

(Article)

Stem/branch Maintenance Respiration of Japanese red pine stand

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Abstract

Stem/branch maintenance respiration for a stand of Japanese red pine (*Pinus densiflora*) during the dormant season was examined using an open flow system. The stem/branch respiration rates per unit of volume were closely related to the thickness of the stems and branches, e.g. it decreased with increasing diameter ($p < 0.0001$). When the respiration rates on the various positions were regressed against the stem temperature of the specific position, Q_{10} values decreased with increasing diameter. The variation of Q_{10} ranged from 1.28 to 6.4. These Q_{10} variations should have represented the variation of stem/branch temperature within the tree. The increase in time lag corresponded with an increase in diameter. We estimated the annual maintenance respiration for stem and branches at stand level based on the respiration rate-diameter relation, the Q_{10} -diameter relation, and the pipe model theory. In the *Pinus densiflora* stand, total annual maintenance respiration was estimated to be $2.55 \text{ tCha}^{-1}\text{yr}^{-1}$ ($1.40 \text{ tCha}^{-1}\text{yr}^{-1}$ for stems, and $1.15 \text{ tCha}^{-1}\text{yr}^{-1}$ for branches). This suggests that branch respiration is an important component of total aboveground woody respiration at the stand-level (about 45%). Within the distribution of annual maintenance respiration rates for each D class, the stem and branch of 25-30 cm D class was the highest, and accounted for 33% and 31% of total stem and branch respiration rates, respectively. According to our results and those of previous studies, maintenance respiration correlated positively with annual mean temperature and

LAI, and correlated negatively with stand age and latitude.

Key words: Japanese red pine; maintenance respiration; pipe model theory; Q_{10} ; stem respiration rate; stem temperature

1. Introduction

Many researchers have emphasized the usefulness of such parameters as living cell volume (Ryan, 1990), sapwood volume (Lavigne et al., 1996; Ryan, 1990; Ryan et al., 1994), and stem nitrogen content (Lavigne et al., 1996) to predict woody respiration rates. Although these parameters may be good predictors of stem respiration, their applicability in modeling efforts is limited by the fact that data on living cell and sapwood volumes, as well as stem nitrogen content, is not widely available.

On the other hand, other researchers have expressed respiration rates on the basis of different measurements of plant size. Respiration rates expressed on a basis of weight (Möller et al., 1954; Yoda et al., 1965; Yoda, 1967, 1983; Hagihara and Hozumi, 1981) or volume (Lavigne et al., 1996; Ryan et al., 1996) decrease with increasing diameter, while surface area based rates (Lavigne et al., 1996) increase with increasing diameter. Yoda et al. (1965) estimated an explicit numerical relationship between the diameter of woody organs (root, trunk, and branch) and their respiration rates. Using the respiration-diameter relation and the pipe model theory (Shinozaki et al., 1964), which is the frequency distribution of diameters in a single tree following a power function, they estimated the total respiration for a whole tree, and further expanded their calculations to estimate respiration rates for stand levels.

However, all of the studies mentioned above did not consider temperature variation within a tree, that is, they estimated the respiration of the whole tree under the assumptions that Q_{10} values would remain constant for the whole tree, and that stem temperature at a given time would have been the same throughout the tree. Many other authors (Kinerson, 1975; Linder and Troeng, 1981; Lavigne, 1996; Ryan et al., 1996) also estimated whole stem respiration under both of the same assumptions. Moreover, in natural conditions, temperature within a tree varies according to the direction it faces (Edwards and Hanson, 1996; Kim and Nakane, 2005), its height, and the depth of the stem tissue (Stockfors, 2000). Therefore, Stockfors (2000) simulated total respiration for the whole stem using the variations of temperature within the stem under the assumption that Q_{10} was constant for all days and all stem positions. In other words, assuming that the fluctuation of stem temperature for a certain given period remains constant throughout the tree, it must follow that Q_{10} would vary with stem position.

