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# Contribution of root respiration to soil respiration in a C<sub>3</sub>/C<sub>4</sub> mixed grassland

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The spatial and temporal variations of soil respiration were studied from May 2004 to June 2005 in a C<sub>3</sub>/C<sub>4</sub> mixed grassland of Japan. The linear regression relationship between soil respiration and root biomass was used to determine the contribution of root respiration to soil respiration. The highest soil respiration rate of 11.54  $\mu\text{mol m}^{-2} \text{s}^{-1}$  was found in August 2004 and the lowest soil respiration rate of 4.99  $\mu\text{mol m}^{-2} \text{s}^{-1}$  was found in April 2005. Within-site variation was smaller than seasonal change in soil respiration. Root biomass varied from 0.71 kg m<sup>-2</sup> in August 2004 to 1.02 in May 2005. Within-site variation in root biomass was larger than seasonal variation. Root respiration rate was highest in August 2004 (5.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and lowest in October 2004 (1.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Microbial respiration rate was highest in August 2004 (5.8  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and lowest in April 2005 (2.59  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). We estimated that the contribution of root respiration to soil respiration ranged from 31% in October to 51% in August of 2004, and from 45% to 49% from April to June 2005.

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## 1. Introduction

Rising atmospheric CO<sub>2</sub> and temperature are probably altering ecosystem carbon cycling, causing both positive and negative feedbacks to climate. Below-ground processes play a key role in the global carbon cycle because they regulate storage of large quantities of C, and are potentially very sensitive to direct and indirect effects of elevated CO<sub>2</sub> and temperature (Norby and Jackson 2000). Grassland soils are high in soil organic carbon and contain an extensive fibrous root system that creates an environment ideal for soil microbial activity (Conant *et al* 2001). Soil respiration includes root respiration (autotrophic) and microbial respiration (heterotrophic) (Raich and Schlesinger 1992). These autotrophic and heterotrophic respiratory processes are likely to respond to the elevated CO<sub>2</sub> and temperature in different ways (Yazaki *et al*

2004). Therefore, the separation of root respiration and microbial respiration in soil is essential for a better understanding of ecosystem responses to global change.

Carbon net balance (NEP-net ecosystem productivity) in grassland ecosystems is determined as the difference between net primary production (NPP) of vegetation and heterotrophic respiration ( $R_h$ ) of soil. Therefore, separately estimating root respiration and microbial respiration is necessary for interpreting and partitioning NEP. The contribution of each component to soil respiration needs to be understood to evaluate implications of environmental change on soil carbon cycling and sequestration (Hanson *et al* 2000).

The studies of root respiration in large part dealt with forest ecosystems and included the instructive work of Lee *et al* (2003), Masaki *et al* (1998), Mizue *et al* (2000) and Werner *et al* (2001). The approaches for separating

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root and soil microbial contributions to soil respiration in forest ecosystems have been reviewed by Hanson *et al* (2000). In contrast to the relative abundance of published data in forest ecosystems, relatively few studies have been focused on the contribution of root respiration to soil respiration in grassland ecosystems.

In this study, soil respiration and root biomass were measured from May 2004 to June 2005 in a C<sub>3</sub>/C<sub>4</sub> mixed grassland of Japan. We established a linear regression relationship between soil respiration and root biomass. Extrapolation of the regression line yields a y-intercept, which represents microbial respiration in the absence of root. Furthermore, root respiration was estimated by the differences between soil respiration and microbial respiration.

## 2. Materials and methods

### 2.1 Study site

The study site is located at a permanent grassland observation field at the Terrestrial Environmental Research Center, University of Tsukuba (36°06'N, 140°06'E, 27.0 m asl). The field is circular with a diameter of 160 m (approximately 20,000 m<sup>2</sup>) and has a 30 m tall scaffolding observation tower at the center to monitor long-term meteorological and hydrological processes. The study site is in a zone of marine humid climate characterized by a pronounced plum rain season, a period (mid-June to late-July) with continuous rainy and cloudy days. The mean annual air temperature recorded at this center from 1982 to 2001 was 14.1°C. Mean annual precipitation was 1207 mm. The maximum value of daily accumulative evapotranspiration was 6.7 mm d<sup>-1</sup> (Li *et al* 2003). The predominant wind direction is from south to north in summer and vice versa in winter. The parent material of the soil at the site is volcanic ash, light brown in colour.

