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Components and seasonal variation of night-time total ecosystem respiration in a Japanese broad-leaved secondary forest

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ABSTRACT

The Yamashiro Experimental Forest is a broad-leaved secondary forest in Kyoto, Japan. On its complex terrain, low wind speed, high air stability, and local advection are common at night. To reduce the uncertainty in measuring woody-tissue respiration at night, we used automated stem chambers to measure stem respiration continuously (for 5 min at 30 min intervals) on stems of *Quercus serrata* Murr. (deciduous) and *Ilex pedunculosa* Miq. (evergreen) throughout 2003. Using these data, we estimated night-time respiration for the total ecosystem and its various components, and we report foliar and soil respiration rates for 2003. Annual average night-time respiration of soil, evergreen leaf, deciduous leaf, evergreen woody tissue and deciduous woody tissue were estimated as 0.0794 (63.2%), 0.0101 (8.0%), 0.0160 (12.7%), 0.0064 (5.1%) and 0.0137 (10.9%) mg CO_2 m^{-2} s^{-1}, respectively. The contribution of soil respiration to the total ecosystem respiration rate reached its minimum (49.1%) on 12 June (DOY 163) and its maximum (82.4%) on 29 November (DOY 333). Seasonal change of growth respiration was marked, indicating that the seasonal variation of growth respiration must be evaluated carefully to estimate total ecosystem respiration. Therefore, long-term continuous measurement using automated chambers and averaging provides an effective means of evaluating the annual night-time ecosystem respiration.

1. Introduction

The eddy covariance (EC) method has proved to be a successful tool for studying net ecosystem exchange of CO_2 in forest ecosystems (Baldocchi et al., 2001). However, uncertainties in the annual carbon balance arise from systematic underestimation of night-time flux measurements (Goulden et al., 1996). On the complex terrain of the Yamashiro Experimental Forest (YMS), a broad-leaved secondary forest in Kyoto, Japan, low wind speed and high air stability are common at night, such that sufficient mixing of air is often inhibited. Even when CO_2 storage is taken into account, there is still uncertainty about the accuracy of measurements of night-time respiration, caused by the effect of local advection (Kominami et al., 2005). In such cases, interpolation using the relationship between night-time CO_2 flux and temperature (usually an exponential curve) under appropriate turbulent transfer conditions is commonly used to fill data gaps. In many cases, usable data are chosen on the basis of the threshold value (e.g. friction velocity, u^*), which represents the stability of the atmosphere (Barford et al., 2001; Falge et al., 2001). In a previous study that used the EC method in the YMS (Kominami et al., 2005), the estimated night-time respiration increased as the threshold of u^* rose, but there were insufficient usable data (e.g. when u^* threshold was set to 0.3 m s^{-1}, there was 29% usable data). Moreover, in deciduous forests like the YMS, the relationship between respiration and temperature is suspected to change seasonally depending on phenological and biological

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factors (Lavigne et al., 1997). Thus, in the YMS it is necessary to evaluate the night-time total ecosystem respiration in each season using another method.

To estimate night-time total ecosystem respiration and growth respiration in the deciduous forest in 2003, we summed woody-tissue respiration and previously reported values of foliar respiration (Miyama et al., 2005) and soil respiration (Tamai et al., 2005a,b) gathered using the automated chamber method. In the present study, we measured night-time woody-tissue respiration of *Quercus serrata* Murr. (deciduous broad leaved) and *Ilex pedunculosa* Miq. (evergreen broad leaved) using automated stem chambers, which allow long-term continuous data to be measured in a forest under natural conditions. Bolstad et al. (2004) noted that scaling uncertainty of total ecosystem respiration may be particularly large for sapwood flux estimates. Thus, we scaled up woody-tissue respiration using measured allometric relationships rather than models (e.g. the pipe model; Chiba, 1998). Using the previously reported foliar and soil respiration data from the YMS and the new stem respiration data, in this study we estimated total night-time ecosystem respiration and partitioning and evaluated the seasonal characteristics of the total ecosystem respiration. Because the automated chamber system allows us to directly measure the seasonal change of growth respiration, we were able to analyse how the ecosystem respiration was controlled by growth respiration. In addition, we compared night-time total ecosystem respiration values estimated using the EC method and the automated chamber method.

2. Site Description and Methods

2.1. Site description

Deciduous and evergreen mixed broad-leaved forests grow widely in Japan. The YMS is located in a valley in Yamashirocho (34°47′N, 135°50,E; 220m a.s.l.), Soraku-gun, Kyoto, in a mountainous region of western Japan. The valley is underlain by weathering granites, and the soil layer is generally thin, immature, and sandy. The forest consists of more than 50 deciduous broad-leaved species (mainly *Quercus serrata*) and evergreen broad-leaved species (mainly *Ilex pedunculosa*).

The YMS is a typical mixed forest with a dramatic seasonal variation in CO_2 flux. For example, in a previous study (Miyama et al., 2005) we measured large increases of leaf area index (LAI) and growth foliar respiration in spring; biometric and optical techniques were used to measure biomass density, LAI, net primary productivity, and litter fall. Every 5 yr (from 1994) a census of diameter at breast height (DBH) of all trees (>3 cm) was done in the YMS (Goto et al., 2003). The census area of the study site is 1.7 ha. Based on these censuses, within the YMS the tree density was 5953 stems ha^{-1} and the total basal areas were 6.3 m^2 ha^{-1} for evergreen species and 13.3 m^2 ha^{-1} for deciduous species. The forest is composed of many small trees: the average DBH was only 7.4 cm. Based on the allometric relationship between DBH and biomass and the DBH census, deciduous trees accounted for 68% of the total aboveground biomass (52.53 $tCha^{-1}$).

