冷温帯落葉広葉樹林の土壌呼吸の動態:
土壌呼吸における降雨と根の呼吸の季節的影響

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Dynamic Changes of Soil Respiration in a Cool-Temperate Deciduous Broad-Leaved Forest: Effects of rainfall and seasonal contribution of roots to the soil respiration

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Summary

CHAPTER I　General Introduction

The Kyoto protocol agreement of December 1997 has focused the attention of the public and policymakers on the earth's carbon (C) budget. It has fostered a continuing search for a more accurate quantification of global terrestrial C sources and sinks to mitigate global climate change by conserving or increasing C sequestration (Bachelet et al. 2001). It was requested that developed countries cut down their total CO_2 emission by 2008-2012 to 92-95% of the levels in 1990, taking the balance of CO_2 in their forest ecosystems into consideration. Thus, carbon balance in forest ecosystems should be measured or estimated more correctly in the near future (Nakane 2001).

Forest C balance, which is given by net primary production (NPP), is the balance between CO_2 fixation by net photosynthesis occurring aboveground and CO_2 release from the belowground compartment through soil respiration. Carbon net balances (NEP: Net Ecosystem Productivity) in forest ecosystems were determined by the balance of NPP of vegetation and heterotrophic respiration (HR) of soil. These heterotrophic bacteria and fungi active in the organic and mineral soil horizons, and soil faunal activity (HR) is difference between forest soil respiration (SR) and the activity of autotrophic roots and associated rhizosphere organisms (RR: root respiration) (Edwards & Harris 1977). It is important that these components need to precise assessment for quantifying the NEP.

Interest in the factors that control soil respiration rate is growing because of the potential for changing climate, including temperature and precipitation, to affect NEP and carbon exchange between terrestrial ecosys-

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tems and the atmosphere (Raich & Schlesinger, 1992; Davidson et al. 2000). Therefore, information about soil respiration and/or root respiration is limited surrounding methods, especially in forest ecosystems of the world.

The primary objective of this study is to examine the effects of rainfall events on soil respiration and provide recommendations for field measurement. Secondarily, this study provides the seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperate deciduous broad-leaved forest, in central Japan. The final goal of this study is to clarify the carbon balance in the temperate forest ecosystem based on the analysis using the bioprocess approach.

CHAPTER II Study Area

The study area is on the northeast slope of Mt. Norikura, Gifu Prefecture, Japan (36°8'N, 137°26'E, 143 m a. s. l.). The area is in the cool-temperate zone. The annual means of air temperature and precipitation for 21 years (1980 to 2000) were 6.1 °C and 2175 mm, respectively. Vegetation consisted of an approximately 40-year-old secondary deciduous broad-leaved forest, which was primarily composed of oak (*Quercus Mogolica var. grosseserrata*) and birch (*Betula ermanii, Betula platyphylla*). The forest floor is covered with dense dwarf bamboo (*Sasa senanensis*).

CHAPTER III Effects of Rainfall Events on Soil Respiration Rate

Several researchers have proposed models or equations to predict soil respiration rate from more readily available biotic and abiotic measurements. Two commonly used abiotic variables are soil temperature (ST) and soil water content (SWC). However, there are some evidences that abrupt changes in soil respiration rate take place following rainfall events in the field. To date, however, no attempt has been made to evaluate the importance of rainfall events on soil respiration rate in forest ecosystems.

The soil CO_2 fluxes were measured using an open-flow gas exchange system with an infrared gas analyzer (IRGA) in the snow-free season from August 1999 to November 2000. The open-flow IRGA method was used for the flux measurements. The measuring system setup was comprised of one reference line and four identical sample lines, an IRGA in the absolute mode and a data logger. Four chambers were placed 4-5 m apart. The soil respiration rate was determined by using a chamber similar to that described by Mariko *et al.* (2000). Each chamber consisted of two parts. The lower body, with two ports for the inlet and outlet of air, was a 15-cm-high PVC cylinder with a 21 cm internal diameter. When the bottom edge of the cylinder was pushed 4 cm into the soil, the bottom circumscribed an area of 346 cm^2. The upper part, a 2.5-cm-high PVC lid, was placed on the top of the body immediately before starting measurements.

ST was measured in each chamber during the flux measurement at 5-10 cm below the top of the forest litter layer, which is about 4-8 cm below the surface of the mineral soil, depending on local variation in the thickness of the litter layer. Continuous measurements of ST were carried out at two points near the flux measuring points at 30-min intervals (10 cm below the top of the litter layer) over the entire study period.

SWC was measured by time domain reflectometry (TDR). Two 15-cm-long rod-balanced probes were placed horizontally at a soil depth of 15 cm below the top of the litter layer as described by Davidson *et al.* (1998).

