temperature (T_s) and soil water content (W_s) which control soil respiration. The result showed that temporal variations of soil respiration were dominantly controlled by T_s during the days. The variation in R_s and R_h showed a similar pattern of seasonal change in T_s (0.69 to 4.17 $\mu\text{mol m}^{-2}\text{s}^{-1}$ and 0.45 to 2.95 $\mu\text{mol m}^{-2}\text{s}^{-1}$, respectively). R_h ranged from 36% - 86% of R_s . The R_s was limited by W_s while T_s played as a secondary role; R_h , however, appeared to be correlated with both T_s and W_s . These results suggested that the factors controlling the variation in soil respiration differed between R_h and R_s . Additionally, two-variable equations could be better used to model the relationships of soil respiration to both T_s and W_s together, with the R^2 ranging from 0.53 to 0.83.

Key words: Heterotrophic respiration, Soil respiration, Soil temperature, Soil water content

INTRODUCTION

Carbon dioxide (CO_2) emission from the soils is an important component of the global carbon (C) cycle and has been shown to play a role in global warming. Extensive evidence suggests that this is associated with the increasing atmospheric CO_2 concentration (Schlesinger and Andrews, 2000). Soil respiration typically accounts for more than three-quarters of the CO_2 released through ecosystem respiration (Law et al., 2001) and is primarily controlled by temperature and soil moisture (Lloyd and Taylor, 1994; Davidson et al., 1998; Fang and Moncrieff, 1999; Jassal et al., 2008). It is thought that even a small increase in global

warming leading to a higher soil temperature is likely to increase soil CO₂ emissions through increased respiration which, in turn, are thought to lead to an appreciable increase in atmospheric CO₂ concentration. Therefore, it is important to obtain a good estimates of soil respiration and its relation to environmental controls.

The total respiration from the soil surface usually refers to soil respiration which mainly includes respiration from plant roots (autotrophic respiration) and microorganisms (heterotrophic respiration). Since autotrophic and heterotrophic respiration react differently to change in environmental conditions, it is crucial to get more insight into both components of soil respiration. However, the separation of heterotrophic respiration from total soil respiration under a field conditions remains difficulty since there are no effective, non-intrusive methods to separate them without disturbing the root and microbial organisms activities (Buchmann, 2000; Wang and Yang, 2007). In addition, data that might otherwise have been obtained from the greenhouse or laboratories are not likely faithfully reflect natural outdoor soil-atmosphere conditions. Three primary methods have generally been used to separate heterotrophic respiration from total soil respiration, i.e. (1) the integration of components, (2) the root exclusion method (trenching method), and (3) the use of stable isotopes (Hanson et al., 2000). The trenching method calculates the difference between CO₂ emission rates from soil volumes in which roots are either present or excluded to determine heterotrophic respiration. This method is relatively simple and can provide realistic estimates of heterotrophic respiration. Although the trenching method has been used in forest ecosystems and grassland ecosystems (Lee et al., 2003; Tang et al., 2005; Ngao et al., 2007) but it is still unknown whether this method is suitable in the measurements of heterotrophic respiration in agricultural fields. Thus, the bias introduced by using the trenching method should be quantified in order to accurately estimate heterotrophic respiration.

Numerous efforts have been made to understand the mechanisms behind the variation of soil respiration and empirical models have been developed to predict soil respiration using biophysical factors such as soil temperature, soil water content and their interaction (Lloyd and Taylor, 1994; Davidson et al., 1998; Tang et al., 2005; Vincent et al., 2006). However, none of these models appears to be consistently better than the others. In addition, models or equations have seldom been validated against independent data sets. Generally, soil respiration is related to many processes such as photosynthesis, root respiration, organic matter decomposition and microbial activity (Bunnell et al., 1997) and these processes are influenced by multiple biophysical factors. Therefore, root and heterotrophic respirations may respond and adapt to environmental variables (soil temperature and soil water content) differently and thus lead to different carbon flux patterns in a scenario of global climatic warming. The ability to separate soil respiration is thus essential to understand below-ground C processes and the dynamic processes and environmental controlling-factors of these components in agricultural soils have yet to be investigated.

In this study, we used the trenching plot combined with the soil CO₂ gradient method to determine heterotrophic respiration and total soil respiration in a wheat

field. The objectives of this paper were to (1) determine the temporal variation of total soil respiration and heterotrophic respiration and (2) investigate the relative effect of soil temperature and soil water content which control soil respiration.