The grassland vegetation is composed of 54 perennials (46 C<sub>3</sub> species and 8 C<sub>4</sub> species). C<sub>3</sub> species, mainly *Solidago altissima* and *Festuca arundinacea*, dominate the early part (April and May) of the growing season when air temperature is low, and C<sub>4</sub> species, mainly *Imperata cylindrica* and *Miscanthus sinensis*, dominate in mid-summer and autumn when air temperature is high (Tanaka and Oikawa 1999). The grassland is managed by mowing once a year in late autumn or winter when most of aboveground parts of vegetation are dead.

### 2.2 Soil respiration

**2.2a Diurnal change of soil respiration:** Soil respiration was measured at two hour intervals from 06:00 to 18:00 using a dynamic chamber method on June 5, 2005.

Soil temperature at 10 cm depth was measured with a soil temperature probe, connected to the LI-6400, at the same time as the measurements of soil respiration were made.

**2.2b Seasonal change of soil respiration:** Soil respiration was measured on May 26, August 8 and October 29 2004 and April 15, May 10 and June 5, 2005. The soil respiration rate was determined using dynamic closed chamber method with an LI-6400 (Li-Cor, NB, USA) fitted with a soil respiration chamber (LI-6400-09; LiCor). The measurements of soil respiration were made using a soil collar inserted 3 to 4 cm into the soil as an interface between the soil and the chamber. Ten collars were installed at least 24 h prior to measurement for each time. Litter was removed one day before the measurement. An individual measurement took a maximum of 5 min to carry out and the time differences between site measurements were approximately 10 min. All the measurements for each time were conducted between 10:00 and 12:00 h to minimize the impact of the diurnal variation in soil respiration. Soil temperature at 10 cm depth was measured with a soil temperature probe, connected to the LI-6400, at the same time as the measurements of soil respiration were made. Volumetric soil water content at 10 cm depth was measured using a hydrosense soil moisture meter (Cambell Scientific, Inc. Logan, UT).

### 2.3 Microbial biomass carbon, total carbon and nitrogen contents of the soil

Microbial biomass carbon, total carbon and nitrogen contents of the soil were measured on May 26, August 8 and October 29, 2004. Microbial biomass carbon of the soil was measured by chloroform fumigation-extraction procedure (Joergensen 1996). Ten soil cores at 10 cm depth were taken near the location for soil respiration measurements in each sampling time. Soil was passed through a 2 mm mesh sieve to separate roots and debris. Soil moisture content was adjusted to 55% of the water-holding capacity. After the pre-incubation at 25°C for 10 days, sieved 50 g soil samples were placed in a 100 ml beaker and a 250 ml HDPE bottle for the fumigated and control samples, respectively. The fumigated samples were incubated in ethanol-free chloroform in evacuated desiccators for 24 h at 25°C. The fumigated and control samples were extracted with 100 ml of 0.5 M K<sub>2</sub>SO<sub>4</sub>, shaken for 1 h, and filtered through Whatman No. 42 filter paper into 60 ml HDPE bottles. Dissolved organic carbon (DOC) was analysed using a Phoenix 8000 auto-analyser (Takmar-Dormann, Cincinnati, OH, USA). A correction factor (0.45) was used to convert DOC to microbial biomass carbon, which also accounted for the efficiency of extracting DOC and lyses by fumigation (Joergensen 1996).