Table 1. Characteristics of the automated stem chambers

Volume of chamber	910 cc.
Size of chamber	L20 × W15 × H3 (cm)
Material of chamber	Acrylic resin, 5 mm thickness
Gas analyser (IRGA)	LI-800 (Li-cor)
Precision	±2%
Method	Closed chamber method
Measurement time	3 min
Interval time	30 min
Circulation rate	1 L min^{-1}

2.2. Measurement of night-time stem respiration

To measure the night-time stem respiration, we installed two automated stem chambers on the north face of a *Q. serrata* (DBH: 17.4 cm) and an *I. pedunculosa* (DBH: 15.3 cm) on the bark at breast height in November 2002. This automated system was based on the automated foliage chamber described in Miyama et al. (2003). The two chambers automatically measured night-time stem respiration for 5 min at 30 min intervals. Table 1 lists the characteristics of the automated stem chambers, and Fig. 1 illustrates a chamber, showing the circulation and ventilation pumps, electromagnetic valve, programmable relay, and infrared CO_2 gas analyser (IRGA; LI-800, Li-Cor, Lincoln, NE, USA). The electromagnetic valves and pumps were controlled by a programmable relay (ZEN-10C1AR-A-V1, Omron, Japan). To minimize the risk of leaks, the system was lightly pressurized and tested once a month. The chamber was cleaned at least once a week, and the LI-800 was calibrated to 0 and 400 ppm CO_2 once a month.

In Fig. 1, white and black arrows indicate the air flow for the measurement and ventilation periods, respectively. During the measurement period, the inside air was circulated between the chamber (on the stem of *Q. serrata* or *I. pedunculosa*) and the IRGA for 5 min; for the next 25 min, the inside air was ventilated with the pump. The flow rates for circulation and ventilation were 1 and 8 L min^{-1}, respectively. The LI-800 is an absolute, non-dispersive IRGA based on a single-path, dual-wavelength infrared detection subsystem. The optical bench is maintained at a constant temperature of 52 °C by a heater. The heater and a desiccant ($CaCl_2$) minimize the influence of moisture. The air temperature in the chamber was measured with a copper-constantan thermocouple and collected by the data logger (NR-1000, Keyence, Japan) with the CO_2 gas density in the stem chamber every 10 s. The average value of eight data from 2200 to 0200 h was used for the analysis of the night-time stem respiration.

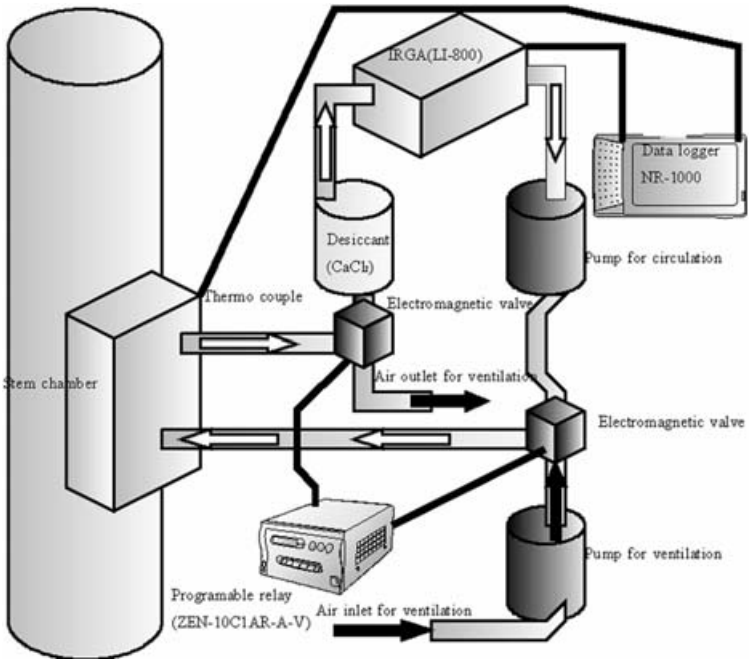

Fig. 1. Diagram of the stem chamber.

Stem respiration (F_{stem}) was calculated using the following equation:

$$F_{\text{stem}} = (\rho V/A)(\Delta c/\Delta t), \quad (1)$$

where ρ is the CO_2 gas density, V is the volume of the system, A is surface area of the stem in the chamber, and $\Delta c/\Delta t$ is the rate of increase of CO_2 concentration (c) with time (t). After the chamber starts circulation it takes 20 s for the change in air concentration to reach the IRGA, so $\Delta c/\Delta t$ was calculated from the difference in CO_2 concentration between 30 and 210 s (3 min).

Using two chambers, night-time stem respiration was measured continuously throughout 2003. However, lightning sometimes interrupted measurements by cutting off the electricity. The data covered 74.0% of the year and 92.8% of the growing season. The relationship between daily average night-time air temperature in the canopy at 10 m height (T_a) and in the stem chamber at 1.3 m height (T_{stem}) was evaluated in 2003. The relationship was linear [$T_a = 1.0017(T_{\text{stem}}) - 0.0494$, $R^2 = 1.00$], because sunlight had no influence on the air temperature at night. Moreover, the trees at our site were small. Thus, in this study we assumed both daily average night-time temperatures of woody tissue and leaf to be represented by T_a.

Continuous measurement of the DBH growth rate and the seasonal variation of the stem moisture at breast height were conducted as well. For the continuous measurement of stem growth, an inductance displacement meter (M-11-30S, Kyowa, Japan) was used; this meter allows the influence of changes in temperature to be reduced. A time domain reflectometry (TDR) soil moisture sensor (HYD-10, Stevens Vitel Inc., Chantilly, VA, USA) was used for the measurement of stem moisture. The TDR sensor was inserted into a hole drilled into the stem and covered with putty to reduce the influence of stem flow. These sensors were installed outside of the stem respiration chambers in November 2002.

