管理されたC3寒地芝群落における呼吸CO2フラックスとその分離

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Partitioning of respiratory CO_2 fluxes in a managed C_3 turfgrass field

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Abstract

To evaluate the respiration and temperature dependence of each component of a managed C_3 cool-season turfgrass (Kentucky bluegrass, *Poa pratensis*) field and to elucidate the characteristics of the carbon budget, respiratory CO_2 fluxes from leaves, non-assimilatory organs, and decomposition (soil heterotrophic respiration) were measured using a closed dynamic chamber method. Analysis of temperature dependence using the Arrhenius function was performed for partitioning of the components of ecosystem respiration. The activation energy for respiration was 40,200 J mol^{-1} for non-assimilatory organs, 41,600 J mol^{-1} for leaves, and 69,800 J mol^{-1} for heterotrophic respiration. Total ecosystem respiration at 25℃ was 9.0 μmol m^{-2} s^{-1} in June 2006 and 8.2 μmol m^{-2} s^{-1} in August 2007. Leaf, non-assimilatory organ, and heterotrophic respiration at 25℃ was 1.7 (19%), 4.8 (53%), and 2.5 (28%) μmol m^{-2} s^{-1}, respectively, in June 2006, and 1.8 (22%), 4.1 (50%), and 2.3 (28%) μmol m^{-2} s^{-1}, respectively, in August 2007. A large proportion of non-assimilatory organ respiration coincided with the non-assimilatory organ biomass. At the study site, soil respiration as the sum of non-assimilatory organ and heterotrophic respiration formed 78-81% of the total ecosystem respiration, and the proportion of autotrophic respiration (non-assimilatory organ respiration) to total soil respiration was 64-66%. The total ecosystem respiration and soil respiration were very large in comparison with the values reported for other ecosystems.

Key words: Activation energy, Autotrophic respiration, Ecosystem respiration, Heterotrophic respiration, Temperature dependence.

1. Introduction

For the planning and maintenance of C_3 cool-season turfgrass fields in warm climates and transitional regions, evaluating the balance between temperature and plant carbon uptake (photosynthesis) and loss (respiration) is essential. The balance is evaluated as the difference between total carbon assimilation from photosynthesis and carbon loss from plant respiration (*i.e.*, from leaves, stems, and roots). A few studies have examined the depression of canopy photosynthesis and mass decline of C_3 turfgrass at high temperatures (Xu and Huang, 2000a, b, 2001a, b, 2003; Huang and Liu, 2003; Su *et al.*, 2007) and the partitioning of net photosynthesis, total ecosystem respiration, and soil respiration in a C_3 turfgrass field using chamber measurements (Bremer and Han, 2005). However, partitioning of the respiration rate for each component

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in relation to temperature has not been reported.

Total ecosystem respiration (leaf, stem, root, and the decomposition of soil organisms) can be estimated as the CO_2 efflux from the entire ecosystem at night or in the dark. CO_2 efflux from the soil surface (*i.e.*, soil respiration) is one of the largest components (Raich and Schlesinger, 1992). The partitioning of soil respiration into autotrophic (root) and heterotrophic (decomposition of soil organisms) respiration is necessary to separate the carbon lost through plant respiration from the total ecosystem respiration. Hanson *et al.* (2000) reviewed 50 studies and found that the integrated root contribution to total soil respiration throughout an entire year or growing season was 45.8% on average for forest vegetation and 60.4% for non-forest vegetation, but with considerable scatter, from less than 10% to more than 90%. For C_3 turfgrass and other types of vegetation, very few studies have partitioned ecosystem respiration based on direct flux measurements of every component. To better understand and manage C_3 turfgrass fields, more information on each component of ecosystem respiration is required, as are comparisons with other types of vegetation.

The objective of this study was to evaluate the respiration rate and temperature dependence of each component of a C_3 turfgrass field, and to compare the results with other vegetation types to clarify the characteristics of ecosystem respiration in turfgrass fields.

2. Masterials and Methods

2.1 Site

This study was conducted at a turfgrass nursery (34°39'N, 134°10'E;<20 m a.s.l.) in Kobe, Hyogo Prefecture, Japan. Kentucky bluegrass (*Poa pratensis* L.) turf was established in the nursery in April 2004 on a 1:1 blend of decomposed granite soil (masa soil) and sand. The canopy was homogeneous and completely closed. Adequate water and soil nutrients (N:P:K= 30-40:20-30:35-45 g m^{-2}) were supplied during the growing season to prevent drought or nutrient stresses. The mowing height was approximately 0.03 m.

2.2 Measurements

Using a closed dynamic chamber method, total ecosystem, total soil (heterotrophic+non-assimilatory organ), heterotrophic, and non-assimilatory organ respiration in a well watered C_3 turfgrass field were measured with 'dark', 'clipped', and 'plant-excluding' chambers, and with 'extracted plant' samples, respectively. We conducted two types of observations as follows.

On 13-14 June 2006, nine 0.1×0.2×0.2 m chambers were set up in the field. Collars were installed on the morning of 13 June 2006. Within three of the nine chambers, whole-ecosystem respiration, including leaves, was measured under 'dark' conditions. In three other chambers, total soil respiration (*i.e.*, non-assimilatory organ and heterotrophic respirations) was measured after clipping of the leaves ('clipped' chambers). In the remaining three chambers, the entire plant was extracted from the soil and carefully washed in water. Heterotrophic respiration in the remaining was measured in situ. In these 'plant-excluding' chambers, soil organic matter and dead roots that were washed off of the extracted plants was not included; thus the 'plant-excluding' chambers measured only a partial and not the total amount of heterotrophic respiration. Following stabilization of the CO_2 efflux from the chambers, flux measurement began in the afternoon and continued into the next day. Extracted and washed living parts of the non-assimilatory organs (*i.e.*, 'extracted plants') were immediately placed into PP chambers (0.0009 m^3) and the CO_2 flux was measured. After completion of flux measurements, living and dead portions of the leaves and non-assimilatory organs were sampled from the nine plots, and the dry weight of each component was determined.