Microbial biomass carbon was then calculated from the following equation:

$$\text{Microbial biomass carbon} = (\text{Carbon in fumigated soil} - \text{Carbon in non-fumigated soil})/K_{EC}$$

The soils from the ten cores close to soil respiration chambers for each time were dried at 31°C for 72 h, crushed to pass a 2 mm sieve, ground to 200 µm, and stored in glass bottles. Total carbon and nitrogen contents were determined by dry combustion using a Carlo Erba model NA 1500 automatic carbon-nitrogen analyser (Hake Buckler Instruments, Inc., Saddle Brook, NJ, USA).

#### 2.4 Estimation of root respiration

Root biomass was measured on May 26, August 8 and October 29, 2004 and April 15, May 10 and June 5, 2005. The root biomass was estimated by collecting soil samples at 10 cm depth from the same location where the soil respiration was measured. The roots were washed in tap water, oven dried (70°C), and weighted. The CO<sub>2</sub> attributable to roots and microorganisms were apportioned following the regression method (Behara *et al* 1990), in which soil respiration was plotted against root biomass. A regression line between the two has a y-intercept, which estimates the respiration in the absence of root, i.e. microbial respiration. Root respiration can be estimated by the differences between soil respiration and microbial respiration.

#### 2.5 Statistical analysis

Coefficient of variation (CV) was calculated to provide a measure of within-site variation of soil respiration, soil temperature, soil moisture content, root biomass, microbial biomass carbon, and total carbon and nitrogen contents of the soil. Linear regression was used to establish the relationship between soil respiration and root biomass. Significance was defined as at the 95% confidence level. All the statistical analyses were performed with SPSS 10 (SPSS Science, Birmingham, UK).

### 3. Results

#### 3.1 Spatial and temporal variation of soil respiration rate and root biomass

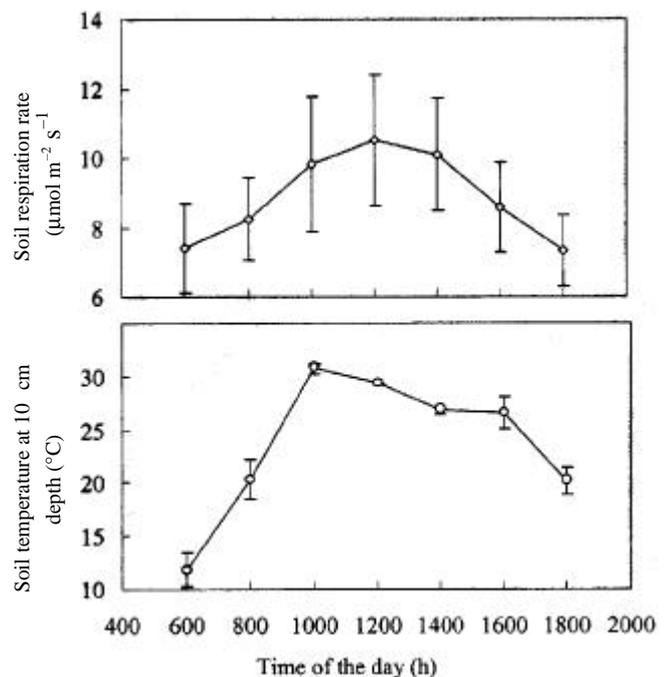
Soil respiration rate was highest at 12:00 (10.53 µmol m<sup>-2</sup> s<sup>-1</sup>) and lowest at 18:00 (7.3 µmol m<sup>-2</sup> s<sup>-1</sup>) during a daytime (figure 1). Spatial variations among soil collars were large. Within-site differences of soil respiration among replicated collars were up to 5.7 µmol m<sup>-2</sup> s<sup>-1</sup> and diurnal variations were 6.3 µmol m<sup>-2</sup> s<sup>-1</sup>. During the 12 h

period, soil temperature at 10 cm depth was highest at 10:00 and lowest at 06:00.