2.3. Scaling up of night-time woody-tissue respiration

In most studies, estimates of whole-tree woody-tissue respiration rates are obtained by scaling up sample measurements acquired using chambers at one or more positions on the stems. Because high respiratory rates are observed at the cambium and phloem (Ryan 1990), the stem surface area beneath the chamber has often been used as an index of the amount of living tissue associated with the measured respiration rate (Kinelson, 1975; Landsberg 1986). Bolstad et al. (2004) reported that the stem respiration per unit area shows less variation than respiration per unit volume, probably because the latter includes the variation of heartwood volume. The stem respiration rate per unit area can be extrapolated to the entire surface area of the stem and from there to the whole forest. Because at our site there are few large stems (average DBH, 7.4 cm; Goto et al., 2003), the thickness of sapwood may be assumed to be nearly constant, and thus stand-level woody-tissue respiration would be closely related to surface area including all twigs. Thus, after confirming the linearity of the relationship between woody-tissue surface area and respiration rate using samples of different diameter, we estimated the relationship between DBH and the surface area of woody tissue per tree. We then estimated total surface area in the YMS using the DBH census data and scaled up the woody-tissue respiration to the whole forest.

To estimate the relationship between DBH and the surface area in the YMS, we evaluated the relationship between branch base diameter and branch surface area. In September 2004 we

destructively sampled 17 trees and measured branch base diameter, stem surface area and DBH. At the same time, we measured the surface area and respiration rate of woody-tissue samples of various diameters cut to 20 cm lengths, and we confirmed the linear relationship between branch surface area and woody-tissue respiration. At our site, there was no clear size difference between main stems and branches in broad-leaved trees. Therefore, we defined the stem as the part between the tree base and the top of the tree, and a branch as extending from the stem outward. We calculated the stem surface area using diameter measurements of the stem at intervals of 1 m. To calculate the relationship between branch base diameter and branch surface area, all branch base diameters and joint diameters of randomly sampled branches were measured with digital callipers (to the nearest 1 mm). To avoid the influence of extreme thickening of the joint, the length of all branches of 17 sampled trees was measured with a tapeline, and the branch base diameter was measured with a digital micrometer calliper at 10 equidistant positions along the length of the branch. Branch surface area (S) was calculated from the following equation:

$$S = \pi(r_1 + r_2)l, \tag{2}$$

where r_1 and r_2 are radii at the upper and lower joints, and l is the length between the joints. Using S data, we estimated the relationship between DBH and the surface area of woody tissue on the sample trees. We defined surface areas of woody tissue per tree from the sum of total S and measured stem surface areas.

2.4. Estimation of night-time total ecosystem respiration

We used the following equations to express night-time total ecosystem respiration (F_{eco}) in the YMS:

$$F_{wD} = F_{wQ}S_D, \tag{3}$$

$$F_{wE} = F_{wI}S_E, \tag{4}$$

$$F_{eco} = F_{wD} + F_{wE} + F_{fD} + F_{fE} + F_{soil}, \tag{5}$$

where F_{wD} and F_{wE} are the night-time woody-tissue respiration rates of deciduous and evergreen trees per unit ground area, respectively; F_{wQ} and F_{wI} are night-time respiration rates of woody tissue per unit woody-tissue surface area of *Q. serrata* and *I. pedunculosa* measured in the automated stem chambers; S_D and S_E (ha ha^{-1})are the surface areas of woody tissue per unit ground area of the deciduous and evergreen species estimated from a database of DBH values for the YMS; F_{fD} and F_{fE} are the corresponding night-time foliar respiration rates per unit ground area of the deciduous and evergreen species; and F_{soil} is night-time soil respiration per unit ground area. F_{fD} and F_{fE} (Miyama et al., 2005) and F_{soil} (Tamai et al., 2005a and 2005b) were measured using the chamber method in 2003. We assumed that the stem respiration of *Q. serrata* and *I. pedunculosa* were representative of deciduous and evergreen woody-tissue respiration; we then multiplied the respective night-time stem respiration values by the surface areas of deciduous or evergreen trees to estimate the forest-level night-time woody-tissue respiration.

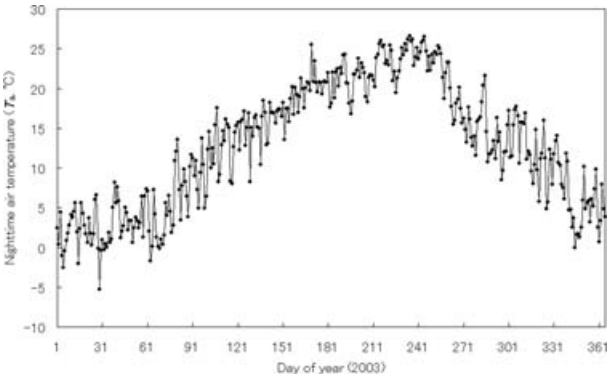

Fig. 2. Seasonal variation in air temperature (T_a).