Respiration can be subdivided into growth (respiration used to build dry matter) and maintenance (respiration used to maintain ion gradients, replace enzymes, and repair membranes) components (McCree, 1970; Penning de Vries et al., 1974; Penning de Vries, 1975; Ryan et al., 1994). The most common method for measuring maintenance respiration in trees, and the one that was used in this study, is to assume that measurements taken after the growing

season represent maintenance respiration rates (Butler and Landsberg, 1981; Sprugel, 1989; Ryan, 1990; Sprugel and Benecke, 1991; Lavigne, 1996). Using this method, the relationship between temperature and maintenance respiration is able to be viewed as being either more or less constant throughout the year, while growth respiration is calculated as the difference between total respiration and maintenance respiration. A weakness in this method may be that the CO₂ efflux from the stem has, in some studies, appeared to arise from a combination of the CO₂ released by local respiring cells and the CO₂ that was transported through the xylem to the site of measurement (Teskey and McGuire, 2005).

In the present study, we assumed the measured stem/branch respiration rates to be the maintenance respiration, because the investigation was conducted from September 27 to October 3, 2003 when the growth of pine trees ceases. Stem temperature was measured at a specific position (at a bark depth of 1.5-2 cm and at 2.5 m aboveground), and was employed to discover the relationship between respiration rate and temperature. Based on the intra- and inter-tree variability of Q_{10} and respiration rate, and the pipe model theory (Shinozaki et al., 1964; Yoda et al., 1965; Yoda, 1967), individual and stand woody tissue maintenance respiration rate was estimated.

2. Materials and Methods

2.1 Site description

The study was conducted on a 40-year-old *Pinus densiflora* Sieb. et Zucc (Japanese red pine) forest situated in Yoshikawa, Higashi-Hiroshima City, west Japan (34°23'N, 132°39'E). The study site is located on the lower southern aspect of a hill, with an elevation of ca. 208 m a.s.l., and an inclination of ca. 5 degrees. According to a June 29, 2002 tree census at the study site (10 m × 40 m), the basal area (a cross-sectional area at breast height) of Japanese red pine, which is the dominant species of the tree layer, was 29.5 m² ha⁻¹, and accounts for 86% of the total basal area. The tree density of Japanese red pine was 1000 trees ha⁻¹, mean diameter at breast height (D) was 18.7 (± 2.33) cm, and mean height was 14.3 (± 1.02) m.

The region belongs to the warm-temperature monsoon zone. At a station located ca. 5 km northeast from the study site, the average of annual mean temperature is 13.5°C and the average annual precipitation is 1,494 mm (Hiroshima Prefecture Research Center, based on records from 1992 to 2001). The monthly mean air temperature reached at a maximum (25.6°C) in August and decreased to a minimum (2.4°C) in January.

2.2. Respiration measurement

In order to measure the respiration rates (Table 1), stems and branches which varied in thickness (3.1 to 34.8 cm) and height (1.8 to 15.9 m) were selected from eleven Japanese red pine trees (23 points; 17 points for stem, and 6 points for branch). Measurements were made from September 27 to 29 for samples 1 – 9, and from September 30 to December 3, 2003 for samples 10 – 23 (Table 1).

Stem or branch respiration rates (R_{stem} or R_{branch}) were estimated by the difference in CO_2 concentration between air outflow from the chamber and air inflow into the chamber using an open flow system (Kim and Nakane, 2005). The system was comprised of a reference line and a sample line, consisting of an air pump, a flow meter, an electromagnetic valve, an air filter, a digital flow meter (SEF-21A, STEC Inc., Kyoto) and an infra-red gas analyzer (IRGA) (LI-6252, LiCor Inc., Lincoln). Continuous air flow through the chambers was controlled with a pump and flow meter, and maintained at 1.2 l min^{-1} . Among all the reference and sample lines, the air in only one of these lines was passed through an electromagnetic valve controlled by KV700 (Keyence, Tokyo) to IRGA. Chambers were made of a flexible acrylic film (1 mm thickness). After loose bark was removed from the stems/branches, these chambers were attached to the stems with a silicone gasket, or with putty. While measurements were being made, the chambers were covered with aluminum foil to prevent bark photosynthesis and stem/branch heating caused by direct sun exposure.