Seasonal variations of the soil respiration rate were greater than within-site spatial variations (table 1). Soil respiration rate was highest in August (11.54 µmol m<sup>-2</sup> s<sup>-1</sup>) and lowest in April (4.99 µmol m<sup>-2</sup> s<sup>-1</sup>). Soil temperature showed the same pronounced temporal pattern as the soil respiration rate. In contrast, soil moisture content at upper 10 cm showed a different pattern from soil temperature, with the highest value of 48% in May 2004 and the lowest value of 21% in June 2005. Within-site variation in root biomass was larger than seasonal variation (table 1). Root biomass varied from 0.71 kg m<sup>-2</sup> in August 2004 to 1.02 in May 2005. Our samples of root biomass were from 0–10 cm soil layer. More than 90% of the total root biomass at the site distributed within 50 cm soil depth (Liu *et al* 2004). The root biomass at upper 10 cm depth accounted for 70% of that within 50 cm soil depth (Liu *et al* 2004).

#### 3.2 Spatial and temporal variability of microbial biomass carbon, total carbon content and total nitrogen content of the soil

Microbial biomass carbon was higher in May (2.3 g C m<sup>-2</sup>) than those in October (1.5 g C m<sup>-2</sup>) and August (1.2 g



**Figure 1.** Diurnal changes of soil respiration rate and soil temperature at upper 10 cm depth. Means and standard deviations were given ( $n = 10$ ). Collars were installed 24 h prior to measurement.

**Table 1.** Seasonal and within-site variations of SR, ST, VSWC, and RB in a C<sub>3</sub>/C<sub>4</sub> mixed grassland.

Date	2004				Date	2005			
	SR	ST	VSWC	RB		SR	ST	VSWC	RB
May 26	7.54 ± 1.4 (CV = 19)	18.6 ± 0.4 (CV = 2)	48 ± 3.0 (CV = 6)	0.72 ± 0.20 (CV = 28)	Apr. 15	4.99 ± 1.0 (CV = 20)	10.4 ± 0.4 (CV = 4)	46 ± 4.0 (CV = 9)	0.81 ± 0.2 (CV = 25)
Aug. 8	11.54 ± 2.3 (CV = 20)	36 ± 0.6 (CV = 2)	26 ± 2.0 (CV = 8)	0.71 ± 0.18 (CV = 25)	May 10	6.27 ± 1.2 (CV = 19)	15.3 ± 0.5 (CV = 3)	24 ± 2.0 (CV = 8)	1.02 ± 0.3 (CV = 29)
Oct. 29	5.41 ± 0.9 (CV = 17)	11 ± 0.6 (CV = 5)	45 ± 4.0 (CV = 9)	0.83 ± 0.19 (CV = 23)	Jun. 5	10.53 ± 1.9 (CV = 18)	22.6 ± 0.6 (CV = 3)	21 ± 2.0 (CV = 10)	1.01 ± 0.3 (CV = 30)

Data are mean ± standard deviation. Ten measurements were averaged for each data. Coefficient of variation was calculated to describe within-site variations.

SR, soil respiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ); ST, soil temperature at 10 cm depth ( $^{\circ}\text{C}$ ); VSWC, volumetric soil water content (%); RB, root biomass ( $\text{kg m}^{-2}$ ); CV, coefficient of variation (%).

$\text{C m}^{-2}$ ). The highest within-site variation of microbial biomass carbon was found in August. Soil total carbon content in May ( $69.5 \text{ g C kg}^{-1}$ ) was similar to that in August ( $69.8 \text{ g C kg}^{-1}$ ), but higher than that in October ( $60.1 \text{ g C kg}^{-1}$ ). Within-site spatial variation of soil total carbon was up to  $27.2 \text{ g C kg}^{-1}$ , whereas, the biggest temporal difference among the three months was  $9.7 \text{ g C kg}^{-1}$ . Soil total nitrogen content was higher in August ( $3.3 \text{ g N kg}^{-1}$ ) than those in October ( $2.6 \text{ g N kg}^{-1}$ ) and in May ( $1.5 \text{ g N kg}^{-1}$ ). The highest within-site variation of soil total nitrogen content was found in August (table 2).