Another observation was conducted on 23-24 August 2007. In the morning on 23 August, we collected whole-vegetation samples using a hexagon-shaped large sampler (area: 0.02104 m^2, height :0.15 m). The soil bottom and side face of the three whole-vegetation samples were sealed with PP film and placed in separate PP chambers (0.0057 m^3). Flux measurement began in the morning on 23 August following stabilization of the CO_2 efflux from the disturbed samples and continued into the next day. Whole-ecosystem respiration, including leaves, was first measured in a 'dark' chamber. After that, the leaves were clipped and total soil respiration was measured in a 'clipping' chamber in the afternoon on 23 August. The soil water content was kept constant during all observation periods. Temperature fluctuations were tightly controlled; the range was smaller than that in our in situ experiments conducted in June 2006. In the morning on the next day, dead and living portions of the non-assimilatory organs were extracted from the samples and washed in water. The flux from the remaining soil was then

measured with a 'plant-excluding' chamber. Extracted and washed dead and living portions of the non-assimilatory organ were measured using a small PP chamber (0.0009 m^3). Flux measurement was done immediately after preparation of the washed samples. After measurements, the dry weights of the dead and living parts of the leaves and non-assimilatory organs were determined.

For in situ flux measurements, soil temperature at a depth of 0.01 m and the air temperature adjacent to the chamber were measured using thermistors (Thermo Recorder RT-10; Espec Mic Corp., Aichi, Japan). For the extracted samples, the organ or soil temperature was measured using a thermistor (RT-10) or a radiation thermometer (THI-500; Tasco Japan Co., Osaka, Japan).

The temperature dependences of each part of the non-assimilatory organs was measured by the oxygen electrode method. Non-assimilatory organs from the extracted plants were subdivided into four components: fine roots, lateral roots, subterranean stems, and terrestrial stems. The temperature dependence of respiration in three pieces (0.003-0.02 g dry weight) from each of the four components was measured by the oxygen electrode method using 6-ml dissolved oxygen electrodes (Rank Brothers Ltd., Cambridge, UK) at 5, 10, 15, 20, 25, 30, 35, 40, and 45℃. Samples were taken with a 0.05-m-diameter core sampler from neighboring plots between 13 June and 27 July 2006. The dry weight of each component from the subplot samples was measured.

The temperature dependence of leaf respiration on a leaf-area basis was measured in situ on three intact leaves using a portable photosynthesis system (CIRAS-2; PP Systems Inc., Hitchin, UK) on four occasions between February and November 2006 at 5, 10, 15, 20, 25, 30, 35, and 40℃. Leaf temperature was estimated from the energy budget using the CIRAS-2 system. The temperature range was dependent on the season.

2.3 Closed dynamic chamber system

The respiratory CO_2 flux was measured using an infrared gas analyzer (LI-840 and LI-820; LI-COR, Lincoln, NE, USA) equipped with a closed dynamic acrylic or PP chamber and PE tubing. After the chamber was closed and the CO_2 concentration in the chamber had stabilized, the CO_2 concentration was recorded every 2 s for 90 s; the respiration rate was calculated from the increase in the CO_2 concentration using a regression of the linear section of the record. The measurement periods were brief, and linearity was assessed for each measurement to avoid noise due to pressure artifacts or disturbances in the diffusion gradients (Davidson *et al.*, 2002). Periods of 20 or 60 s after the concentration began to increase linearly were used to calculate CO_2 flux, depending on the flux rate and linearity. The zero and span of the IRGA were calibrated in the laboratory before the field campaign.

The in situ acrylic chambers were 0.2 m tall and had stainless steel collars 0.1×0.2 m in size that were inserted 0.03 m into the soil (as in Kosugi *et al.*, 2010). At the time of measurement, the lid and midportion of the chamber were closed and air was circulated in a loop between the chamber headspace and IRGA at a flow rate of 1.0 L min^{-1} using a pump (MP-15CF; Shibata, Tokyo, Japan). Air was also circulated into another pumping line and dried through perchloric acid magnesium to prevent the accumulation of water vapor in the chamber.

The CO_2 flux of the extracted samples was measured using box-type PP chambers (0.0057 or 0.0009 m^3) with a similar system but without an air-drying line.

2.4 Optimization procedure

Analysis using the Arrhenius function of temperature dependence was performed for the partitioning of each component of ecosystem respiration as follows:

$$f(T_k) = R_{25} \cdot \exp\left[\left(1 - \frac{T_{ref}}{T_k}\right) \cdot \frac{\Delta H_a}{RT_{ref}}\right],$$

where $f(T_k)$ is respiration at a given temperature T_k (K), R_{25} is the reference respiration (μmol m^{-2} s^{-1}) at a reference temperature T_{ref} (298 K), R is the gas constant (8.314 Pa m^3 mol^{-1} K^{-1}), and ΔH_a is the activation energy (J mol^{-1}). R_{25} indicates the reference value for each component of respiration at 25℃, while ΔH_a represents the sensitivity of respiration to increasing and decreasing temperatures.