Air temperature was measured at 1.3 m above ground, and a thermocouple was used to measure stem temperature at a bark depth of 1.5 – 2 cm. Air/stem temperatures and CO₂ concentration of reference/sample lines were recorded by a data logger (NR1000, Keyence, Tokyo). The constant for stem temperature which was used to calculate the relationship between stem temperature and stem/branch respiration rate was arrived at by averaging measurements taken at 2.5 m above ground, and at four azimuth angles, from sample stem 1. Stem temperature measurements were taken over 2002 – 2003. Several missing portions of the data, which were absent data due to a system shutdown, were extrapolated from the values induced by calculating the relationship between the air temperature measured at the study site and the air temperature recorded at the Hiroshima Prefectural Agricultural Research Center, and then by comparing this relationship with the ratio between air temperature and stem temperature measurements which had been taken measured at the study site. Annual maintenance respiration was calculated on the basis of the relationships between stem temperatures and the Q₁₀ or respiration rates.

The response of stem/branch respiration rates to temperature changes for the individual chambers can be expressed in the form of the following exponential function,

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

where R_0 is R_{stem} at 0 , β is the coefficient for temperature response and T is the stem temperature () at a specific point (2.5m above ground). The Q_{10} value used to describe this relationship is the factor by which the change of the respiration rate is expressed for a 10 change in temperature. The Q_{10} value is expressed as $\exp(10\beta)$.

To compare the respiration rates measured in each sample segment, the stem/branch respiration rate at 20 °C (R_{20}) was calculated. Equation 1 can be transformed as the following function,

$$R_{\text{stem}} = R_{20} Q_{10}^{\left(\frac{T-20}{10}\right)} \quad (2)$$

Equation 2 was fitted for each sample segment using surface area (m^2) and volume (m^3) as the basis for expressing respiration rate. The time interval between the responses of R_{stem} and stem temperature is called the ‘time lag’. The temperature which best fits this exponential relationship is called the ‘lagged temperature’. It was used for all equations in this study.

2.3. Maintenance respiration for both forest and trees

The method used in this study to estimate the total aboveground woody maintenance respiration of a single tree was based on the one employed by Yoda et al. (1965), and Yoda (1967, 1983). According to their theory, when the diameter of woody organs (stem, branches, and roots) in a single tree is

measured at regular intervals of length, starting from the stem base to the tips of the most minute twigs and rootlets, along all courses of branching, and the figures obtained thereby are grouped in successive diameter classes, the frequency (f) per class can be expressed as a function of diameter (x), which has been calculated as the median value of the corresponding diameter class, as follows:

$$f = K x^{-\alpha} \quad (3)$$

where K and α are coefficients specific to respective parts. In the case of the values for stems, the shape can roughly be described as a cone, and the value of α is therefore nearly equal to 0. For the branches of *Pinus densiflora*, α was nearly equal to 1.5 (Yoda et al., 1965).

Rewriting equation 3 as a continuous function,

$$\phi(x)dx = K x^{-\alpha} dx \quad (4)$$

where $\phi(x)dx$ is equivalent to f in equation 3.

The volume of woody tissue ($dV(x)$) if a function of the diameter, which ranges between x and $x+dx$ is given by

$$dV(x) = K' \phi(x) x^2 dx \quad (5)$$

The total volume (V) of a woody organ (stem/branches) is then obtained by integrating equation 5 over the whole range of diameters from x_{\min} to x_{\max} .

$$V = \int_{x_{\min}}^{x_{\max}} dV(x) = KK' \int x^{2-\alpha} dx = \frac{KK'}{3-\alpha} \left[x^{3-\alpha} \right]_{x_{\min}}^{x_{\max}} \quad (6)$$

$$\text{Therefore, } KK' = \frac{V(3-\alpha)}{(x_{\max})^{3-\alpha} - (x_{\min})^{3-\alpha}} \quad (7)$$

On the other hand, the total maintenance respiration rate (R_t) in stem or branches per tree can be calculated by the integration of their entire range from the minimum diameter, x_{\min} (cm), to the maximum diameter, x_{\max} (cm), as follows:

$$R_t = \int_{x_{\min}}^{x_{\max}} r(x) dV(x) \quad (8)$$

where $r(x)$ is stem/branch respiration rate at x diameter.