MATERIALS AND METHODS

Site description

The experiment was conducted in a 6 ha of non-irrigated wheat field at the Southwest Georgia's Research and Education Center, Plains, Georgia, USA, (32.050° N, 84.367° W; 156 m elevation) during November 2006 to May 2007. The field was relatively flat in our sampling area. Wheat (*Triticum aestivum* L., var. Ag South 2000) was planted on November 15, 2006 and harvested on May 14, 2007 with a yield of 5,043 kg ha⁻¹. The soil was ploughed for land preparation prior to sowing. The sowing density of winter wheat was 56 kg per ha at a 0.06 m spacing. Basal fertilizer of N, P₂O₅, K₂O (4-22-6) was applied at 448 kg ha⁻¹ during planting and 56 kg ha⁻¹ of urea was applied before heading. The soil type was relatively uniform and dominated by sandy clay loam. The soil for planting wheat was composed of 52% of sand, 20% of silt and 28% of clay with a bulk density of 1.03 g cm⁻³ and 2.24% of organic matter. The crop was protected against pests and diseases throughout the study.

Soil respiration measurements

Soil respiration was measured by using soil CO₂ gradient measurement systems during the period of February to May 2007. Soil respiration was also measured at two locations, i.e., inside a trenched plot and an untrenched plot. We created open space and established a small plot of 3 m x 3 m for the trenching method. We dug a trench 0.40 m deep and 1.20 m wide around the plot. After lining the trench with a polyethylene sheet, we put the soil back into the trench plot according to its original soil profiles while minimizing any disturbance. The trench cut down most live roots that extended into the plot. The barrier sheets were installed to inhibit future root growth. The trenched plot was then kept free of any vegetation by periodic manual removal. Thus, we assumed that there were no root influences within this plot. The untrenched plot was installed at one location and at a lateral distance of 3 m away from the center of the trenched plot. Thus, we also assumed that the trenched and untrenched plots were installed in a homogenous location.

In this study, total soil respiration (Rs) in the untrenched plot is defined as the combined root respiration of living root tissues and the respiration of symbiotic mycorrhizal fungi and associated microorganisms. Heterotrophic respiration (Rh) in the trenched plot is defined as the respiration of soil microorganisms and microorganisms not directly under the influence of the live root system.

All plots were installed with solid-state infrared gas analyzers (GMP343, Vaisala Inc., Finland) to continuously monitor soil CO₂ concentration profiles by burying two sensors at 4 and 8 cm soil depths during the vegetation period in the center of the trenched plot and in the soil beneath a wheat canopy in the untrenched

plot. The probe was 0.18 m in length and 0.055 m in diameter. Before installation, the sensors were covered with a sintered PTFE (polytetrafluoroethylene) filter and a cap made of POM (polyoxymethylene) with a diffusion slot enabling gas exchange between the soil and the probe and protecting the probe from water. The sensor's dynamic range is 0-5,000 $\mu\text{mol mol}^{-1}$. The technical specification indicated that the accuracy of the CO_2 sensors is ± 5 ppm plus 2% of reading. The sensors were logged continuously and data were stored as 5-min averages in a datalogger (CR1000, Campbell Scientific Inc., Logan, UT). The sensors were installed in a horizontal face of a soil pit excavated at the site, keeping the different soil layers separated (Fig. 1). Then, soil layers were placed back in the same order to minimize the disturbance. The gradient measurement was applied to Fick's gradient diffusion equation to calculate the CO_2 efflux from the soil:

$$F_z = -D_s \frac{dC}{dz} \quad (1)$$

where F_z is the soil respiration, D_s is the gaseous CO_2 diffusion coefficient in the soil that varies with soil, C is the CO_2 mole concentration at a certain depth of the soil, and z is the depth. For flux determination, the gradient is approximated by discrete differences ΔC and Δz .

Diffusivity was computed with the Moldrup model (Moldrup et al., 2000)

$$\frac{D_s}{D_a} = \frac{\varepsilon}{\phi}^{2.5} \quad (2)$$

where D_a is the CO_2 diffusion coefficient in the free air, ε is the volumetric air content (air-filled porosity), ϕ the porosity or sum of the volumetric air content ε and the volumetric water content (W_s).