We calculated R_{25} (per unit land area, μmol m^{-2} s^{-1}) and ΔH_a for non-assimilatory organ, heterotrophic, leaf, total soil, and total ecosystem respiration. Total soil respiration is expressed as the sum of the non-assimilatory organ and heterotrophic respiration values, while total ecosystem respiration is expressed as the sum of non-assimilatory organ, heterotrophic, and leaf respiration. The optimization procedures for R_{25} and ΔH_a for each part were made as follows.

(a) Optimization of ΔH_a for non-assimilatory organ respiration using the results obtained by the dis-

solved oxygen electrode method. We calculated weighted averages using the results for each part of the non-assimilatory organs to obtain a single curve. This procedure also produces R_{25}; this value was not used in our later calculations. Calculating the absolute value of the respiration per unit dry weight using the oxygen electrode method is inadequate because this method measures the respiration in water, which is quite different from the original growth environment. Thus we refer only to the relative amplitude for each organ and optimized ΔH_a from this experiment (Fig. 2).

(b) Optimization of ΔH_a for leaf respiration using our CIRAS-2 leaf-area base gas exchange measurements. The leaf-area base R_{25} for leaf respiration was also optimized in this procedure; however, it was not used afterward, as this value is at the single-leaf scale and not at the canopy scale, which is required for partitioning (Fig. 3).

(c) Optimization of ΔH_a and R_{25} for partial heterotrophic respiration using the results obtained from the 'plant-excluding' chambers in June 2006 (see line [3] in Fig. 4). This ΔH_a value was assumed to be the ΔH_a for whole heterotrophic respiration.

(d) Optimization of R_{25} for partial heterotrophic respiration using the results obtained from the 'plant-excluding' chambers and ΔH_a for whole heterotrophic respiration, during July 2007 (see line [3] in Fig. 4).

(e) Optimization of R_{25} for non-assimilatory organ respiration using the results obtained for the 'extracted plant' samples and ΔH_a for non-assimilatory organ respiration, for June 2006 and July 2007 separately (see line [5] in Fig. 4).

(f) Optimization of R_{25} and ΔH_a for total soil respiration and R_{25} for whole heterotrophic respiration simultaneously, using our 'clipped' chamber results, and R_{25} and ΔH_a for non-assimilatory organ and partial heterotrophic respiration, for June 2006 and July 2007 separately (see lines [2] and [4] in Fig. 4).

(g) Optimization of R_{25} and ΔH_a for total ecosystem respiration and the land-area base value of R_{25} for leaf respiration, using our 'dark' chamber results, R_{25} and ΔH_a for total soil respiration, and ΔH_a for leaf respiration, for June 2006 and July 2007 separately (see line [1] in Fig. 4).

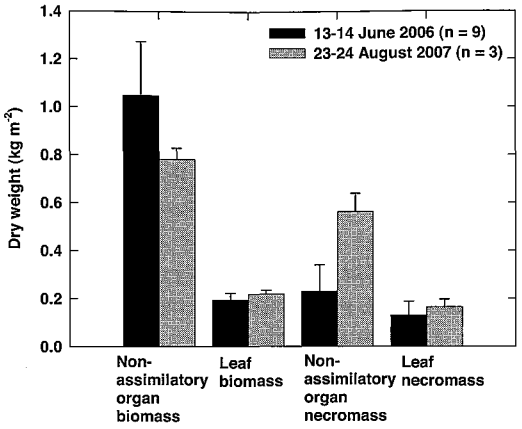

Fig. 1. The average and standard deviation of the dry weight of non-assimilatory organs, dead non-assimilatory organs, leaves, and dead leaves in nine chambers sampled on 13-14 June 2006 and in three chambers sampled on 23-24 August 2007 in a managed C_3 turfgrass (Kentucky bluegrass, *Poa pratensis*) field.

3. Results

3.1 Partitioning of the dry weight for each component

Fig. 1 shows the average and standard deviation of the dry weight of the non-assimilatory organs, dead non-assimilatory organs, leaves, and dead leaves from nine plots in June 2006 and three plots in August 2007. In June 2006, dry weight of non-assimilatory organs was 1.05±0.23 kg m^{-2} and formed 84% of the total biomass; the leaf biomass was 0.19±0.03 kg m^{-2} (16% of total biomass), the non-assimilatory organ necromass was 0.23±0.22 kg m^{-2}, and the leaf necromass was 0.13±0.06 kg m^{-2} (n=9). The non-assimilatory organ biomass consisted of 51% fine roots, 8% lateral roots, 16% subterranean stems, and 25% terrestrial stems in the subplot sample on 13 June 2006. In August 2007, the dry weight of non-assimilatory organs was 0.78±0.05 kg m^{-2} and formed 78% of the total biomass; the leaf biomass was 0.22±0.02 kg m^{-2} (22% of the total biomass), the non-assimilatory organ necromass was 0.56±0.08 kg m^{-2}, and the leaf necromass was 0.16±0.03 kg m^{-2} (n=3).

3.2 Temperature dependence of respiration for each component

The temperature dependence of respiration for fine roots, lateral roots, subterranean stems, and terrestrial

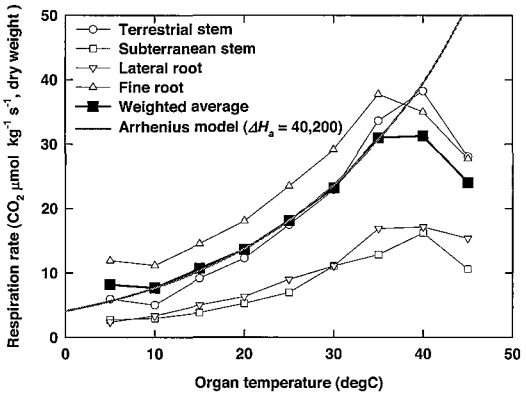

Fig. 2. Temperature dependence of fine roots, lateral roots, subterranean stems, and terrestrial stems of Kentucky bluegrass (*Poa pratensis*) as measured with the oxygen electrode method.