### 3.3 Estimation of the contribution of root respiration to soil respiration

**3.3a Diurnal change in the contribution of root respiration to soil respiration:** The relationship between soil respiration rate and root biomass was described by the linear regression equation (table 3). By this regression line, we estimated the root respiration fraction in the total soil respiration, which varied from 42% at 14:00 h to 56% at 18:00 h with an average of 50% (table 3).

**3.3b Seasonal change in the contribution of root respiration to soil respiration:** The linear regression relationships between soil respiration and root biomass were established (figure 2). Soil respiration was significantly positively related to root biomass for each measuring periods ( $P < 0.05$ , table 4). Approximately 41% to 50% of variation in soil respiration could be explained by the variability in root biomass (table 4). Root respiration rate was highest in August ( $5.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and lowest in October ( $1.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Microbial respiration rate was highest in August ( $5.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and lowest in April ( $2.59 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) (figure 3). The contribution of root respiration to soil respiration ranged from 31% in

**Table 2.** Temporal and within-site variations of microbial biomass carbon ( $\text{g C m}^{-2}$ ), total carbon ( $\text{g C kg}^{-1}$ ) and total nitrogen ( $\text{g N kg}^{-1}$ ) of the soil.

Date	Microbial biomass carbon	Total carbon	Total nitrogen
May 26	2.3 ± 0.5 (CV = 22)	69.5 ± 10 (CV = 14)	1.5 ± 0.3 (CV = 20)
Aug. 8	1.2 ± 0.3 (CV = 25)	69.8 ± 8.7 (CV = 12)	3.3 ± 1.1 (CV = 33)
Oct. 29	1.5 ± 0.3 (CV = 20)	60.1 ± 13.6 (CV = 23)	2.6 ± 0.7 (CV = 27)

Data are expressed as mean ± standard deviation, averaged from 10 measurements. CV, coefficient of variation (%).

October to 51% in August of 2004, and from 45% to 49% from April to June 2005 (figure 3).