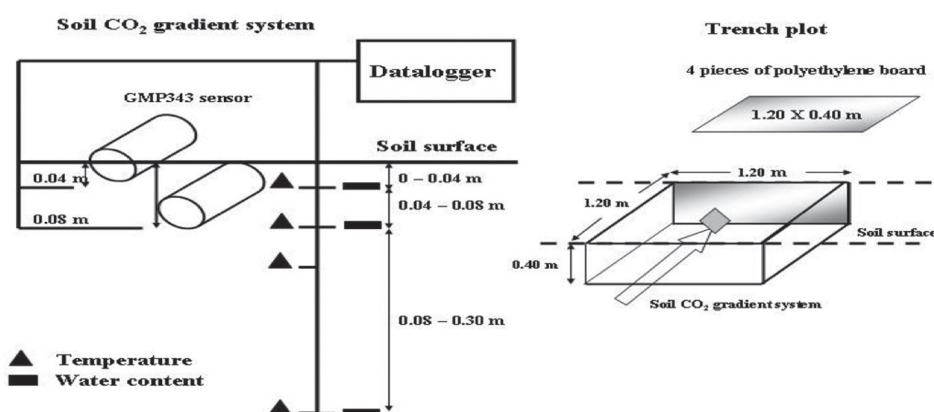


Figure 1. A schematic presentation of the system for measuring soil CO_2 profile using solid-state CO_2 sensors (left) and trenching method (right).

Measurements of environmental factors

In tandem with soil respiration measurements, soil temperature was measured using thermocouples (type E, Omega Engineering, Inc, CT.) at depths of 4, 8, 12 and 30 cm near the CO₂ concentration sensors but at a lateral distance of 10 cm away from the probe. Volumetric soil water content was measured at depth of 0-4, 4-8 and 8-30 cm at the same location using time-domain reflectometry probes (CS616, Campbell Scientific Inc., Logan, UT). The CO₂ concentration, soil temperature and the data of the profile of volumetric soil water content were stored as 5-min average in a datalogger (CR1000, Campbell Scientific Inc., Logan, UT).

Half-hourly cumulative rainfall was measured above the canopy with a tipping bucket rain gauge with a resolution of 0.1 mm (TE525, Campbell Scientific Inc., Logan, UT). The 12 soil samples (0-15 cm depth) were collected using a soil corer. The soil samples were weighed, dried at 105°C for at least 48 hr and then re-weighed to calculate total soil porosity.

Data analysis

Linear and non-linear regression analyses were used to examine the relationships between soil respiration and environmental variables. Generally, soil temperature (T_s) and soil moisture (W_s) are considered to be the most influential environmental factors controlling soil respiration. Linear and non-linear regressions were performed to fit a simple empirical model to the daily soil CO₂ efflux mean data:

$$F_s(T_s) = ae^{bT_s} \quad (\text{Lloyd and Taylor, 1994; Davidson et al., 1998}) \quad (3)$$

$$F_s(W_s) = a + bW_s + cW_s^2 \quad (\text{Qi and Xu, 2001}) \quad (4)$$

$$F_s(T_s, W_s) = ae^{bT_s} e^{cW_s + dW_s^2} \quad (\text{Tang and Baldocchi, 2005}) \quad (5)$$

where F_s is soil CO₂ efflux ($\mu\text{mol m}^{-2}\text{s}^{-1}$), T_s is the soil temperature (°C), W_s is the volumetric soil water content (m^3m^{-3}) and a , b , c and d are coefficients estimated by non-linear regression. Parameter a from Equation 3 denotes the reference soil respiration at 0 °C and b provides an estimate of the Q_{10} coefficient (dependence of soil respiration on soil temperature). All statistical analyses were performed using Origins package, Version 7 (Origins Cooperation, Massachusetts, USA). Unless otherwise stated, significant differences of all statistical tests were evaluated at the level $\alpha = 0.05$.

RESULTS AND DISCUSSION

Diurnal and seasonal variations of soil respiration

Diurnal variations in soil respiration were highly associated with variation of soil temperature at 8 cm depth (Fig. 2) during the growing season. Diurnal soil water content at all depths changes were small on the days when rainfall did not

occur, indicating that soil water content was not strong predictor of diurnal soil respiration patterns. In the untrenched plot, total soil respiration (R_s) followed the increasing trend of soil temperature in the morning and then decreased slightly when soil temperature decreased in the afternoon. R_s reached the peak values between 12:00-13:00 h. In contrast, heterotrophic respiration (R_h) was highest at 18:00 h, 2 h later than soil temperature at 8 cm depth and lowest at 11:00 h during a daytime (Fig. 2). Parkin and Kaspar (2003) reported that the CO_2 flux increased in response to soil warming in the morning and decreased when soil temperature started to cool, which is consistent with our soil respiration results from the trenched plot. It indicates that the diurnal variations in R_h closely resembled those in soil temperature. The mechanistic explanation of diurnal R_s in the untrenched plot is yet unclear. The effect may be due to a lag in production of CO_2 in the soil regulated by photosynthesis (Liu et al., 2006) or changes in photosynthate allocation to roots (Högberg et al., 2001; Liang et al., 2004).