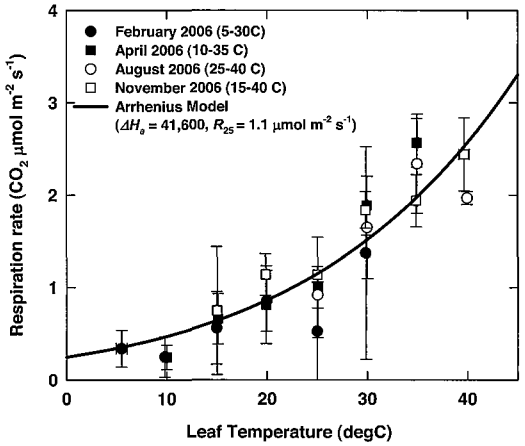

Fig. 3. Temperature dependence of intact leaves of Kentucky bluegrass (*Poa pratensis*) as measured using an in situ gas exchange method in darkened chambers four times between February and November 2006.

stems is shown in Fig. 2. A decline in respiration in all non-assimilatory organs occurred above 40℃. We still used the Arrhenius function to fit the temperature dependence, because 40℃ is perhaps beyond the upper temperature limit for the sample leaves. A weighted average temperature dependence curve was calculated from the ratio of the dry weight and temperature dependence for each of the four plant parts (Fig. 2). From the weighted average curve based on the ratio of the dry weight for each of the four parts, the activation energy (ΔH_a) was determined to be 40,200 J mol^{-1} for non-assimilatory organ respiration.

The temperature dependence of respiration in intact leaves was obtained from in situ gas exchange measurements collected in a darkened chamber between February and November 2006. The reference leaf respiration at 25℃ (R_{25}) at the single-leaf scale was 1.1 μmol m^{-2} s^{-1}, and the ΔH_a was 41,600 J mol^{-1} for intact leaves (Fig. 3).

Fig. 4 shows the measurements from the 'dark,' 'clipped,' and 'plant-excluding' chambers, as well as the measurements from the 'extracted plants' (*i.e.* non-assimilatory organs) in relation to the soil or organ temperature in June 2006 and August 2007. In June 2006, R_{25} for partial heterotrophic respiration (measured with the 'plant-excluding' chambers) was 1.1 μmol m^{-2} s^{-1}, and the ΔH_a was 69,800 J mol^{-1}. We used this ΔH_a for whole heterotrophic respiration. As mentioned above, the R_{25} value represents only a portion of heterotrophic respiration.

3.3 Partitioning of respiration for each component

Based on our measurements for 'extracted plants' (non-assimilatory organs) and using a ΔH_a value of 40,200 J mol^{-1} (derived from Fig. 2), R_{25} for the non-assimilatory organs was optimized to 4.8 and 4.1 μmol m^{-2} s^{-1} in June 2006 and August 2007, respectively. Line [5] in Fig. 4 shows the temperature dependence of non-assimilatory organ respiration, while line [3] in Fig. 4 shows the temperature dependence of partial heterotrophic respiration. Combining the non-assimilatory organ respiration (line [5]) with the whole heterotrophic respiration (line [3] * multiplier) yielded the soil respiration (line [2] in Fig. 4), which was measured in the 'clipped' chambers. Combining lines [3] and [5], we simultaneously estimated the optimum R_{25} for whole heterotrophic respiration (2.5 and 2.3 μmol m^{-2} s^{-1} in June 2006 and August 2007, respectively; line [4] in Fig. 4) and the temperature dependence curves for total soil respiration (line [2]). The optimized R_{25} for soil respiration was 7.3 and 6.4 μmol m^{-2} s^{-1} in June 2006 and August 2007, respectively, while ΔH_a was 50,400 and 52,300 J mol^{-1} in June 2006 and August 2007, respectively. Finally, we combined the temperature dependence curves for soil respiration (line [2]) and the leaves to obtain temperature dependence curves for the total ecosystem respiration (line [1]). A ΔH_a of 41,600 J mol^{-1}, as derived from Fig. 3, was used for the leaves. The R_{25} for the total ecosystem respiration was found to be 9.0 and 8.2 μmol m^{-2} s^{-1} in June 2006 and August 2007,