Effects of rainfall events on diurnal soil respiration rate

Soil CO_2 flux showed no significant diurnal trend on days without rain. In contrast, rainfall events caused a significant increase in soil CO_2 flux. To determine the effect of rainfall events and to evaluate more precisely the daily and annual soil carbon flux, we constructed a multiple polynomial regression model that included two variables, soil temperature and soil water content, using the soil CO_2 flux data recorded on sunny days. Daily soil carbon fluxes on sunny days calculated by the model were almost the same as those determined by the field measurements.

On the contrary, the fluxes measured on rainy days were significantly higher than those calculated daily from the soil carbon fluxes by the model. The model can explain approximately 96% of variance of the daily soil carbon fluxes calculated from daily average ST and SWC on sunny days. The relationship between measured and calculated daily soil carbon fluxes was also highly significant ($r^2 = 0.87$) on rainy days. However, on rainy days, measured soil carbon fluxes were significantly higher than calculated values. The relationship between the calculated and measured daily soil carbon flux on rainy days was expressed as follows:

Measured daily soil carbon flux (g CO_2-C m^{-2} d^{-1})

$$= 1.96 \times \text{calculated daily soil carbon flux} \quad (1)$$

Some causes of these post-rainfall increases in soil respiration rate have been suggested. One possible explanation is that post-rainfall increases in soil respiration rate are caused mainly by the increased microbial activity and/or population (Buyanovsky & Wagner 1983; Rochette *et al.* 1991; Borken *et al.* 1999). Borken *et al.* (1999) and Franzluebbers et al. (2000) indicated that increases of soil respiration rate following rewetting were most likely caused by enhanced activity of the decomposer community. There is some evidence that microbial biomass and activity are higher in surface soil layers than in deeper soil layers (Uchida *et al.* 1998; Mishima *et al.* 1999).

Importance of rainfall events on annual soil carbon flux

Annual soil carbon fluxes in 1999 and 2000 were estimated using models that both do and do not take rainfall effects into consideration. The result indicates that post-rainfall increases in soil CO_2 flux represent approximately 16-21% of the annual soil carbon flux in this cool temperate deciduous forest. The contribution of the post-rainfall increases to annual soil carbon flux depends on the amount of rainfall as well as the length of dry period between rainfalls, which vary with location. It is expected that the effect of rainfall is especially important in areas with frequent soil drying and rewetting. The results demonstrated that rainfall events make a significant influence on the annual soil carbon flux even in a cool temperate forest with abundant precipitation.

CHAPTERⅣ Seasonal Changes in the Contribution of Root Respiration to Total Soil Respiration

The contribution of root respiration to total soil respiration is difficult to determine, as reflected by the wide range of published estimates for forest soils (10 to 90%). The trenching method is relatively simple and its use is most common in forest ecosystems (Rochette *et al.* 1999; Hanson *et al.* 2000). In this method, disadvantage is the influence of residual decomposing roots left in the trenched plots and their contribution to soil respiration. Thus, trenching method can be modified using the root-bag method to eliminate the decomposition of the residual roots. In addition, to the contribution of root respiration to total soil respiration may change seasonally. Several studies have been differences between the growing season and the dormant season in the contribution of root respiration to total soil respiration (Edwards 1991; Rochette & Flanagan 1997). However, little information is available on seasonal changes in the contribution of root respiration to total soil respiration, especially for forest ecosystems. Seasonal changes in the contribution of root respiration rate ($\boldsymbol{R}_r$) to total soil respiration rate were examined.

A modified trenching method, in which part of the ground was cut vertically with a knife, was employed to eliminate the contribution of root respiration to soil respiration. Soil respiration rates in the trenched plot ($\boldsymbol{R}_{trench}$) and those in the control plot ($\boldsymbol{R}_{control}$) were measured from May 2000 to September 2001 using an open-flow gas exchange system with an IRGA. In addition, carbon emission through the decomposition rate of dead roots ($\boldsymbol{R}_D$) was estimated using the root-bag method. In order to estimate root biomass ($\boldsymbol{B}_r$), three plots (1m × 2m, 0.5 m in depth) were established 40-50 m apart from the control plot. The tree roots were classified into three size classes: fine ($\phi < 2$ mm), medium (2 mm < ϕ 10 mm) and thick (10 mm < ϕ). The Sasa roots were classified into subterranean stem or fine roots. Root samples collected in May 2000 were placed in bags made of 1áo nylon mesh to estimate the relative loss rate constant (k) in the soil. The bags used for the thick tree roots were 50 cm × 50 cm and the bags used for the other roots types were 25 cm × 25 cm. A total of 58 bags were prepared. They were buried at soil depth of 10-20 cm in May 2000, and the decrease of dry weight of the roots was measured at 83 and 181 days after the burial.

