Jour. Korean For. Soc. Vol. 95, No. 2, pp. 168~173 (2006)

JOURNAL OF KOREAN FOREST SOCIETY

Diurnal and Seasonal Changes of Stem Respiration in Black Locust (*Robinia pseudoacacia*)

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Abstract : Stem respiration rate (R_{stem}) was examined using an open flow system on black locust (*Robinia pseudoacacia* L.). R_{stem} exponentially increased with increasing air and stem temperature during measurement period and was most closely correlated with stem temperature. It was more closely correlated with stem temperature observed 0.5-2.0 hrs earlier than with current stem temperature, that is, there was time lag between the increase of stem temperature and the efflux of CO_2 from stem. R_{stem} gradually increased from spring to summer, and then decreased during autumn. R_{stem} ranged from 0.13 to 4.44 μmol CO_2 $m^{-2}s^{-1}$. Q_{10} decreased with increasing stem temperature, and varied along position (or diameter) within trees during the same period, especially during the growing season. On the other hand, time lag was shortened with increasing temperature.

Key words **:** *black locust, Q_{10}, stem respiration, stem temperature, time lag*

Introduction

Carbon dioxide (CO_2) is a major green house gas and its concentration in the atmosphere increased by 18% in the mean annual concentration from 316 ppm in 1959 to 373 ppm in 2002 (Keeling and Whorf, 2003). Forest ecosystem is an important part of the global carbon cycle, having large capacities to both store and release carbon (Dixon *et al.*, 1994; Valentini *et al.*, 2000) and covering more than 4.1×109 hectares of the Earth's land area (Dixon *et al.*, 1994).

Recently, the direct measurements of CO_2 exchange between a forest and atmosphere have been conducted by a flux tower (eddy covariance technique) to account for the capacities (store and release) of a forest ecosystem (Law *et al.*, 1999; Valentini *et al.*, 2000; Milyukova *et al.*, 2002). The advantages of this technique are as follows: 1) fluxes are integrated over a large area, 2) total flux is measured, and 3) vegetation is not distributed by measurement. However, this technique needs an expensive instrument and cannot explain the fluxes for each flux (photosynthesis, autotrophic respiration, and heterotrophic respiration) within forest ecosystem. Therefore it needs combining each flux data to perfectly understand the carbon cycle of forest ecosystem.

Autotrophic respiration in plants or forest ecosystems consumes approximately 50% of the carbon fixed by photosynthesis (Ryan, 1991; Ryan *et al.*, 1997). Since research of autotrophic respiration has been mainly foliar and root rather than stem respiration, relatively few studies of stem respiration have been conducted. However, stem respiration is a considerably important part of the carbon cycle in forest ecosystems because stems account for the largest portion of forest biomass and increase continuously with stand development. Recently, interest in stem and branch respiration is increasing (Sprugel and Benecke, 1991; Damesin *et al.*, 2002).

Although the effects of temperature in woody respiration are not clear, many studies are commonly assumed that the respiration increases exponentially with increasing temperature (Amthor, 1989; Martin *et al.*, 1994). The response is usually expressed in terms of Q_{10}, the change in respiration with increasing each 10°C. Amthor (1984) suggested a close value to 2.0 using for Q_{10}, and Sprugel and Beneke (1991) suggested that Q_{10} values were between 2.0 and 2.3 based on previous studies. Many authors used 2.0 of Q_{10} in the studies of stem respiration (Linder and Troeng, 1981; Lavigne, 1987; Ryan, 1990; Sprugel, 1990; Stocfors and Linder, 1998).

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On the other hand, Hagihara and Hozumi (1981) calculated Q_{10} of 3.7, 3.6, 3.3, and 3.4 for stems, branches, coarse roots and fine roots of *Chamaecyparis obtusa*, respectively. In studies carried out over a year, some authors reported that Q_{10} decreased with increasing temperature (Carey *et al.*, 1997; Lavigne, 1996; Maier, 2001; Paembonan *et al.*, 1991; Stockfors and Linder, 1998). While, other authors have found no seasonal variation in Q_{10} (Linder and Troeng, 1981; Lavigne and Rayn, 1997; Butler and Landsberg, 1981). In this study we examine the spatial and seasonal variations of Q_{10} based on field measurements of stem respiration and microclimate.