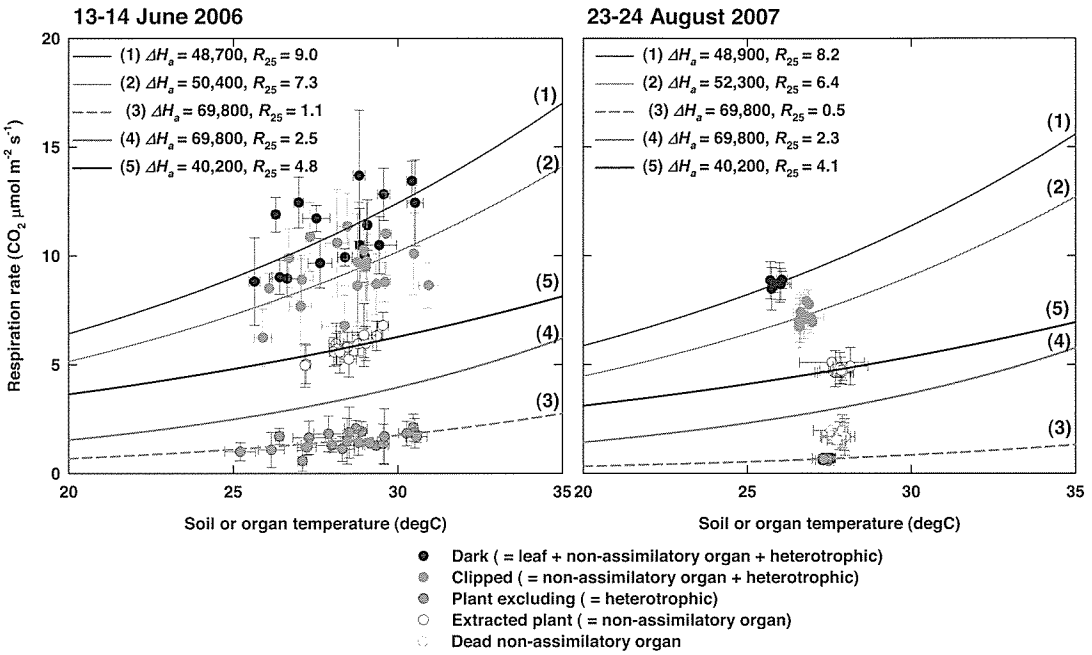

Fig. 4. Measurements made in June 2006 and August 2007 from 'dark', 'clipped', and 'plant-excluding' chambers in a Kentucky bluegrass (*Poa pratensis*) field, and from 'extracted plants' (*i.e.* non-assimilatory organs) in relation to soil or organ temperature. Lines show the optimized temperature dependence curves for (1) total ecosystem, (2) soil, (3) partial heterotrophic, (4) whole heterotrophic, and (5) non-assimilatory organ respiration.

Table 1. Optimized activation energy (ΔH_a, J mol^{-1}) and reference value at 25℃ (R_{25}, μmol m^{-2} s^{-1}) for the respiration of each component, and their partitioning as the result of two measurements at a managed C_3 turfgrass (Kentucky bluegrass, *Poa pratensis*) field in June 2006 and August 2007.

	July 2006			August 2007		
	ΔH_a (J mol^{-1})	R_{25} (μmol m^{-2} s^{-1})	Ratio (%)	ΔH_a (J mol^{-1})	R_{25} (μmol m^{-2} s^{-1})	Ratio (%)
Total ecosystem respiration	48,700	9.0	100	48,900	8.2	100
Soil respiration	50,400	7.3	81	52,300	6.4	78
Non-assimilatory organ respiration	40,200	4.8	53	40,200	4.1	50
Partial heterotrophic respiration	69,800	1.1	–	69,800	0.5	–
Whole heterotrophic respiration	69,800	2.5	28	69,800	2.3	28
Leaf respiration	41,600	1.7	19	41,600	1.8	22

respectively, while ΔH_a was calculated to be 48,700 and 48,900 J mol^{-1} in June 2006 and August 2007, respectively. The R_{25} for leaves at the canopy scale was simultaneously optimized through this procedure to 1.7 and 1.8 μmol m^{-2} s^{-1} in June 2006 and August 2007, respectively. The results of optimization and partitioning are listed in Table 1.

The partitioning of respiration at 25℃ was 19 and 22% for the leaves, 53 and 50% for the non-assimilatory organs, and 28 and 28% for soil decomposition in June 2006 and August 2007, respectively (Table 1).

4. Discussion

4.1 Temperature dependence

The respiration activation energy was 40,200 J mol^{-1} for non-assimilatory organs, 41,600 J mol^{-1} for leaves, and 69,800 J mol^{-1} for decomposition of dead roots and soil organic matter. Although data

are lacking concerning the activation energy for each plant component, Kosugi and Matsuo (2006) scanned the literature on the activation energy for plant leaves and found that it ranged widely from 9,593 J mol^{-1} in an evergreen conifer (*Pinus radiata* D.) to 95,400 J mol^{-1} in a deciduous broadleaf tree (*Quercus serrata* Thunb.) and 84,450 J mol^{-1} in cotton; no significant plant life-form-specific trend, however, was noted. For turfgrass, the calculated activation energies of 40,200 J mol^{-1} for respiration in non-assimilatory organs and 41,600 J mol^{-1} for respiration in leaves were very close to the median published values (41,500 J mol^{-1}). These values correspond to Q_{10} (temperature sensitivity) values of 1.73 and 1.77. The larger values (69,800 J mol^{-1}) produced for the decomposition of dead roots and soil organic matter suggest that the contribution of heterotrophic respiration is higher in summer.