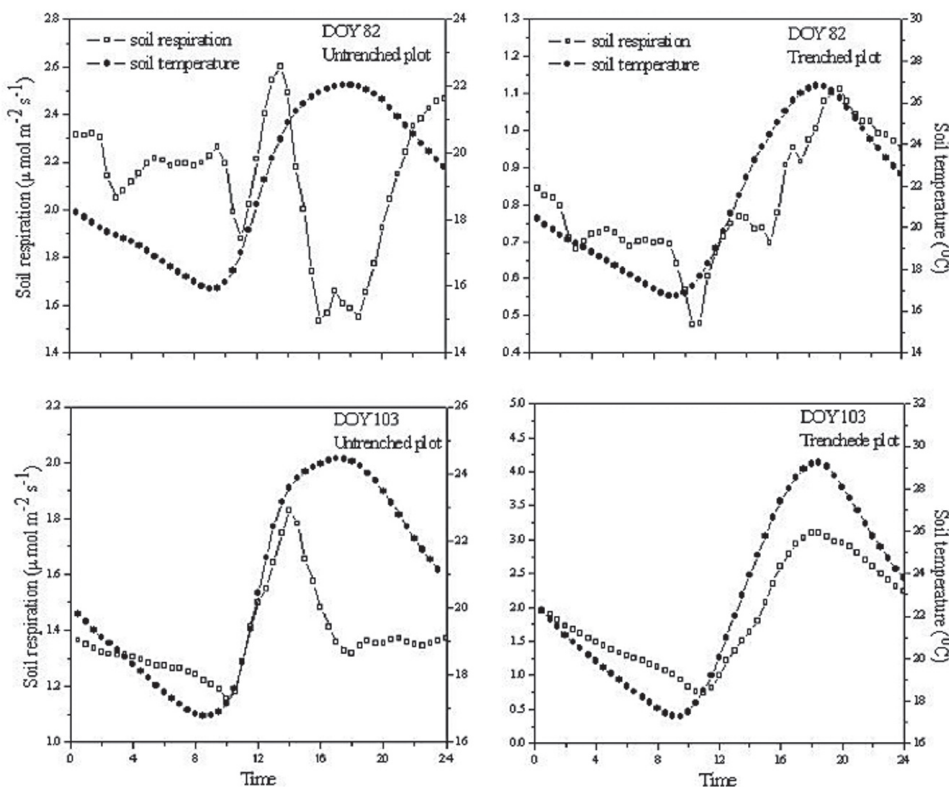


Figure 2. Diurnal patterns of soil respiration and soil temperature at a depth of 8 cm in the untrenched and trenched plots. Open circles, increasing temperatures during the day.

The seasonal evolutions of the soil respiration components are presented in Fig. 3. Daily total soil respiration (R_s) and heterotrophic respiration (R_h) changed from 0.69 to 4.17 $\mu\text{mol m}^{-2}\text{s}^{-1}$ and from 0.45 to 2.95 $\mu\text{mol m}^{-2}\text{s}^{-1}$, respectively. These results are consistent with the previous reports from many croplands under different conditions (Lee and Jose, 2003; Han et al., 2006; Shi et al., 2006). The pattern of seasonal change in R_h in the trenched plot was similar to R_s in the untrenched plot during the day of year (DOY) 67-90. This may be attributed to the differences in root respiration and their exudates within the trenched plot. Soil temperature also showed the same pronounced seasonal pattern as the soil respiration. In contrast, soil water content at 4-8 cm depth showed a different pattern from soil temperature and soil respiration. Similar results have been reported by Xu and Qi (2001) and Han et al., (2006), suggesting that soil temperature was the primary factor controlling seasonal soil respiration.