Stem respiration at a given moment was more closely correlated with the stem temperature observed earlier than with the current stem temperature (Linder and Troeng, 1981; Ryan *et al.*, 1995; Lavigne *et al.*, 1996; Stockfors and Linder, 1998; Kim and Nakane, 2005). The time interval between the responses of R_{stem} and stem temperature is called 'time lag'. The temperature most fitting to the exponential relationship is called 'lagged temperature' (Kim and Nakane, 2005). The mechanism of time lag between stem respiration and stem temperature is not clear, therefore simultaneous and continuous measurements of stem respiration and microclimate data are needed to clear this mechanism.

The objectives of the present study are to: (1) determine the relationships between stem respiration rate and environmental factors (temperature, relative humidity, precipitation, photosynthetic photon flux density, and ambient CO_2 concentration), and (2) estimate temperature responses, and diurnal and seasonal changes in stem respiration rate on black locust.

Materials and Methods

The study was conducted in Yoshikawa, Higashi-Hiroshima City, west Japan (34°23'N, 13°239'E). Two black locust (BL) trees that are healthy and not stressed were chosen as sample trees. The sample trees are growing in the edge, a sunny location, of Japanese red pine forest. Characteristics and four sample points of the sample trees are given in Table 1.

Measurements were conducted at four sample points in the sample trees with the open flow system (Kim and Nakane, 2005). The system is comprised of a reference line and sample line, consisting of an air pump, a flow meter and an electromagnetic valve. Behind the electromagnetic valve, the air stream was passed through an air filter and a digital flow meter (SEF-21A, STEC Inc., Kyoto) to an infra-red gas analyzer (LI-6252, LiCor Inc., Lincoln) with absolute mode.

Stem chambers were made from a flexible acrylic file (thickness = 1 mm). A chamber that completely encircled the tree was used. After loose barks were removed from the stems, chambers were attached to stems with adhesive tape. While measurements were being made, the chambers were covered with aluminum foil to prohibit bark photosynthesis and stem heating caused by direct sun exposure. Ambient CO_2 concentration was measured at 1.3 m above ground by LI-6252. Air temperature was measured at 1.3 m above ground, and stem temperatures were measured in a bark depth of 1.5-2.0 cm with a thermocouple. Photosynthetic photon flux density (PPFD) was measured above the canopy (ca. 18 m) by a quantum sensor (IKS-25; Koito Industries, Tokyo). The data were recorded with a data logger (NR1000; Keyence, Tokyo). Relative humidity was measured and logged by a thermo recorder (TR-72S; T&D, Tokyo).

Table 1. Characteristics of black locust (BL) trees selected for measurements of diurnal and seasonal changes in stem respiration rates.

Sample trees	Tree height (m)	DBH (cm)	Height of sample point (m)	Diameter of sample point (cm)
BL I-(1)			0.60	10.3
BL I-(2)	6.9	10.6	2.40	7.0
BL I-(3)			3.30	5.0
BL II-(1)	6.9	6.0	3.30	4.3

Stem respiration rate (R_{stem}) was estimated by difference in CO_2 concentration between air outflow out of the chamber (sample line) and air inflow into the chamber (reference line). The response of stem respiration to temperature changes can be expressed in the form of the following exponential function (Ryan *et al.*, 1995),

$$R_{stem} = R_0 \exp(\beta T) \quad (1)$$

where R_0 is R_{stem} at 0°C, β is a coefficient for temperature response and T is stem temperature (°C). The Q_{10} value is given by $\exp(10\beta)$. Measurements were taken from January, 2002 to March, 2003.

Stem respiration and microclimate data were processed in an Excel 2003 spreadsheet. Regression analysis was used to examine the relationships between stem respiration rate and environmental factors. For each chamber, a paired t-test was used to compare R_0, β, and coefficients of determination (R^2) based on current and previous stem temperatures.