From equations 6, and 8,

$$R_t = \int_{x_{\min}}^{x_{\max}} r(x) KK' x^{2-\alpha} dx \quad (9)$$

Inserting equation 7 to 9,

$$R_t = \frac{V(3-\alpha)}{x_{\max}^{3-\alpha} - x_{\min}^{3-\alpha}} \int_{x_{\min}}^{x_{\max}} r(x) x^{2-\alpha} dx \quad (10)$$

In order to collect the fundamental data needed for equation 10, a tree census was conducted. The total volume of each tree in the study site was calculated using the allometric relationship based on measurements taken from five sample trees.

3. Results

The respiration rate per unit of surface area at 20 (${}_{20}R_{sur}$) was not

significantly correlated with stem/branch diameter ($p=0.407$). Its value on average was $0.81 (\pm 0.31) \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Fig. 1A). The respiration rates per unit of stem volume at 20 $(_{20}R_{vol})$ decreased with increasing diameter in both stems and branches ($p<0.0001$, Fig. 1B).

$$_{20}R_{vol} = 168.55 x^{-0.7841} \quad (R^2=0.67, n=23) \quad (11)$$

where x is stem/branch diameter (cm). In this study, the diameter can explain approximately 67% of the variation in respiration rate.

Q_{10} values also decreased with increasing diameter in both stems and branches (Fig. 2A), and the time lag became longer with increasing diameter (Fig. 2B).

$$Q_{10} = 5.8023 x^{-0.4516} \quad (R^2=0.75, n=23) \quad (12)$$

From the results above, stem/branch respiration rate at x diameter, $r(x)$, can be calculated by inserting equations 11 and 12 to equation 2, as follows:

$$r(x) = A x^B \quad (13)$$

where $A=168.55 \times 5.8023^t$, and $B=-0.7841-0.4516t$. $t=(T-20)/10$. T is an hourly mean stem temperature.

Inserting equation 13 to 10,

$$R_t = \frac{V(3-\alpha)}{x_{\max}^{3-\alpha} - x_{\min}^{3-\alpha}} \int_{x_{\min}}^{x_{\max}} A x^{2-\alpha+B} dx \quad (14)$$

Equation 14 means that a stem (R_{stem}) or branch (R_{branch}) maintenance

respiration rate for any given tree can be calculated only if the values of α , A , B , x_{\min} , x_{\max} , and V are known. Since x_{\min} is usually far smaller than x_{\max} in trees of ordinary size, it is possible to put $x_{\min} = 0$. Then equation 14 can further be transformed as follows:

$$R_{stem} = \frac{3V_s}{x_{\max}^3} \frac{A}{B+3} x_{\max}^{(B+3)} \quad (\text{for stem, } \alpha=0) \quad (15)$$

and

$$R_{branch} = \frac{1.5V_b}{x_{\max}^{1.5}} \frac{A}{B+1.5} x_{\max}^{(B+1.5)} \quad (\text{for branch, } \alpha=1.5) \quad (16)$$

where V_s and V_b are the total volume of stem and branch per tree, respectively.

On the other hand, x_{\max} of stem and branch were estimated by the empirical formula of Yoda et al. (1965) as follows:

$$x_{\max} = 1.065 \times D \quad (\text{for stem}) \quad (17)$$

and

$$x_{\max} = 0.25 \times D \quad (\text{for branch}) \quad (18)$$

where D is the diameter (cm) at breast height (1.3 metres above the ground).

The total volume of stems (V_s , m^3) and branches (V_b , m^3) per tree can be estimated from D and tree height (H , m) by the following allometric equations.

$$V_s = 0.0001(D^2 H)^{0.8974} \quad (R^2=0.99, n=5) \quad (19)$$

and

$$V_b = 2 \times 10^{-5} (D^2 H)^{0.8801} \quad (R^2=1, n=5)$$

(20)

Based on the tree census (D and H) used in the present study site, x_{\max} , V_s , and V_b were estimated by equation 17, 18, 19, and 20 for all trees in the study area.