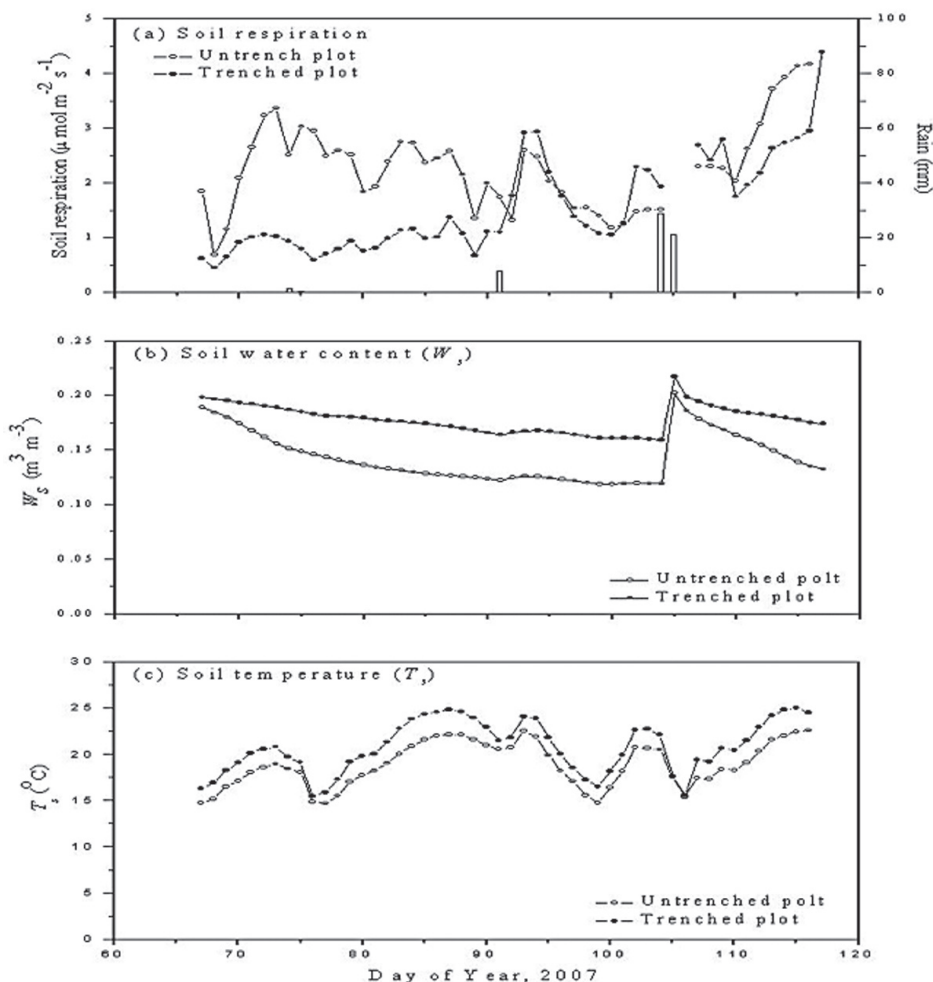


Figure 3. Seasonal variation of soil respiration in relation to soil temperature at 8 cm depth, volumetric soil water content at 4-8 cm depth and rainfall in the untrenched and trenched plots.

Soil respiration and its correlation with soil temperature and soil moisture

By plotting soil respiration with soil temperature and soil water content at different depths, we found the correlation to be highest at the depth of 8 cm and 4-8 cm, respectively. This result indicated that soil temperature and soil water content at this depth were suitable to study the relationship between soil respiration and environmental factor. Table 1 summarizes the coefficients of determination and best single- and multiple-factor models obtained from evaluating the influences of the soil temperature and soil water content factors on the soil respiration. For the untrenched plot, the R_s showed a highly positive correlation with soil water content and the soil water content explained 58% variability in the R_s . For the trenched plot, 65% variability in the R_h during DOY 67-90 could be ascribed to the variability in the soil water content while 83% variability in the R_h during DOY 91-116 could be ascribed to the total variability in both soil temperature and soil water content.

Table 1. Parameters estimated for the models of soil respiration from the untrenched (R_s) and trenched (R_h) plots against soil temperature (T_s , °C) at 8 cm depth and soil water content (W_s , m³ m⁻³) at 4-8 cm depth.

Environmental factors	a*	b*	c*	d*	R ²
<i>Models for the untrenched plot (R_s)</i>					
1. T_s					
$W_s < 0.13$	0.32	0.08	-	-	0.41
$0.13 < W_s < 0.16$	0.66	0.07	-	-	0.55
$W_s > 0.16$	0.37	0.23	-	-	0.59
2. W_s					
DOY 67-116	-33.20	482.08	-1,600.48	-	0.58
3. T_s and W_s					
DOY 67-116	-11.19	0.06	140.86	-444.18	0.53
<i>Models for the trenched plot (R_h)</i>					
1. T_s					
DOY 67-90	0.26	0.06	-	-	0.54
DOY 91-116	0.15	0.11	-	-	0.65
2. W_s					
DOY 67-90	-	-	-	-	-
DOY 91-116	-173.22	2,013.84	-5,764.91	-	0.44
3. T_s and W_s					
DOY 67-90	-37.44	0.08	387.41	-1,049.83	0.65
DOY 91-116	-20.01	0.12	208.04	-594.30	0.83

*a, b, c, d are significant coefficients ($\alpha < 0.05$). R² stands for determination coefficient.