Results and discussion

3.1. Diurnal change

Figure 1 shows the diurnal changes in environmental

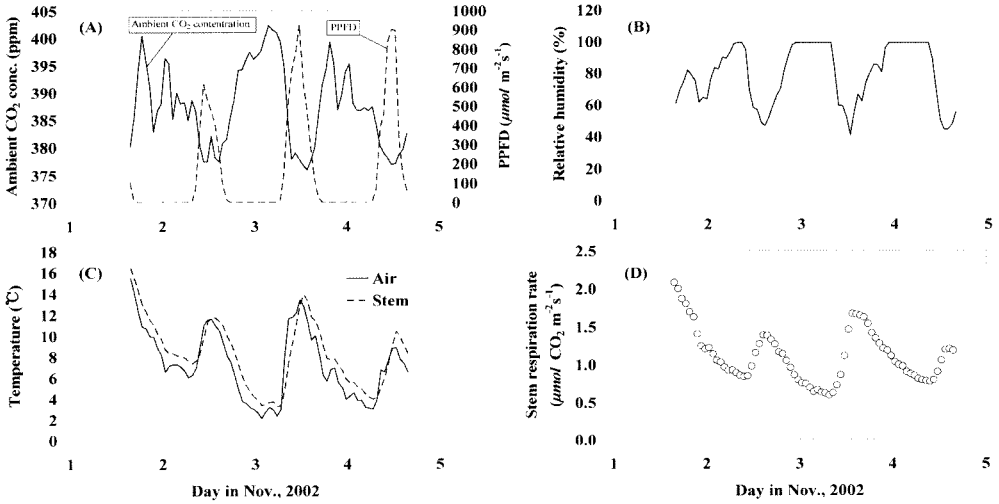

Figure 1. Diurnal changes in the ambient air CO_2 concentration and photosynthetic photon flux density (PPFD) (A), in the relative humidity (B), in the air and stem temperatures (C), and in the stem respiration rates for BL I-(1) (D).

factors (ambient CO_2 concentration, PPFD, relative humidity, air temperature, and stem temperature) and R_{stem}, which were measured from November 1 to 5, 2002. Ambient air CO_2 concentration was high during the night time and low during the daytime, and ranged between 376 and 402 ppm during the measurement period (Figure 1A). The fluctuation of photosynthetic photon flux density (PPFD) was inversely related to the ambient air CO_2 concentration (Figure 1A). The fluctuation of relative humidity was similar to the pattern of the ambient air CO_2 concentration, and ranged between 41% (daytime) and 99% (nighttime) (Figure 1B). The fluctuation patterns of air temperature and stem temperature (Figure 1C) were similar to that of the PPFD. The coefficients of variation (CV) of air and stem temperature were 46% and 40%, respectively during the measurement period. The difference on the CV of air and stem temperature might be due to difference between the responses of air and stem to sunlight. Because changes in air temperature did not affect stem temperature and respiration rates rapidly, it is better to use stem temperature than air temperature for analyzing the relationship between temperature and respiration rate. The diurnal fluctuations in respiration rates were paralleled with those in the PPFD (>0), and air and stem temperatures, but not with the diurnal fluctuations in other environmental factors (ambient CO_2 concentration, relative humidity; Figure 1).

R_{stem} was more closely correlated with the stem temperature observed before than with the current stem temperature (Figure 2, Table 2). The lagged responses of stem respiration to temperature were observed in all the samples throughout the year (Table 2). The fact that R_{stem} have a lagged response to stem temperature is especially important when measurements cannot be conducted for

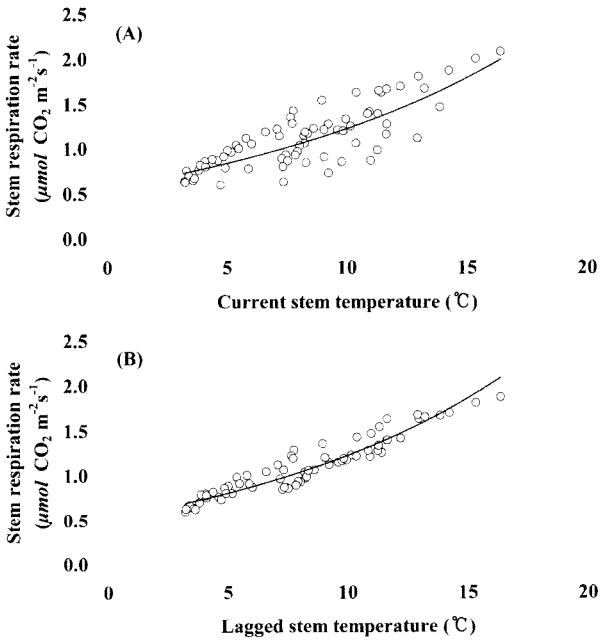

Figure 2. Relationships between stem respiration rates and the current stem temperature (A) or the lagged stem temperature (B) for BL I-(1). Parameters of the exponential regression curves are the same as Table 2.

both daytime and nighttime, because at the current stem temperature, R_{stem} were lower during the daytime than during the nighttime (Kim and Nakane, 2005). Many authors reported lagged response of respiration to temperature (Linder and Troeng, 1981; Ryan *et al.*, 1995; Lavigne *et al.*, 1996; Stockfors and Linder, 1998; Kim and Nakane, 2005). On average for all samples in table 2, coefficients of determination (R^2) was about 21% higher when respiration rate was regressed against the lagged stem temperature than the current stem temperature, and the differences were statistically significant

Table 2. Parameters of the exponential equations fitted the relationship between stem respiration rates and current or lagged stem temperature.