The soil respiration rates in the control plot increased from May to August, and then decreased during autumn. The soil respiration rates in the trenched plots showed a similar pattern of seasonal change, but the rates were usually lower than those in the control plot except during 2 months following the trenching. Root respiration rate ($\boldsymbol{R}_r$) and heterotrophic respiration rate ($\boldsymbol{R}_h$) were estimated from $\boldsymbol{R}_{control}$, $\boldsymbol{R}_{trench}$ and $\boldsymbol{R}_D$. There was a significant relationship between $\boldsymbol{R}_h$ and soil temperature, whereas $\boldsymbol{R}_r$ had no correlation with soil temperature. It was estimated that the contribution of $\boldsymbol{R}_r$ to total soil respiration in the growing season was within the range 27%-71%.

These values are similar to those reported for many forest ecosystems (Hanson *et al.* 2000). The data presented in this paper demonstrate that the pattern of seasonal change in $\boldsymbol{R}_r$ is somewhat different from that in $\boldsymbol{R}_h$. The root respiration rate was highest in early summer (June) and then decreased. In contrast, no marked reduction in $\boldsymbol{R}_h$ was observed at least in the summer season of 2001. The high root respiration rate in early summer may have resulted from the high physiological activity associated with root growth (growth respiration). The time period from mid-May through June is characterized by high root growth and root turnover (Edwards & Harris 1977; Joslin 1983). Hanson *et al.* (1993) found that the contribution of $\boldsymbol{R}_r$ to total soil respiration can change dramatically throughout an annual cycle as a result of changes in soil respiration rate associated with root construction costs. Ohashi *et al.* (2000) and Hogberg **et al**. (2001) suggest that root growth respiration, which is associated with the synthesis of new tissue, fluctuates irrespective of environmental conditions such as temperature. The data of the present study supported these studies. There was a significant relationship between $\boldsymbol{R}_h$ and soil temperature, whereas $\boldsymbol{R}_r$ had no correlation with soil temperature. These data suggest that the factors controlling the seasonal change of respiration are different between the two components of soil respiration, i.e. roots and heterotrophic organisms.

CHAPTER V Conclusions

Estimation of NEP (Net Ecosystem Productivity)

In this study, the NEP of the cool-temperate deciduous broad-leaved forest at Takayama Site was investigated. According to Koizumi *et al.* (unpublished) for this study area in the cool-temperate deciduous broad-leaved forest, the tree biomass of this study area was 129.6 t C ha^{-1} of aboveground and 26.8 t C ha^{-1} of belowground. The NPP was estimated as about 4.32 t C ha^{-1} yr-^{1} from tree (3.14 t C ha^{-}1 yr^{-1}) and emitted it from *Sasa* (1.18 t C ha^{-1} yr^{-1}). However, the contribution of root respiration to total soil respiration has been unknown in the cool-temperate deciduous forest stand. Soil respiration was estimated as about 5.61 t C ha^{-}1 yr^{-1} (average from 1994 to 1996), and root respiration was stimulated as approximately 2.52 t C ha^{-1} yr^{-1} (45% of total soil respiration). From the result, NEP was estimated approximately 1.23 t C ha^{-1} yr^{-1}. Therefore, the study area as a whole was estimated to act as a sink of carbon. According to flux tower result, the net uptake rate of carbon was 1.1 t C ha^{-1} yr^{-1} in 1994-1996 (Yamamoto et al. 1999).

In this study, a better assessment of the soil respiration and to understand the dynamic change of soil respiration in the cool-temperate deciduous broad-leaved forest at Takayama Site was investigated. First, the effects of rainfall events on the soil respiration rates were examined. Rainfall events caused a significant increase in soil respiration rate. The rates measured on rainy days were significantly higher than those calculated daily from the soil carbon fluxes by the model using the soil respiration rate data recorded on sunny days. Second, seasonal changes in the contribution of root respiration rate ($\boldsymbol{R}_r$) to total soil respiration rate were examined. The soil respiration rates in the trenched plots showed a similar pattern of seasonal change, but the rates were usually lower than those in the control plot except during 2 months following the trenching. It was estimated that the contribution of $\boldsymbol{R}_r$ to total soil respiration in the growing season was within the range 27%–71%.

This study has achieved remarkably in (1) to examine the effects of rainfall events on soil respiration, (2) to evaluate the dynamic of the post-rainfall increases in annual soil carbon flux, (3) to determine the seasonal changes in the contribution of root respiration to total soil respiration, (4) to seasonal estimation of the root respiration to total soil respiration in a cool-temperate deciduous broad-leaved forest, and (5) to clarify the carbon budget in the temperate forest ecosystem as a sink of carbon in a cool-temperate deciduous broad-leaved forest, in central Japan. These results may provide to improve the precision of future forest carbon estimation of forest ecosystem.