We used simultaneously-measured of soil respiration to compare with the estimated soil respiration data. Three empirical models that predicted soil respiration were selected and fitted against the measurement of soil respiration data (Fig. 4a-c). The results show that the estimated of soil respiration data correlated well with the measured of soil respiration. About 76% and 87% of measured soil respiration was explained by the $F_s(\theta_s)$ and $F_s(T_s, \theta_s)$ equation in the untrenched and trenched plots, respectively. This result agrees with the finding of many researchers that the soil respiration are generally predicted by soil temperature (Lloyd and Taylor, 1994; Davidson et al., 1998; Xu and Qi, 2001; Han et al.,

2006), soil water content alone (Keith et al., 1997; Epron et al., 2004), or both (Bunnell et al., 1977; Mielnick and Dugas, 1999; Tang et al., 2005). In contrast to the single-factor model above, the R^2 of the multiple-factor model increased (Fig. 4b-c), therefore, the application of multiple-factor model was better than a single-factor model in predicting soil respiration.

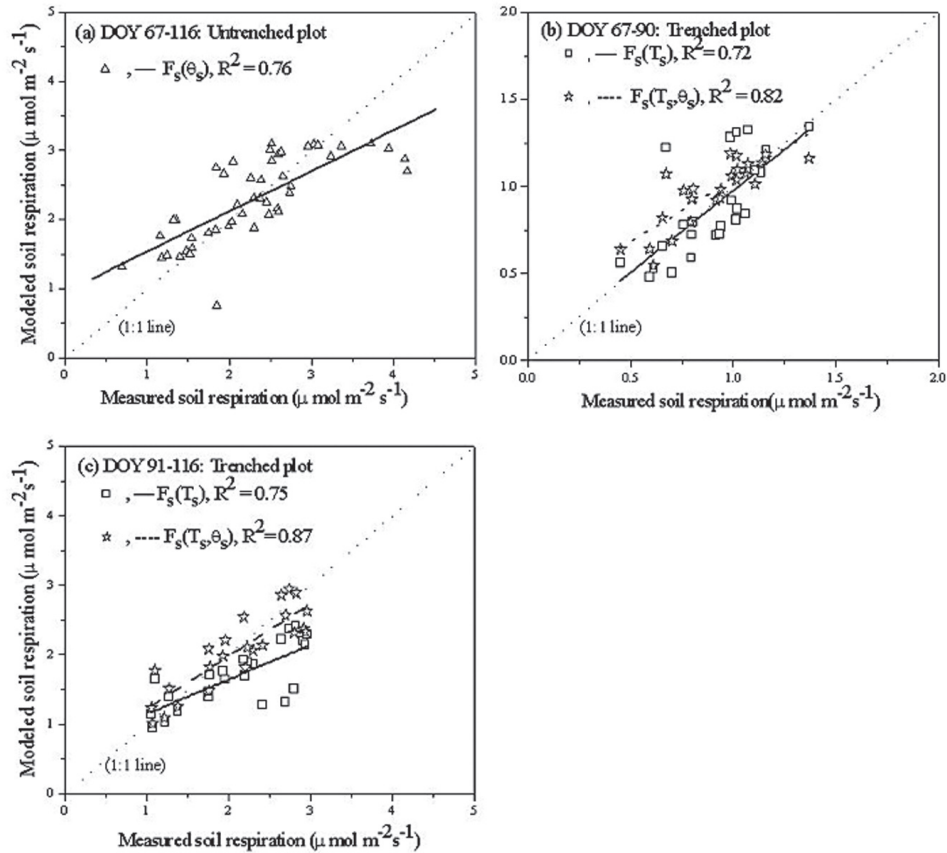


Figure 4. Comparison of measured and modeled soil respiration in the untrenched and trenched plots: function of soil water content, $F_s(W_s)$ in the untrenched plot (a) and function of soil temperature, $F_s(T_s)$ and function of soil temperature and soil water content $F_s(T_s, W_s)$ in the trenched plot (b-c).