4.2 Contribution of autotrophic respiration to soil respiration

Leaf, non-assimilatory organ, and heterotrophic respiration at 25℃ was 19-22, 50-53, and 28%, respectively. A large proportion of non-assimilatory organ respiration is consistent with that of the non-assimilatory organ biomass. Autotrophic respiration (*i.e.*, non-assimilatory organ respiration) to total soil respiration was 64-66%, which is close to the mean value for non-forest vegetation (60.4%; Hanson *et al.*, 2000), smaller than that found by Dörr and Münnich (1986) using ^{14}C-labeling of grass in winter (80%) and summer (98%), and larger than that found in a tallgrass prairie in Missouri (40%; Kucera and Kirkham, 1971), and a tropical grassland in Kurukshetra (42%; Gupta and Singh, 1981). We assume that the results of partitioning will change seasonally, as reported for a C_4 grassland (22-53%; Yazaki *et al.*, 2004), a C_3/C_4 mixed grassland in Japan (31-51%; Wang *et al.*, 2005), a managed grassland in southern Ireland (38-50%; Byrne and Kiely, 2006), a grassland in northeast China (25-76%; Wang *et al.*, 2007), and a deciduous broadleaf forest in Japan (25-60%; Dannoura *et al.*, 2006). Our results indicate that normalized non-assimilatory organ respiration was a little larger in June 2006 (4.8 μmol m^{-2} s^{-1}) than in August 2007 (4.1 μmol m^{-2} s^{-1}). This difference might have been caused by the difference in the non-assimilatory organ biomass between June 2006 (1.05 kg m^{-2}) and August 2007 (0.78 kg m^{-2}). At this site, both non-assimilatory organ biomass and total ecosystem respiration showed large seasonal variations (Kosugi *et al.*, 2010). These results strongly suggest that both the amount and partitioning of soil respiration change considerably with the seasons.

4.3 Contribution of soil respiration to total ecosystem respiration

At the study site, soil respiration as the sum of respiration from non-assimilatory organs and decomposition formed 78-81% of total ecosystem respiration, and non-assimilatory organ respiration, especially in fine roots, was the largest contributor to ecosystem respiration. Table 2 compares the total and each component of ecosystem respiration for various types of vegetation based on the chamber measurements. Previous studies using this method have estimated that soil respiration accounts for 46-61% of the total ecosystem respiration in C_3 turfgrass fields (Bremer and Han, 2005), 52% in an Amazonian rainforest (including coarse litter respiration; Chambers *et al.*, 2004), 48% in a temperate Japanese cypress (evergreen conifer) forest (Ohkubo *et al.*, 2007), 68% in a deciduous broadleaf forest (Goulden *et al.*, 1996), 77% in a ponderosa pine forest with a low LAI (1.5) (Law *et al.*, 1999), and 75-88% in three northern deciduous forests (Bolstad *et al.*, 2004). Seasonal fluctuations of 39-58% were reported in a Japanese cypress forest (Ohkubo *et al.*, 2007). The contribution of soil respiration to total ecosystem respiration at the C_3 turfgrass field in this study was close to the values reported for northern deciduous forests (Bolstad *et al.*, 2004) and larger than those for most forest ecosystems and other C_3 turfgrass fields (Bremer and Han, 2005).

4.4 Total ecosystem respiration and the contribution of each component

Total ecosystem respiration (8.2-9.0 μmol m^{-2} s^{-1}) and soil respiration (6.4-7.3 μmol m^{-2} s^{-1}) at 25℃ in this study were among the largest reported in the literature for the various ecosystems (Table 2; Raich and Schlesinger, 1992; Falge *et al.*, 2002; Kato and Tang, 2008). If we compare the results of this study with those reported for a tropical rainforest (Chambers *et al.*, 2004), summer data for a Japanese cypress forest (Ohkubo *et al.*, 2007), and summer data for a deciduous broadleaf forest (Goulden *et al.*, 1996), considering the temperature differences, the C_3 turfgrass field investigated in this study exhibited extremely high root respiration, a decomposition rate as high as a tropical rainforest (Chambers *et al.*, 2004), and leaf respiration similar to a cool-temperate forest (Goulden *et al.*, 1996). Total ecosystem respiration during the summer in this study was quite large despite its small biomass

Table 2. Ecosystem respiration and its partitioning based on chamber measurements for various types of vegetation in the literature.

Vegetation type		$R_{ecosystem}$	R_{soil}	R_{root}	$R_{heterotrophic}$	R_{trunk}	R_{foliar}	
Managed C_3 turfgrass field in Japan *Poa pratensis*	at 25℃ June 2006	9.0	7.3 (81)	4.8 (53)	2.5 (28)		1.7 (19)	This study
	at 25℃ August 2007	8.2	6.4 (78)	4.1 (50)	2.3 (28)		1.8 (22)	
Managed C_3 turfgrass field in Kansas *Lolium perenn*	Oct 2003	7.2	3.9 (54)				3.3 (46)	Bremer and Han (2005)
Managed C_3 turfgrass field in Kansas *Festuca arundinacea*	Oct 2003	7.7	4.7 (61)				3.0 (39)	Bremer and Han (2005)
Managed C_3 turfgrass field in Kansas *Poa pratensis*	Oct 2003	4.6	2.1 (46)				2.5 (54)	Bremer and Han (2005)
Managed turfgrass field in southern Ireland *Lolium perenne*	maximum	22			13			Byrne and Kiely (2006)
	annual average	6.2			3.5 (56)			
Managed grassland in Hokkaido, Japan (fertilizer plot) *Phalaris arundinacea*, *Alopecurus pratensis*	maximum		7.2	2.7	4.5			Shimizu *et al.* (2009)
	annual average		2.6	1.6	1.0			
C_4 grassland in Japan *Miscanthus sinensis*	July 2001		11.2					Yazaki *et al.* (2004)
	annual average		3.7	1.8	1.9			
C_3/C_4 mixed grassland in Japan	August 2004		11.5	5.7	5.8			Wang *et al.* (2005)
Undisturbed grassland in northeast China *Leymus chinensis*	June 2002		3.1	1.2	1.9			Wang *et al.* (2007)
	annual average		1.0	0.6	0.4			
Tropical rainforest	annual average	7.8	4.1 (52)	2.9 (24)	2.2 (28)	1.1 (14)	2.6 (33)	Chambers *et al.* (2004)
Japanese cypress	June-September	6.23	3.18 (51)			0.74 (12)	2.31 (37)	Ohkubo *et al.* (2007)
	annual average	3.84	1.84 (48)			0.48 (13)	1.52 (40)	
Mature red oak and red maple (50–70 years old)	June-September	6.5	4.4 (68)			0.3 (5)	1.8 (28)	Goulden *et al.* (1996)
Ponderosa pine	annual average	2.35	1.80 (77)			0.14 (6)	0.41 (17)	Law *et al.* (1999)
Northern hardwood	annual average	3.11	2.34 (75)			0.62 (20)	0.15 (5)	Bolstad *et al.* (2004)
Mature aspen	annual average	3.65	2.95 (81)			0.41 (11)	0.29 (8)	Bolstad *et al.* (2004)
Intermediate aspen	annual average	2.67	2.36 (88)			0.05 (2)	0.26 (10)	Bolstad *et al.* (2004)