To estimate CO_2 flux by the EC method, we built meteorological towers in the forest. A 26.5-m-high tower was situated along a ridge and equipped with an EC system using a three-dimensional ultrasonic anemometer (DAT-600-3TV, Kaijo, Japan) and a closed-path CO_2 analyser (LI-6262, Li-Cor). The sampling frequency was 10 Hz, and the EC was measured at the top of the meteorological tower (Kominami et al., 2005). In this study, we used night-time EC flux data (F_{EC}) obtained at the ridge tower from 1 January 2000 to 31 December 2003, and we compared these data with F_{whole} calculated from the chamber data. Using only the 2003 EC flux data to evaluate seasonal variation was not possible owing to insufficient usable data (<29%). Therefore, we used data from 4 yr (2000–2003) in which the weather conditions were similar to those of 2003. The annual average air temperatures ranged between 15.0 °C and 15.5 °C, and the 4 yr average was 15.2 °C ($SD = 0.20$); the average in 2003 was 15.0 °C.

3. Results and Discussion

3.1. Seasonal variation of night-time stem respiration

Figure 2 shows the seasonal variation of the night-time air temperature (T_a) in 2003. The maximum T_a was observed on 23 August (DOY 235) and the minimum on 29 January (DOY 29). Neither soil freezing nor drought was observed in 2003. Figure 3 shows the seasonal variation of cumulative DBH. *Quercus serrata* began growing earlier in the season than did *I. pedunculosa* and had a cumulative growth rate nearly three times as great. The growth rate of *Q. serrata* was high at the beginning of the growing season and decreased gradually, whereas the growth rate of *I. pedunculosa* was low at first and increased gradually.

Figure 4 shows the relationship between daily average night-time air temperature (T_a) and stem respiration of *Q. serrata* (F_{wQ}) and *I. pedunculosa* (F_{wI}), respectively. Using diameter growth rate data (Fig. 3), we estimated the growing season (DOY 123–249) and the dormant season (DOY 1–122, 250–365), and we analysed the relationship between T_a and night-time

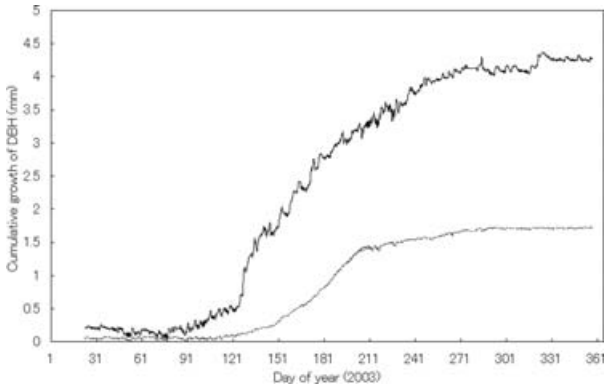

Fig. 3. Seasonal changes in cumulative growth of diameter in *Quercus serrata* (solid line) and *Ilex pedunculosa* (broken line) at breast height.

stem respiration during the dormant season. During the growing season, relatively high respiration was observed and there was a hysteretic relationship between T_a and night-time stem respiration of both trees. The equation for each relationship is as follows:

$$F_{wQm} = 0.0054 \exp(0.0593 T_a); (R^2 = 0.76), \quad (7)$$

$$F_{wIm} = 0.0030 \exp(0.0979 T_a); (R^2 = 0.90), \quad (8)$$

$$F_{wQ} = F_{wQm} + F_{wQg}, \quad (9)$$

$$F_{wI} = F_{wIm} + F_{wIg}, \quad (10)$$

where F_{wQm} and F_{wIm} are night-time stem respiration values in the dormant season, representing maintenance woody-tissue respiration of *Q. serrata* and *I. pedunculosa*, respectively; F_{wQg} and F_{wIg} are growth woody-tissue respiration of the species; and F_{wQ} and F_{wI} are the sum of maintenance respiration and growth respiration. We assumed the respiration estimated for the dormant season to be maintenance respiration, and we defined the difference between the total respiration and the maintenance respiration (eqs. 7 and 8) in the growing season to be the growth respiration. Such a high respiration rate during the growing season was reported previously (Tianshan et al., 2004), and our measured maintenance respiration rate and Q_{10} range were within the range of reported values for Japanese broad-leaved trees (Sasa et al., 1984). In addition, the stem respiration of *Q. serrata* and *I. pedunculosa* during the growing season was approximated using the following equations:

$$F_{wQ} = 0.0049 \exp(0.0745 T_a); \quad (R^2 = 0.79, \text{DOY } 123 - 249) \quad (11)$$

$$F_{wI} = 0.0088 \exp(0.0541 T_a); \quad (R^2 = 0.81, \text{DOY } 123 - 249). \quad (12)$$

However, the main factor controlling growth respiration was not the temperature but the growth rate. Figure 5 illustrates the seasonal change of night-time growth woody-tissue respiration. The pattern of the seasonal change in growth respiration is complex, and it is difficult to continuously measure the increase of dry weight by non-destructive methods. Edwards and Hanson (1996) tried to calculate the growth respiration using diameter growth, but their attempt failed because the growth rate did not directly reflect the period of cell expansion. We had the same difficulty. Thus, to estimate the forest-level woody-tissue respiration, we used the seasonal pattern of observed respiration rates measured using the automated chamber method.