Effects of trenching plot on the measurements of heterotrophic respiration and environmental factors

The results show that trenching can modify soil environmental conditions. The plot trenching tends to increase in both T_s and W_s (Fig 2-3) leading to a significant difference in T_s and W_s between the untrenched and trenched plots. It was found that heterotrophic respiration (R_h) was underestimated in this study. This is likely an artifact of the experimental design, as the trenched plot's was

higher in temperatures which are likely to be an artifact resulting from an imperfect technique: (1) it is virtually impossible to prevent any soil disturbance by trenching the plot and (2) the radiation load over that plot is vastly different from that of the untrenched plot, making a true separation of the respiration components rife with uncertainties pertaining to the role of the higher temperature in the dataset. Another reason for obtaining the lower rates of R_h from the trenched plot soil could be the depletion of labile carbon. Since the trenched plot did not receive the labile carbon from the plant roots, its might have become depleted of the labile carbon compared to the untrenched plot. This could explain the lower rate of R_h that obtained from the trenched plot (Jiang et al., 2005; Ngao et al., 2007).

CONCLUSION

The present study sought to separate the contribution of heterotrophic respiration from the total soil respiration using a trenching method. Results suggest that total soil respiration (the untrenched plot) was more sensitive to soil water content than soil temperature. However, heterotrophic respiration (the trenched plot) was controlled by both soil temperature and soil water content, but soil temperature appeared to be a more important variable. Moreover, the seasonal variation in soil respiration can be predicted by the combination of soil temperature and soil water content in our field. Based on the multivariate regression analysis, the bi-variable model was better fitted well with the observed data and explained approximately 83% accounted of the total variation in daily soil respiration. By using of the trenching method for the purpose of separating heterotrophic respiration from the total soil respiration in agricultural soils should be carefully considered as it perturbs the soils and thus alters both soil water content and temperature, rendering any robust distinction of the role of heterotrophic and autotrophic respiration measurements. Results from the present experiment suggest that the characterization of the partitioning of total soil CO_2 emissions between autotrophic and heterotrophic respiration can be achieved provided that (1) smaller-area trenched plots should be used to reduce the radiation load on the plot and that (2) the plot should be shielded by placing a net or some material partly filtering the light to ensure that the soil temperatures between both plots are equivalent.

ACKNOWLEDGEMENTS

This research was funded by Georgia Peanut Commission. We would like to thank the Royal Golden Jubilee (RGJ) Ph.D. program of Thailand Research Fund (TRF) and Chiang Mai University for providing a research scholarship. We especially appreciate the multi-faceted efforts of the staff at the Southwest Georgia Research and Education Center of the University of Georgia Plains Research Center for their logistical support of the present research. Authors are grateful to Professor Dr. John P. Beasley Jr, and Dr. Gengsheng Zhang for their kindly help and many recommendations in conducting this research.

REFERENCES

- Bunnell, F.L., D.Tait, P.W. Flanagan, and K.V. Cleve. 1997. Microbial respiration and substrate weight loss I. A general model of the influences of abiotic variables. *Soil Biol. Biochem.* 3: 33-40.
- Buchmann, N. 2000. Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. *Soil Biol. Biochem.* 32: 1625-1635.
- Curiel-Yuste, J., I.A. Janssens, A. Carrara, and R. Ceulemans. 2003. Annual Q10 of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biol.* 10: 161-169.
- Davidson, E.A., E. Belk, and R.D. Boone. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperature mixed hardwood forest. *Global Change Biol.* 4: 217-227.
- Epron, D.E., Y. Rnouvellon, O. Roupsard, W. Mouvondy, A. Mabiala, L.S. Andre, R. Joffre, C. Jourdan, J.M. Bonnefond, P. Berbigier, and O. Hamel. 2004. Spatial and temporal variations of soil respiration in Eucalyptus plantation in Congo. *For. Ecol. Manag.* 202: 149-160.
- Fang, C., and J.B. Moncrieff. 1999. A model for soil CO₂ production and transport I: model development. *Agric. For. Meteorol.* 95: 225-236.
- Hanson, P. J., N.T. Edwards, C.T. Garten, and J.A. Andrews. 2000. Separating root and soil microbial contributions to soil respiration: A review of methods and observations. *Biogeochemistry* 48: 115-146.
- Han, G., G. Zhou, Z. Xu, Y. Yang, J. Liu, and K. Shi. 2006. Biotic and abiotic factors controlling the spatial and temporal variation of soil respiration in an agricultural ecosystem. *Soil Biol. Biochem.* 39: 418-425.
- Högberg, P., A. Nordgren, N. Buchmann, A.F.S. Taylor, A. Ekblad, M.N. Högberg, G. Nyberg, M. Ottosson-Lofvenius, and D.J. Read. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411: 789-792.
- Jiang, L., F. Shi, B. Li, Y. Luo, J. Chen, and J. Chen. 2005. Separating rhizosphere respiration from total soil respiration in two larch plantation in northeastern China. *Tree Physio.* 25: 1187-1195.
- Jassal, R.S., T.A. Black, M.D. Novak, D. Gaumont-Guay, and Z. Nesic. 2008. Effect of soil water stress on soil respiration and its temperature sensitivity in 18-year-old temperate Douglas-fir stand. *Global Change Biol.* 14: 1-14.
- Keith, H., K.L. Jacobsen, and R.J. Raison. 1997. Effects of soil phosphorus availability, temperature and moisture on soil respiration in *Eucalyptus pauciflora* forest. *Plant and Soil* 190: 127-141.
- Law, B.E., F.M. Kelliher, D.D. Baldocchi, P.M. Anthoni, J. Irvine, D. Mooree, and S. Van Tuyl. 2001. Spatial and temporal variation in respiration in young ponderosa pine forests during a summer drought. *Agric. For. Meteo.* 110: 27-43.
- Lee, K.H., and S. Jose. 2003. Soil respiration and microbial biomass in a pecan-cotton alley cropping system in Southern USA. *Agroforestry Systems* 58: 45-54.