Sample trees	Current stem temperature			Lagged stem temperature			Time lag (hr.)
	R_0	Q_{10}	R^2	R_0	Q_{10}	R^2	
BL I-(1)	0.565	2.15	0.64***	0.521	2.33	0.89***	2
BL I-(2)	0.325	2.00	0.59***	0.312	2.06	0.76***	2
BL I-(3)	0.344	2.34	0.69***	0.340	2.31	0.79***	2
BL II-(1)	0.250	2.47	0.77***	0.249	2.45	0.82***	1

R_{stem} (stem respiration rate) = $R_0 \exp(\beta T)$, where R_0 (μmol CO_2 $m^{-2}s^{-1}$) is R_{stem} at 0°C, β is a coefficient for temperature response, and T is stem temperature. Q_{10} value is $\exp(\beta T)$. *** $p<0.001$

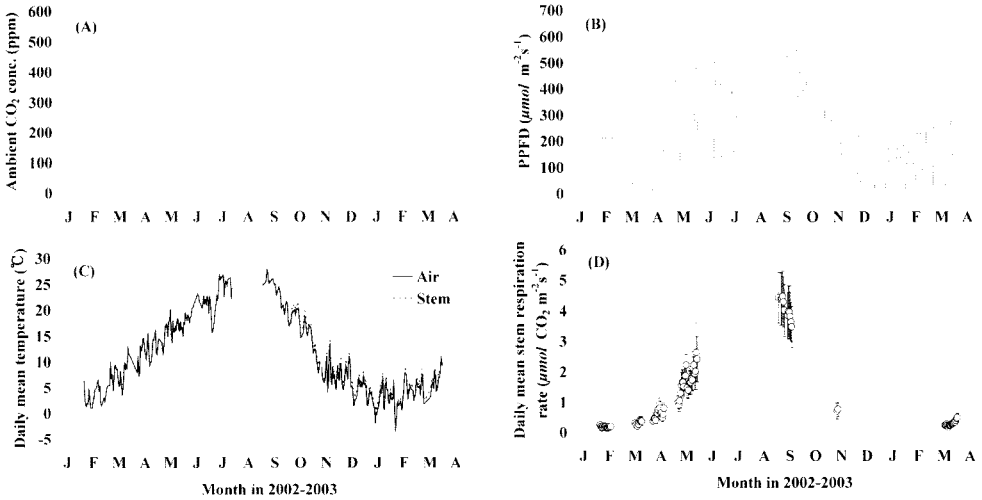

Figure 3. Seasonal changes in the daily mean ambient CO_2 concentration (A), in the daily mean photosynthetic photon flux density (PPFD) (B), in the daily mean air and stem temperature (C), and in the daily mean stem respiration rates (D). Error bars are standard deviation (n=4).

($p < 0.05$). However, R_0 (R_{stem} at 0°C) and Q_{10} estimated from the lagged stem temperature did not statistically differ from those estimated from the current stem temperature ($p = 0.21$ for R_0, and $p = 0.39$ for Q_{10}). The lagged responses of stem respiration to temperature are likely the results of (1) the large resistance to movement of CO_2 from stem to air (Eklund and Lavigne, 1995), (2) stem temperature varies by the position of stem tissue (Derby and Gates, 1966; Stockfors, 2000; Kim and Nakane, 2005), and (3) the transpiration stream (Negisi, 1972, 1979).

3.2. Seasonal change

The environmental factors (ambient CO_2 concentration, PPFD, air temperature, and stem temperature) and R_{stem} were measured throughout different season (Figure 3). Ambient CO_2 concentration was relatively constant (approximately 400 ppm, Figure 3A), but the PPFD, temperature, and respiration rate varied seasonally (Figure 3). The seasonal pattern in stem respiration rate strongly followed the seasonal pattern in air and stem temperature. The stem respiration rate gradually increased from spring to summer, and then decreased during autumn. The decrease of stem respiration rates during the dormant season and its increase during the growing season have been observed in many other studies (Linder and Troeng, 1981; Negisi, 1974; Paembonan *et al.*, 1991).

The relationship between daily mean R_{stem} and stem temperature was an exponential function (Q_{10} was 4.6; Figure 4). However, stem respiration rates were higher at 15 to 20°C and lower at over 20°C than the regression line. Paembonan *et al.* (1991) reported also a lack of strong synchrony between temperature and respiration rate after June. It was explained by the difference of a growth rate throughout the year, i.e., the decrease in respiration rate after June might have been the result of a decrease in growth respiration, which is related to the synthesis of new tissues and temperature-independent (Penning de Vries *et al.*, 1974). The decrease observed in stem respiration rate at more than 20°C of stem temperature also could have been caused by water stress (Negisi, 1975). In this study, stem respiration rate ranged from 0.13 μmol CO_2 $m^{-2}s^{-1}$ in January to 4.44 μmol CO_2 $m^{-2}s^{-1}$ in August.