Unit: μmol m^{-2} s^{-1} Proportion (%) of each flux to the total ecosystem respiration is shown in parentheses.

compared to forests.

In the case of grasslands, considerable scatter over the range of ecosystem respiration has been reported based on both the chamber (Table 2) and eddy covariance methods (Falge *et al.*, 2002; Xu and Baldocchi, 2004; Kato and Tang, 2008). For example, Raich and Schelesinger (1992) reported smaller annual soil respiration values for temperate grasslands (132-830 gC m^{-2} yr^{-1}). Smaller values were also reported in the recent literature (*e.g.*, for undisturbed grassland in northeast China, Wang *et al*, 2007). On the other hand, larger ecosystem or soil respiration values, as reported here, were reported during the summer in some managed grasslands (Bremer and Han, 2005; Byrne and Kiely, 2006; Shimizu *et al.*, 2009) and C_4 or C_3/C_4 grasslands (Yazaki *et al.*, 2004; Wang *et al.*, 2005). Small and large ecosystem respiration values have also been reported in studies with the eddy covariance method (Falge *et al.*, 2002; Xu and Baldocchi, 2004; Kato and Tang, 2008). This large scatter suggests that fertilization and management are among the main factors contributing to the large ecosystem and soil respiration values in

some grasslands, including our site, although Shimizu *et al.* (2009) showed that fertilization did not increase soil and heterotrophic respiration in a managed grassland in southern Hokkaido. Our site was located in a warm climate and transitional region for C_3 cool-season turfgrass; thus, high temperatures might be another trigger for large respiration values. We need much more data to compare and investigate what is the cause of the large scatter in ecosystem respiration of grasslands.

Our results suggest that non-assimilatory organ respiration is a key component in evaluating the carbon balance for planning and maintenance of C_3 cool-season turfgrass fields, especially in warm climates and transitional regions. For the annual estimation of respiration in each component and its influence on the carbon budget and seasonal growth/decline, we should consider both seasonal variations in leaf and root biomass and the temperature dependence of respiration for each component.

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References

Bolstad, P. V., Davis, K. J., Martin, J., Cook, B. D., and Wang, W., 2004: Component and whole-system respiration fluxes in northern deciduous forests. *Tree Physiol.*, **24**, 493–504.

Bremer, J. D., and Han, J. M., 2005: Measurement and partitioning of in situ carbon dioxide fluxes in turfgrasses using a pressurized chamber. *Agron. J.*, **97**, 627–632.

Byrne, K. A., and Kiely, G., 2006: Partitioning of respiration in an intensively managed grassland. *Plant and Soil*, **282**, 281–289.

Chambers, J. Q., Tribuzy, E. S., Toledo, L. C., Crispim, B. F., Higuchi, N., Santos, J. D., Araújo, A. C., Kruijt, B., Nobr, A., and Trumbore, S. E., 2004: Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecol. Appl.*, **14**, 72–88.

Dannoura, M., Kominami, Y., Tamai, K., Jomura, M., Miyama, T., Goto, Y., and Kanazawa, Y., 2006: Development of an automatic chamber system for long-term measurements of CO_2 flux from roots. *Tellus*, **58B**, 502–512.

Davidson, E. A., Savage, K., Verchot, L. V., and Navarro, R., 2002: Minimizing artefacts and biases in chamber-based measurements of soil respiration. *Agric. For. Meteorol.*, **113**, 21–37.

Dörr, H., and Münnich, K. O., 1986: Annual variations in the ^{14}C content of soil CO_2. *Radiocarbon*, **28**, 338–345.

Falge, E., Baldocchi, D., Tenhunen, J., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, C., Burba, G., Clement, R., Davis, K. J., Elbers, J. A., Goldstein, A. H., Grelle, A., Granier, A., Guðmundsson, J., Hollinger, D., Kowalski, A. S., Katul, G., Law, B. E., Malhi, Y., Meyers, T., Monson, R. K., Munger, J. W., Oechel, W., Paw U, K. T., Pilegaard, K., Rannik, Ü., Rebmann, C., Suyker, A., Valentini, R., Wilson, K., and Wofsy, S., 2002: Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agric. For. Meteorol.*, **113**, 53–74.

Goulden, M. L., Munger, J. W., Fan, S- M., Daube, B. C., and Wofsy, S. C., 1996: Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Global Change Biol.*, **2**, 169–182.

Gupta, S. R., and Singh, J. S., 1981: Soil respiration in a tropical grassland. *Soil Biol. Biochem.*, **13**, 261–268.

Hanson, P. J., Edwards, N. T., Garten, C. T., and Andrews, J. A., 2000: Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry*, **48**, 115–146.

Huang, B., and Liu, X., 2003: Summer root decline: production and mortality for four cultivars of creeping bentgrass. *Crop Sci.*, **43**, 258–265.