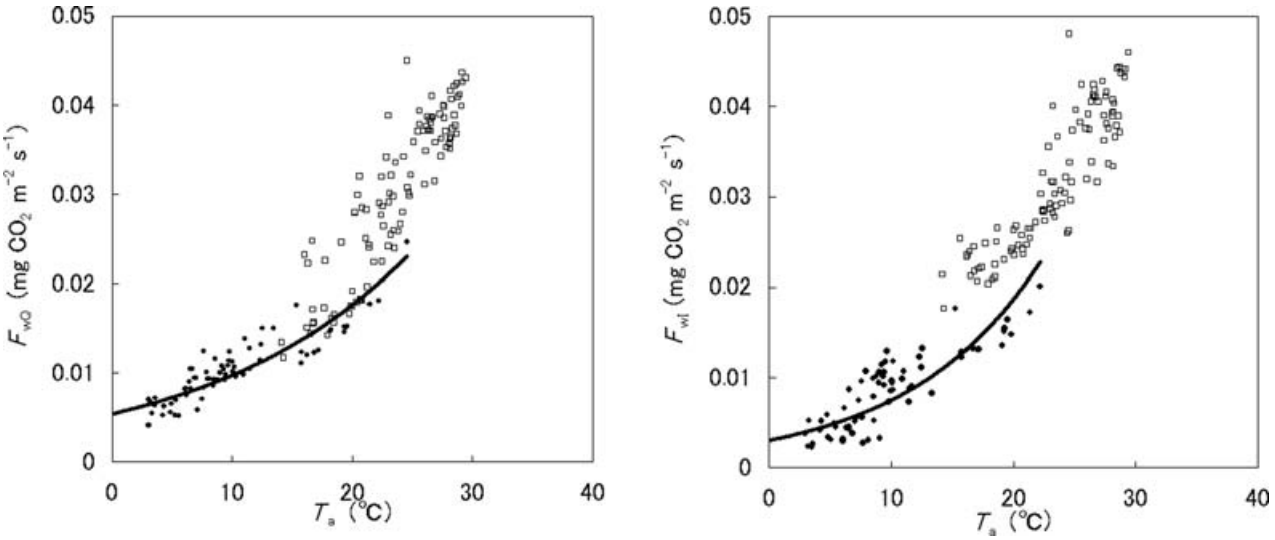

Fig. 4. Relationship between daily average night-time air temperature (T_a) and daily average woody-tissue respiration of *Quercus serrata* (Fig. 4a, left, $F_{wQm} = 0.0053 \exp(0.0598\, T_a)$, $R^2 = 0.73$) and *Ilex pedunculosa* (Fig. 4b, right, $F_{wIm} = 0.0035 \exp(0.0818\, T_a)$, $R^2 = 0.60$) in dormant season (filled circle, DOY 1–123 and 239–365). Stem respiration in growing season (open box, DOY 124–238) were relatively high with growth respiration.

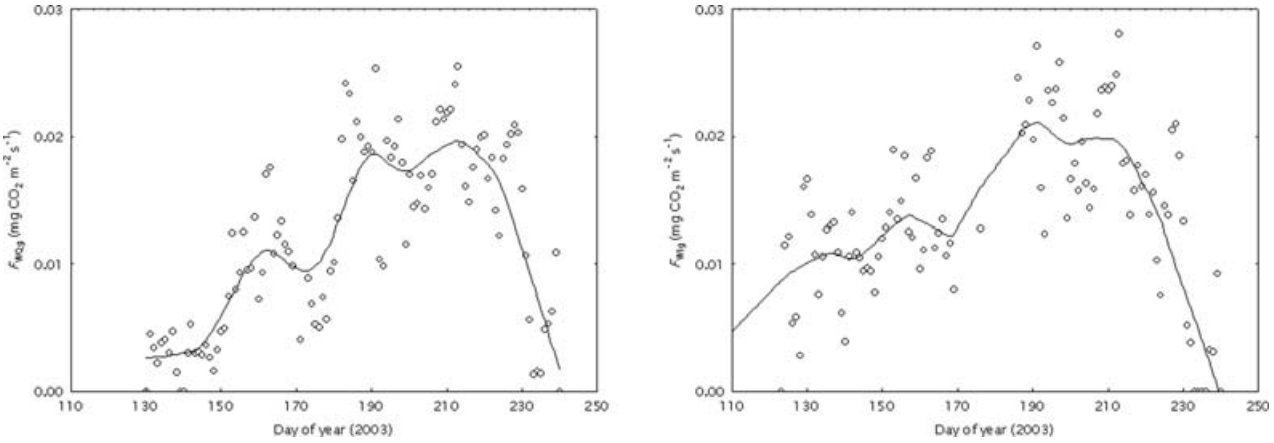

Fig. 5. Seasonal change of growth woody-tissue respiration of *Quercus serrata* (F_{wQg}, Fig. 5a, left) and *Ilex pedunculosa* (F_{wIg}, Fig. 5b, right). The growth respiration is deficit between measured stem respiration (F_{wQ} and F_{wI}) and estimated maintenance stem respiration (F_{wQm} and F_{wIm}) using data in dormant season (eqs. 9 and 10). The broken curve is a smoothing curve by LOESS. Lack of data was 7.2% in a growing season.

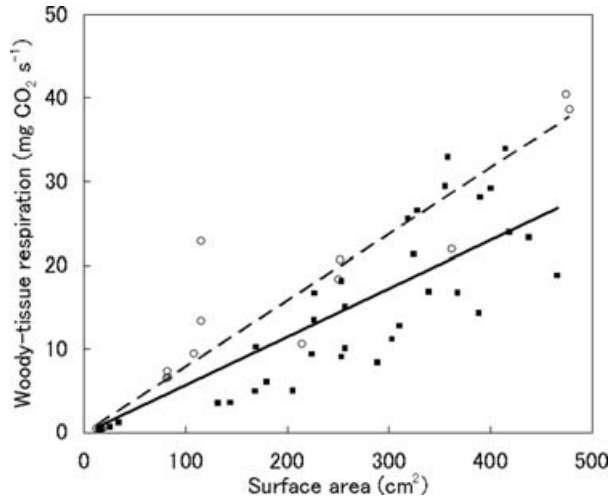

Fig. 6. Relationship between surface area (Sample diameter: 0.2–7.6cm) and woody-tissue respiration in *Quercus serrata* (open circle, brokenline, $F_{wQ} = 0.0791 \times$ Surface area, $R^2 = 0.89$) and *Ilex pedunculosa* (filled box, solid line, $F_{wI} = 0.0577 \times$ Surface area, $R^2 = 0.68$).