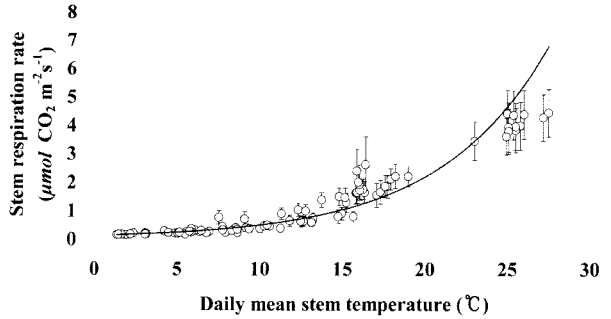

Figure 4. Relationship between the daily mean stem temperature and stem respiration rates. The regression curve is y=0.1064exp (0.152x) (R^2= 0.93*). Error bars are standard deviations (n=4). ***p<0.001**

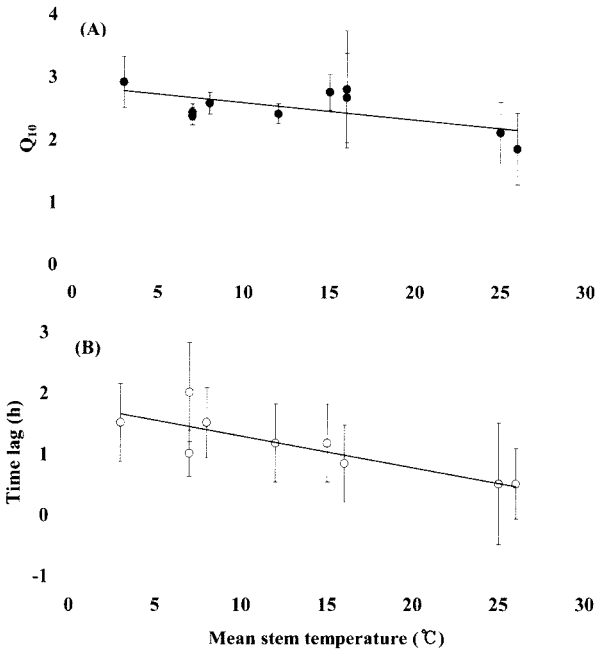

Figure 5. Relationships between each mean stem temperature and Q_{10} (A), or time lag (B). The regression lines: y = -0.0272x + 2.847 (R^2=0.41*, n=10) for Q_{10}, and y = -0.0515x + 1.7957 (R^2= 0.70, n=10). The data were calculated by the average per two-day or more. Error bars are standard deviations (n=4). * p<0.05, ** p<0.01**

In order to estimate seasonal pattern (or temperature response) in Q_{10} or time lag, Q_{10} values were calculated by the data measured continuously for more than two days (Figure 5A). Q_{10} decreased with increasing stem temperature ($p < 0.05$), and the mean value was 2.48± 0.33. Some authors have found no seasonal variation in Q_{10} (Linder and Troeng, 1981; Lavigne and Ryan 1997; Butler and Landsberg, 1981). Other authors have reported that Q_{10} decreased at summer having great metabolic activity with high temperature (Carey et al., 1997; Lavigne, 1996; Maier, 2001; Paembonan *et al.*, 1991; Stoackfors and Linder, 1998). Especially, the studies of Carey *et al.* (1997) for *Pinus ponderosa* and Stockfors and Linder (1998) for *Picea abies* suggested clear differences of Q_{10}, e.g. about 1.6 in September and 2.4 in July in *P. ponderosa*, and 1.92 in August and 2.55 in June in *P. abies*.

On the other hand, time lag ranged from 0.5hr. to 2hrs and became short with increasing temperature ($p<0.001$, Figure 5B). Stockors and Linder (1998) also reported that time lag changed throughout the year on *Picea abies* (L.) Karst., and was short in June and reached to a maximum in September.

Acknowledgements

We thank to Dr. H. Sakugawa for his permission to carry out this study at the ecological tower. We also would like to thank to Dr. S.J. Joo and Dr. M.H. Yim for helpful discussion, and Dr. J.H. Yoon for filed-work help.

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(Received November 29, 2005; Accepted December 26, 2005)