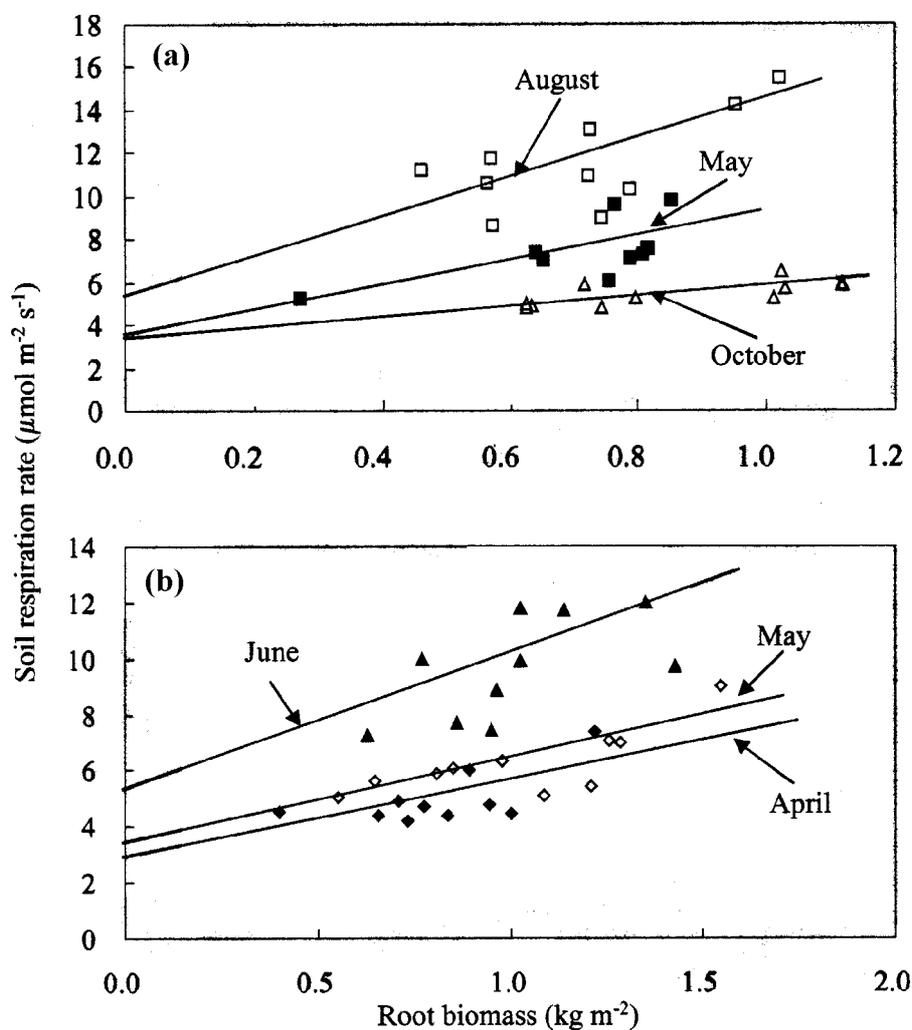
## 4. Discussion

Some attempts have been made to estimate the contribution of root respiration to soil respiration in grassland ecosystems including the work reported for grasslands in Nebraska (15–70%, Norman *et al* 1992), a tallgrass prairie in Texas (90%, Dugas *et al* 1999), a tallgrass prairie in Missouri (40%, Kucera and Kirkham 1971), a tropical grassland at Kurukshetra (42%, Gupta and Singh 1981), a grazed grassland in China (24%, Li *et al* 2002) and a *M. sinensis* grassland in Japan (22–53%, Yazaki *et al* 2004). The ratio between root respiration and microbial respiration is generally quite site-specific and varies between 1 : 9 and 9 : 1 (Hanson *et al* 2000). We compared our results with those obtained in similar grassland ecosystems (table 5). Compared with *M. sinensis* grassland in

**Table 3.** Regression equations between soil respiration (*Y*) and root biomass (*x*) over the course of a daytime.

Hours	Equations	R <sup>2</sup>	MR	RR	RC
06:00	$Y = 4.19x + 3.3$	0.67*	3.3	4.1	55
08:00	$Y = 3.69x + 4.5$	0.59*	4.5	3.74	45
10:00	$Y = 4.42x + 5.16$	0.36*	5.16	4.67	48
12:00	$Y = 5.12x + 5.34$	0.44*	5.34	5.19	49
14:00	$Y = 4.19x + 5.84$	0.42*	5.84	4.26	42
16:00	$Y = 4.41x + 4.08$	0.71*	4.08	4.48	52
18:00	$Y = 3.66x + 3.2$	0.48*	3.2	4.1	56

Microbial respiration was estimated by the intercept of the regression equation. Root respiration was calculated by the differences between soil respiration and microbial respiration. MR, Microbial respiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ); RR, root respiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ); RC, root respiration contribution (%). Degrees of freedom for all the above equations were 9. \* $P < 0.05$ .



**Figure 2.** Relationship between soil respiration and root biomass ( $n = 10$ ) in (a) 2004 and (b) 2005. Microbial respiration rate was estimated by the intercept of the regression line. Root respiration rate was calculated by the differences between soil respiration rate and microbial respiration rate.