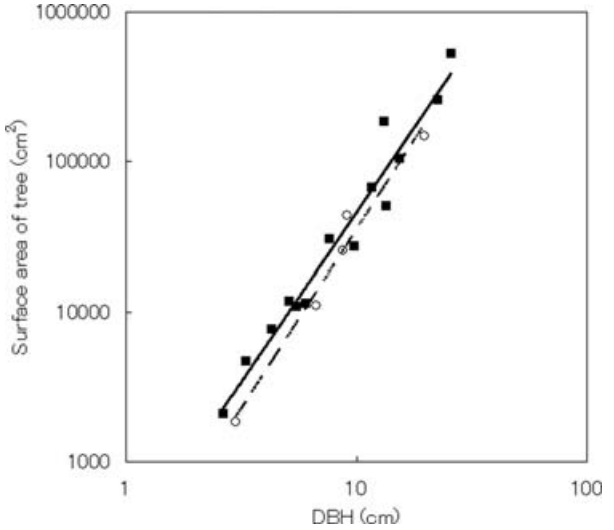

Fig. 7. Relationship between woody-tissue surface area of tree and DBH in *Quercus serrata* (open circle, broken line, Surface area = $145.17 \times$ DBH2.^{3828}, $R^2 = 0.97$, $n = 5$) and *Ilex pedunculosa* (filled box, solid line, Surface area = $251.63 \times$ DBH2.^{2635}, $R^2 = 0.96$, $n = 14$).

Missing data during the growing season (7.2%) were interpolated with a smoothing curve by LOESS (Cleveland and Devlin, 1988).

3.2. Spatial variation of woody-tissue respiration

Figure 6 shows the relationship between surface area and woody-tissue respiration in *Q. serrata* and *I. pedunculosa*. These data were measured from 20-cm-long samples of various diameters. Samples were collected from trees felled to estimate surface area. The cut ends of samples were sealed with silicone. These stem respiration values were converted to values at 25 °C using the automated stem chamber data. The respiration rate rose in proportion to increases in surface area for both the deciduous and evergreen species. The linear relationships (*Q. serrata,* $R^2 =$ 0.89; *I. pedunculosa,* $R^2 = 0.68$) suggest that the respiration is nearly constant per unit of surface area, a finding that corresponds to the results of Sasa et al. (1984). We confirmed the linearity of the relationship between surface area and the respiration rate of woody tissue by destructively sampling trees in the YMS, and we used these relationships to scale up to the woody-tissue respiration.

3.3. Estimation of woody-tissue surface area

Figure 7 illustrates the relationship between DBH (cm) and stand-level aboveground woody-tissue surface area (cm^2) in *Q. serrata* (SA_{wQ}) and *I. pedunculosa* (SA_{wI}) in 14 sample trees.

Table 2. Table of surface area

Elements	Surface area (ha ha^{-1})	
Evergreen woody tissue	0.39	9.4%
Deciduous woody tissue	0.84	20.2%
Woody tissue in YMS	1.23	29.6%
Evergreen leaf	0.64	15.4%
Deciduous leaf (maximum)	2.29	55.0%
Leaf in YMS	2.93	70.4%
Total	4.17	100.0%

The equation for each relationship is as follows:

$$SA_{\mathrm{wQ}} = 145.17\mathrm{DBH}^{2.3828}; (R^2 = 0.97, n = 5) \quad (13)$$

$$SA_{\mathrm{wI}} = 251.63\mathrm{DBH}^{2.2635}; (R^2 = 0.96, n = 14). \quad (14)$$

We used equations (13) and (14) and DBH census data to estimate forest-level woody-tissue surface area in the YMS. The forest-level woody-tissue surface areas of deciduous (S_{D}) and evergreen (S_{E}) trees were estimated as 0.838 and 0.398 ha ha^{-1}, respectively. Using the pipe model (Chiba, 1998), we estimated these values as more than three times as high. The pipe model tends to overestimate the separate twig frequency; thus, directly measured values are important.

SA_{wQ} and SA_{wI} represent the sum of stem and branch surface areas in each sample tree species. The stem surface area of sample trees was measured directly, and the branch surface area was estimated from all measured D_{twig} data of each sample tree by using the following equations:

$$SA_{\mathrm{twigQ}} = 132.71 D_{\mathrm{twig}}^{2.4574}; (R^2 = 0.88, n = 58) \quad (15)$$

$$SA_{\mathrm{twigI}} = 55.84 D_{\mathrm{twig}}^{2.8918}; (R^2 = 0.93, n = 42), \quad (16)$$

where D_{twig} is the base diameter of a branch (cm) and SA_{twigQ} and SA_{twigI} are the branch surface areas (cm^2) of *Q. serrata* and *I. pedunculosa*, respectively. Table 2 shows the estimated surface area and leaf area of each element per ground area in the YMS. The details of seasonal variation of the leaf area were reported by Miyama et al. (2005).

3.4. *Influence of growth respiration on night-time ecosystem respiration*

Figure 8 shows the seasonal variation of forest-level night-time woody-tissue respiration per ground area for deciduous (F_{wD}, eq. 3; Fig. 8a) and evergreen (F_{wE}, eq. 4; Fig. 8b) trees in the YMS. F_{wD} and F_{wE} increased before the peak of the air temperature and maintenance respiration. The growth respiration of deciduous (F_{wDg}) and evergreen (F_{wEg}) trees was estimated to be 22.3% and 26.3% of annual respiration, respectively. This suggests that the influence of growth respiration on the seasonal variation is large.