- Lee, M., K. Nakane, T. Nakatsubo, and H. Hoizumi. 2003. Seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperature deciduous forest. *Plant and Soil* 255: 311-318.
- Lloyd, J., and A. Taylor. 1994. On the temperature dependence of soil respiration. *Functional Ecol.* 8: 315-323.
- Liang, N., T. Nakadai, T. Hirano, L. Qu, T. Koike, Y. Fujinuma, and G. Inoue. 2004. In situ comparison of four approaches to estimating soil CO₂ efflux in a northern larch (*Larix kaempferi* Sarg.) forest. *Agric. For. Meteorol.* 123: 97-117.
- Liu, Q., N.T. Edwards, W. M. Post, L. Gu, J. Ledford, and S. Lenhart. 2006. Temperature-independent diel variation in soil respiration observed from a temperate deciduous forest. *Global Change Biol.* 12(11): 2136-2145.
- Mielnick, P.C., and W.A. Dugas. 1999. Soil CO₂ flux in a tall grass prairie. *Soil Biol. Biochem.* 32: 221-228.
- Moldrup, P., T. Olesen, J. Gamst, P. Schjønning, T. Yamaguchi, and D.E. Rolston. 2000. Predicting the gas diffusion coefficient in repacked soil: Water-induced linear reduction model. *Soil Sci. Soc. Am. J.* 64: 1588-1594.
- Ngao, J., B. Longdoz, A. Granier, and D. Epron. 2007. Estimation of autotrophic and heterotrophic components of soil respiration by trenching is sensitive to corrections for root decomposition and changes in soil water content. *Plant and Soil* 301: 99-110.
- Parkin, T.B., and T.C. Kaspar. 2003. Temperature controls on diurnal carbon dioxide flux: implications for estimating soil carbon loss. *Soil Sci. Soc. Am. J.* 67: 1763-1772.
- Qi, Y., and M. Xu. 2001. Separating the effects of moisture and temperature on soil CO₂ efflux in a coniferous forest in the Sierra Nevada mountains. *Plant and Soil* 237: 15-23.
- Schlesinger, W., and J. Andrews. 2000. Soil respiration and the global carbon cycle. *Biogeochemistry* 48: 7-20.
- Shi, L., X. Zhang, Z. Zhong, and H. Ouyang. 2006. Diurnal and seasonal variability of soil CO₂ efflux in a cropland ecosystem on the Tibetan Plateau. *Agri. For. Meteo.* 137: 220-233.
- Tang, J., and D.D. Baldocchi. 2005. Spatial-temporal variation in soil respiration in an oak-grass savanna ecosystem in California and its partitioning into autotrophic and heterotrophic respiration component. *Biogeochemistry* 73: 183-207.
- Tang, J., L. Misson, A. Gershenson, W. Cheng, and A. H. Goldstein. 2005. Continuous measurement of soil respiration with and without roots in a ponderosa pine plantation in the Sierra Nevada Mountains. *Agri. For. Meteo.* 132: 212-227.
- Vincent, G., A.R. Shahriari, E. Lucot, P.M. Badot, and D. Epron. 2006. Spatial and seasonal variation in soil respiration in a temperate deciduous forest with fluctuating water table. *Soil Biol. Biochem.* 38: 2527-2535.

- Xu, M., and Y. Qi. 2001. Soil-surface CO₂ efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. *Global Change Biol.* 7: 667-677.
- Wang, C., and J. Yang. 2007. Rhizospheric and heterotrophic components of soil respiration in six Chinese temperate forests. *Global Change Biol.* 13: 123-131.

none