Kato, T., and Tang, Y., 2008: Spatial variability and major controlling factors of CO_2 sink strength in Asian terrestrial ecosystems: evidence from eddy covariance data, *Global Change Biol.*, **14**, 2333–2348.

Kosugi, Y., and Matsuo, N., 2006: Seasonal fluctuations and temperature dependence of leaf gas exchange parameters of co-occurring evergreen and deciduous trees in a temperate broad-leaved forest. *Tree*

Physiol., **26**, 1173–1184.

Kosugi, Y., Osaka, K., Itoh, M., Takanashi, S., and Matsubara, T., 2010: Photosynthesis and respiration of C_3 turfgrass fields under various light conditions. *J. Agric. Meteorol.*, **66**, 000–000.

Kucera, C. L., and Kirkham, D. R., 1971: Soil respiration studies in tallgrass prairie in Missouri. *Ecol.*, **52**, 912–915.

Law, B. E., Ryan, M. G., and Anthoni, P. M., 1999: Seasonal and annual respiration of a ponderosa pine ecosystem. *Global Change Biol.*, **5**, 169–182.

Ohkubo, S., Kosugi, Y., Takanashi, S., Mitani, T., and Tani, M., 2007: Comparison of the eddy covariance and automated closed chamber methods for evaluating nocturnal CO_2 exchange in a Japanese cypress forest. *Agric. For. Meteorol.*, **142**, 50–65.

Raich, J. W., and Schlesinger, W. H., 1992: The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus*, **44B**, 81–99.

Shimizu, M., Marutani, S., Desyatkin, A. R., Jin, T., Hata, H., and Hatano, R., 2009: The effect of manure application on carbon dynamics and budgets in a managed grassland of Southern Hokkaido, Japan. *Agric. Ecosyst. Environ.*, **130**, 31–40.

Su, K., Bremer, D. J., Keeley, S. J., and Fri, J. D., 2007: Effects of high temperature and drought on a hybrid bluegrass compared with Kentucky bluegrass and tall fescue. *Crop Sci.*, **47**, 2152–2161.

Wang, W., Ose, K. J., Liu, J. J., Mo, W. H., and Oikawa, T., 2005: Contribution of root respiration to soil respiration in a C_3/C_4 mixed grassland. *J. Biosci.*, **30**, 507–514.

Wang, W., Guo, J., and Oikawa, T., 2007: Contribution of root to soil respiration and carbon balance in disturbed and undisturbed grassland communities, northeast China. *J. Biosci.*, **32**, 375–384.

Xu, L., and Baldocchi, D. D., 2004: Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. *Agric. For. Meteorol.*, **1232**, 79–96.

Xu, Q., and Huang, B., 2000a: Growth and physiological responses of creeping bentgrass to changes in air and soil temperature. *Crop Sci.*, **40**, 1363–1368.

Xu, Q., and Huang, B., 2000b: Effects of differential air and soil temperature on carbohydrate metabolism in creeping bentgrass. *Crop Sci.*, **40**, 1368–1374.

Xu, Q., and Huang, B., 2001a: Morphological and physiological characteristics associated with heat tolerance in creeping bentgrass. *Crop Sci.*, **41**, 127–133.

Xu, Q., and Huang, B., 2001b: Lowering soil temperature improves creeping bentgrass growth under heat stress. *Crop Sci.*, **41**, 1878–1883.

Xu, Q., and Huang, B., 2003: Seasonal changes in carbohydrate accumulation for two creeping bentgrass cultivars. *Crop Sci.*, **43**, 266–271.

Yazaki, Y., Mariko, S., and Koizumi, H., 2004: Carbon dynamics and budget in a *Miscanthus sinensis* grassland in Japan. *Ecol. Res.*, **19**, 511–520.

管理されたC_3寒地芝群落における呼吸CO_2フラックスとその分離

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要　　約

C_3寒地芝(ケンタッキーブルーグラス, *Poa pratensis*)群落の各部呼吸の大きさ・割合および温度依存を調べ炭素収支の特徴を知るために，葉群呼吸，非同化部呼吸，および土壌有機物分解呼吸(従属栄養呼吸)によるCO_2フラックスを閉鎖循環式チャンバー法によって測定した。アレニウス式を用いた温度依存解析から各部の活性化エネルギーを求めたところ，非同化部呼吸について40,200 J mol^{-1}，葉群呼吸について41,600 J mol^{-1}，従属栄養呼吸については69,800 J mol^{-1}の値を得た。25℃で正規化した総生態系呼吸量は2006年6月で9.0 μmol m^{-2} s^{-1}，2007年8月で8.2 μmol m^{-2} s^{-1}であった。25℃で正規化した葉群，非同化部，および従属栄養呼吸はそれぞれ2006年6月には1.7 (19%), 4.8 (53%), 2.5 (28%) μmol m^{-2} s^{-1}，2007年8月には1.8 (22%), 4.1 (50%), 2.3 (28%) μmol m^{-2} s^{-1}となった。非同化部呼吸の割合が大きいことは，非同化部のバイオマス量の割合が多いことと一致した。非同化部呼吸および従属栄養呼吸の合計である土壌呼吸は生態系呼吸全体の78～81%を占め，このうち独立栄養呼吸分である非同化部呼吸は土壌呼吸の63～66%を占めた。対象としたC_3芝群落の生態系呼吸および土壌呼吸の大きさは，文献中にみられる様々な生態系の中でも非常に大きなものであった。

キーワード：温度依存，活性化エネルギー，従属栄養呼吸，生態系呼吸，独立栄養呼吸