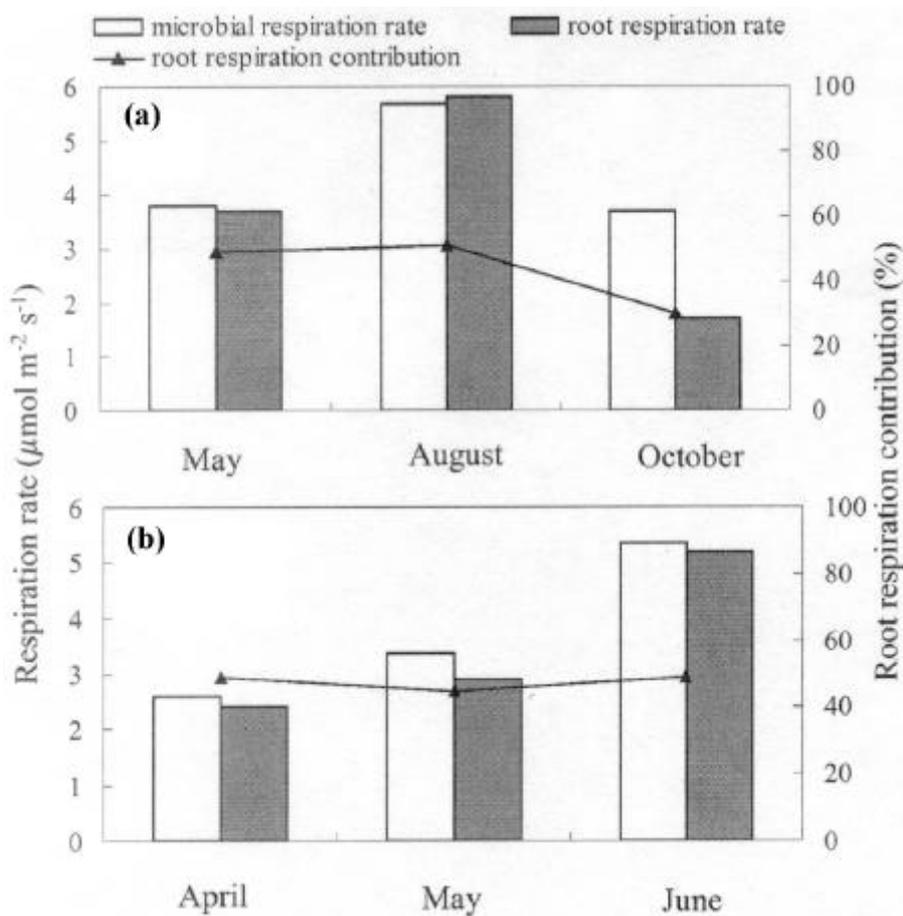
Japan, our study site has more precipitation and higher air temperature. The shorter life cycle of above-ground plant growth in the *M. sinensis* grassland, makes heterotrophic processes the principal source of carbon respired in spring and summer, whereas, in September, the larger contribution of root respiration to soil respiration may result from the high respiratory activity associated with

the increase in the below-ground biomass. The contribution of root respiration to soil respiration was 45%–51% from April to August in our study site, while in late October the lower respiratory activity of root makes microbial respiration the dominant fraction of soil respiration. Our study site has similar annual mean air temperature and precipitation to those in *Solidago altissima* grassland.

**Table 4.** Regression of soil respiration  $Y$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) as a function of root biomass  $X$  ( $\text{kg m}^{-2}$ ).

2004					2005				
Date	Regression equation	Intercept	Slope	$R^2$	Date	Regression equation	Intercept	Slope	$R^2$
May 26	$Y = 5.14x + 3.79$	$3.79 \pm 1.62$	$5.14 \pm 2.0$	0.41*	Apr. 15	$Y = 2.95x + 2.59$	$2.59 \pm 1.01$	$2.95 \pm 1.19$	0.44*
Aug. 8	$Y = 8.03x + 5.71$	$5.71 \pm 2.41$	$8.03 \pm 3.1$	0.44*	May 10	$Y = 2.83x + 3.37$	$3.37 \pm 0.95$	$2.83 \pm 0.89$	0.50*
Oct. 29	$Y = 2.05x + 3.7$	$3.7 \pm 0.64$	$2.05 \pm 0.9$	0.48*	Jun. 5	$Y = 5.12x + 5.33$	$5.33 \pm 2.11$	$5.12 \pm 2.03$	0.44*

Data are expressed as mean  $\pm$  standard error.  
 Degrees of freedom for all the above equations were 9.  
 \* $P < 0.05$ .