In contrast, the pattern of seasonal change in foliar growth respiration (Miyama et al., 2005) was different from that in woody-tissue growth respiration. Figure 9 shows the seasonal change of forest-level foliar and woody-tissue growth respiration. Foliar growth respiration increased and reached a peak before woody-tissue growth respiration. The peak of foliar growth respiration was largely due to the increase in deciduous leaf area during leaf elongation (Miyama et al., 2005). As a result, the seasonal change of growth respiration in the YMS showed two peaks due to the separate increases in foliar and woody-tissue growth respiration. The woody-tissue growth respiration was estimated to be 45.5% of the annual night-time growth respiration.

Figure 10 shows the seasonal change of forest-level growth and maintenance respiration. The forest respiration is the sum of woody-tissue and foliar respiration. The maximum air temperature and maintenance respiration were observed on DOY

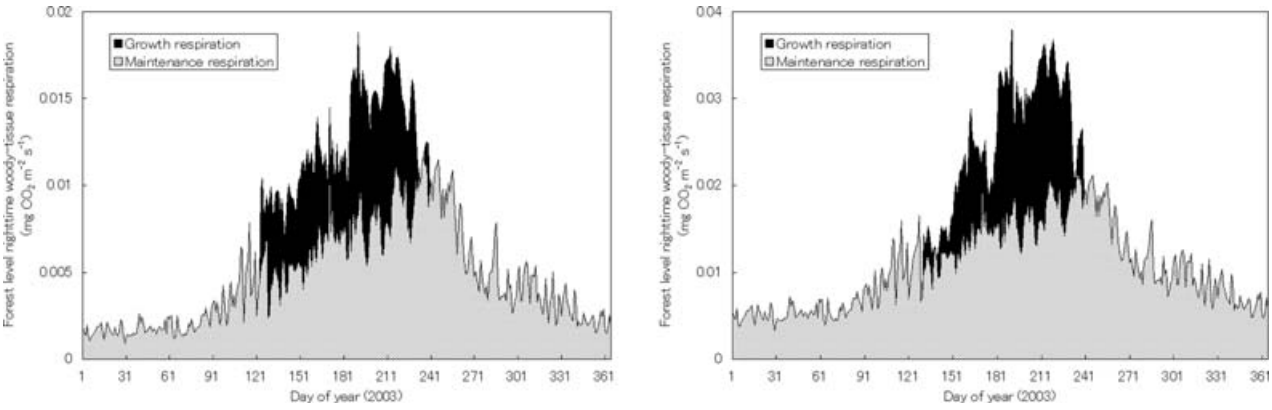

Fig. 8. Seasonal changes of forest level night-time woody-tissue respiration in deciduous tree (Fig. 8a, left) and evergreen tree (Fig. 8b, right). Growth respiration was estimated to 22.3% and 26.3% of each annual respiration, respectively.

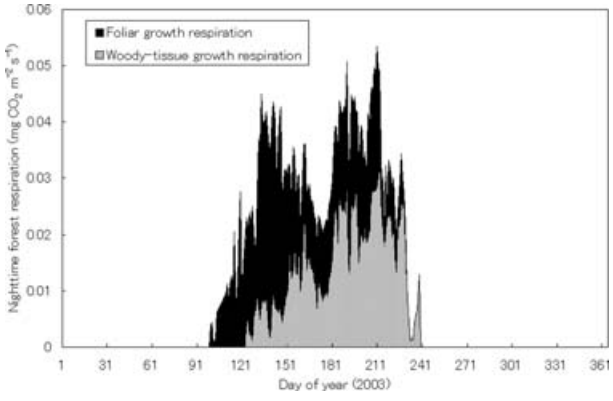

Fig. 9. Seasonal change of forest level foliar and woody-tissue growth respiration. Woody-tissue growth respiration was estimated to 45.5% of annual night-time growth respiration.

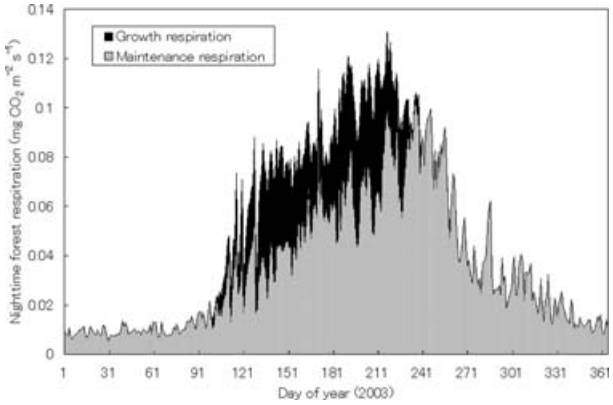

Fig. 10. Seasonal changes of forest night-time respiration (sum of woody-tissue respiration and foliar respiration). Growth respiration was estimated to 22.6 % of annual forest respiration.

235. However, the maximum of woody-tissue plus foliar respiration was observed on DOY 217. The growth respiration was estimated to be 22.6% of the annual forest respiration.