**Figure 3.** Seasonal changes in root respiration rate, microbial respiration rate and the contribution of root respiration to soil respiration in (a) 2004 and (b) 2005.

**Table 5.** Estimates of root respiration contribution (RC) to soil respiration by vegetation type and experimental approach. The time step for which the data are applicable (a, annual and gs, growing season) are also provided.

Vegetation type	Location	Approach	RC (%)	References
<i>Solidago altissima</i> (C <sub>3</sub> ) grassland	Ikeda campus of Osaka Kyoiku University	Trenching method	38% (a)	Yoneda and Okata 1987
<i>Miscanthus sinensis</i> (C <sub>4</sub> ) grassland	Campus of Sugadaira Montane Research Center, University of Tsukuba (36°31'N, 138°21'E, 1300 m asl)	Excised root	22–53% (gs)	Yazaki <i>et al</i> 2004
C <sub>3</sub> /C <sub>4</sub> mixed grassland	Terrestrial Environmental Research Center, University of Tsukuba (36°06'N, 140°06'E, 27.0 m asl)	Regression method	31–51% (gs)	This study

The annual contribution of root respiration to soil respiration was 38% in the *S. altissima* grassland. The contribution of root respiration to soil respiration during the growing season averaged 46% in our study site. Much lower contribution of root respiration to soil respiration has been found during the dormant season than the growing season (Rochette and Flanagan 1997). Therefore, the contribution of root respiration in the *S. altissima* grassland might be larger than our estimate. Some of this variability reflects differences among different types of grassland ecosystems and a considerable proportion of it probably originate from the variety of measurements method used.

Three primary methods have been reported to distinguish hetero-versus autotrophic soil respiration including integration of components *in situ* (i.e. litter, roots, and soil), trenching methods, and stable or radioactive isotope methods (Hanson *et al* 2000). A regression method was used to calculate root respiration from the linear relationship between soil respiration and root biomass in our study. Compared with other methods (see the review, Hanson *et al* 2000), the regression method is simple and inexpensive. The natural conditions for the growth of root and soil microorganism are not interrupted (Gupta and Singh 1981). Comparatively, the method can take multi-samples by placing many sampling collars simultaneously, and thereby reducing the bias caused by soil heterogeneity.

This regression method has two limitations. Firstly, this method assumes that root and microbial respiration rates are equally affected by temperature. However, root respiration may have different temperature sensitivity from microbial respiration (Boone *et al* 1998; Kirschbaum 1995; Lee *et al* 2003). The average contribution fraction of root respiration to soil respiration was 49% from 10 : 00 to 12 : 00, which is very close to the value (50%) averaged over the daytime from 06 : 00 to 18 : 00 (table 3). Therefore, our estimate of root respiration fraction in the soil respiration from 10 : 00 to 12 : 00 can represent

the mean situation of the day. Secondly, the regression method assumes that microbial respiration is independent of root biomass. However, the microbial respiration is influenced by root exudates and turnover (Kuzyakov *et al* 2000). Consequently, the method may increasingly overestimate root respiration with increasing root biomass. In addition, any change in root diameter with increasing biomass would also affect root respiratory rate when expressed on a mass basis (Gupta and Singh 1981).

The factors for controlling root respiration were very complex. Our present work can not illustrate the accurate mechanism for the seasonal change in the contribution of root respiration to soil respiration. Root respiration may fluctuate not only because of temperature but also because of the life cycle of the plants (Marshall and Perry 1987). The high variation of the share of root respiration shows that measurement of soil respiration alone is not sufficient to assess the contribution of soil carbon to the atmospheric CO<sub>2</sub>. Root respiration is very sensitive to changes in photosynthesis, and any alteration in the environmental factors affecting photosynthesis may be expected to affect root respiration (Kuzyakov and Cheng 2001). This also implies that one measurement per day is insufficient for accurate estimation of soil respiration under field conditions. Because the source of carbon for photosynthesis and root growth is periodic, the time of year when the study begins will in part determine the partitioning results.

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