3.5. Comparison of night-time ecosystem respiration between the eddy covariance and chamber methods

The seasonal change of growth respiration affected the seasonal change of components in night-time ecosystem respiration (F_{eco}, eq. 5). Figure 11 shows seasonal change of contributions as a ratio of night-time ecosystem respiration. In the growing season, the ratio of soil respiration decreased greatly. Annual average night-time respiration of soil, evergreen leaf, deciduous leaf, evergreen woody tissue and deciduous woody tissue were estimated as 0.0794 (63.2%), 0.0101 (8.0%), 0.0160 (12.7%), 0.0064 (5.1%) and 0.0137 (10.9%) mg CO_2 m^{-2} s^{-1}, respectively. The contribution of soil respiration to the total ecosystem respiration rate reached its minimum (49.1%) on 12 June (DOY 163) and its maximum (82.4%) on 29 November (DOY 333). The

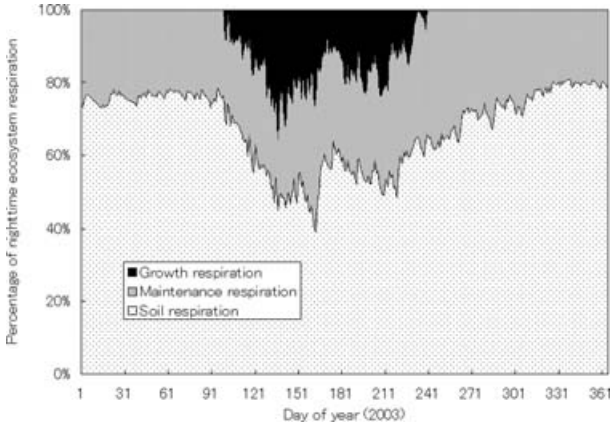

Fig. 11. Seasonal change of contribution ratio per night-time ecosystem respiration. Growth respiration was estimated to 6.2% of annual night-time ecosystem respiration.

proportion of F_{eco} was not constant over the course of the year, which is likely a common characteristic of deciduous forests, due to the change of the deciduous leaf area and growth respiration rate over the year. The seasonal variation in growth respiration was marked in the YMS. In particular, the growth components of foliar and woody-tissue respiration in the forest formed two sequential peaks. The maximum contribution of growth respiration to the night-time ecosystem respiration rate was 35.7% on 13 May (DOY 137). Griffis et al. (2004) measured annual respiration of soil (0.112 mg CO_2 m^{-2} s^{-1}, 73.2%), leaf (0.023 mg CO_2 m^{-2} s^{-1}, 15.1%) and bole (0.018 mg CO_2 m^{-2} s^{-1}, 11.8%) using the automated chamber method in a boreal aspen forest. Our results correspond well with these values, except for soil respiration, which was lower than the value reported by Griffis et al. (2004). One reason for the different soil respiration values may be a difference in soil carbon content. The sandy immature soil in our site likely has less soil carbon than the boreal aspen forest.

Figure 12 illustrates the seasonal change in the deficit between night-time respiration estimated using the EC method (F_{EC}, Kominami et al., 2005) and the chamber method (F_{eco}). Compared to our values measured continuously in automated chambers, during the growing season F_{EC} showed two periods of underestimated values and one period of overestimated values. This seasonal change seems to be controlled by the seasonal change in growth respiration (Fig. 11). Kominami et al. (2005) assumed that the exponential relationship between soil temperature and night-time ecosystem respiration was constant throughout a year. However, the contribution rate of soil respiration in F_{eco} was not constant, showing a dramatic seasonal change caused by growth respiration. These findings indicate that the seasonal variation of growth respiration must be evaluated carefully when estimating the total ecosystem respiration in the YMS. Therefore, long-term continuous measurement using automated chambers and averaging provides an effective means of evaluating the annual night-time ecosystem respiration.

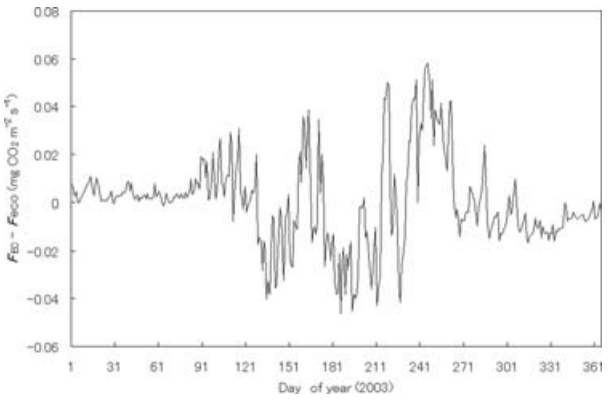

Fig. 12. Seasonal change of deficit between estimated value using by EC method (F_{EC}) and chamber method (F_{eco}).

Many other studies have compared chamber-based and EC respiration data (Goulden et al., 1996; Lavigne et al., 1997; Schmid et al., 2000; Drewitt et al., 2002; Bolstad et al., 2004) and found that chamber-based flux estimates exceeded the EC measurements. At our site, annual estimated F_{eco} exceeded F_{EC} ($u^* >$ 0.35 m s^{-1}; Kominami et al. 2005) by 15.8%. The chamber-method value may have been notably larger than the value measured using the EC method owing to an insufficient evaluation of the growth respiration by the EC method. To improve estimations of night-time respiration, our model should include a phenological parameter. On the other hand, uncertainty still persists regarding the accuracy of quantification of night-time respiration, the underlying causes of annual, seasonal, and spatial variation. To improve our confidence in measurement of CO_2 flux, scaling uncertainty should be clarified by using diversified automated measurement systems, too.

4. Conclusions

According to continuous automated chamber measurements, the seasonal change of night-time ecosystem respiration was controlled by growth respiration in a deciduous broad-leaved forest. The percentage of soil respiration in ecosystem respiration ranged from 49.1% to 82.4%. There were two marked peaks of growth respiration, which were caused sequentially by foliar and woody-tissue respiration. These results indicate the effectiveness of averaging long-term continuous chamber measurements to evaluate the annual night-time ecosystem respiration. Seasonal variation of night-time respiration should be estimated using several parameters, including phenological data. By using the automated chamber method, the total ecosystem night-time respiration was estimated continuously, thus allowing seasonal patterns to emerge.

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