V_s and V_b of the 25-30 cm class was the greater value, and occupied 37.8%, and 37.6% of the total volume, respectively (Table 2). Total V_s and V_b was 236.88 and 40.56 m³ ha⁻¹, respectively.

The annual maintenance respiration rates of the stems and branches of all trees in the stand were estimated for the year 2002 (Table 3) by utilizing equations 15 and 16, the results of the tree census, and the hourly mean stem temperature.

From the distribution of annual maintenance respiration rates for each D class, the stem and branch respiration rates of the D 25-30 cm class were the highest, and accounted for 33% and 31% of the total respiration rate, respectively (Table 3). The annual maintenance respiration of aboveground woody organs was 2.55 tCha⁻¹yr⁻¹. Stem and branch respiration accounted for 55% (1.40 tCha⁻¹yr⁻¹) and 45% (1.15 tCha⁻¹yr⁻¹) of the total respiration, respectively.

Figure 3 shows the seasonal change in the stand maintenance respiration rates of the stem and branch components, and the change in stem temperatures for

Japanese red pine trees. During the summer season, branch respiration rates were higher than those for stem respiration, while during other seasons the relationship was reversed. This was due to the higher Q_{10} value of small diameter branches (Fig. 2A).

Assuming that stem/branch respiration rate per unit of surface area (${}_{20}R_{\text{sur}}$) is constant, the aboveground woody respiration rate can be calculated by exchanging ${}_{20}R_{\text{vol}}$ for ${}_{20}R_{\text{sur}}$ ($0.81 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$), and V_s (or V_b) for S_s (or S_b) in the equations above, where S_s and S_b are the total surface area of stem and branch per tree, respectively.

The total surface area of the stem value (S_s , m^2) and the branch value (S_b , m^2) per tree can be estimated from D and H by the following allometric equations:

$$S_s = 0.024(D^2 H)^{0.6121} \quad (R^2=0.99, n=5) \quad (21)$$

and

$$S_b = 0.0002 \times 10^{-5} (D^2 H)^{1.0527} \quad (R^2=0.98, n=5) \quad (22)$$

The seasonal pattern in respiration rates calculated using ${}_{20}R_{\text{sur}}$ was similar to that calculated using ${}_{20}R_{\text{vol}}$. The annual maintenance respiration rate for stem and branch values calculated using ${}_{20}R_{\text{sur}}$ was 1.13, and 0.59 $\text{tCha}^{-1}\text{yr}^{-1}$, and this was 18% and 49% lower, respectively, than that calculated by ${}_{20}R_{\text{vol}}$.

The relationship between the annual amount of maintenance respiration for

an individual tree and D^2H satisfied the power functions, as shown in equation 23 and 24 (Figure 4).

$$R_{stem} = 0.0002(D^2H)^{0.6193} \quad (R^2=1, n=40) \quad (23)$$

and

$$R_{branch} = 0.003(D^2H)^{0.5271} \quad (R^2=1, n=40) \quad (24)$$

These relationships seem to be adequate for estimating the total aboveground woody respiration in Japanese red pine trees.

4. Discussion

Yoda (1967), Yoda et al. (1965), and Hagihara and Hozumi (1981) reported that the respiration rate per unit of fresh weight decreased with increasing diameter. In this study, the respiration rate per unit of volume decreased with increasing diameter. The result in this study concurs with those of the three aforementioned studies, because woody fresh weight is proportional to volume. Levy and Jarvis (1998) reported that there was a positive linear relationship between the reciprocal of stem diameter and the flux per unit of volume. Their result was the same as our result. However, we used the relationship between the diameter and respiration rate per unit of volume leveling order to estimate the respiration rate for the stand, because the coefficient of correlation (R^2) between the stem diameter and the respiration rate per unit of volume was higher than the

R^2 value obtained by their approach.

Many previous researchers reported that the values of Q_{10} decreased in the summer (Carey et al., 1997; Lavigne, 1996; Maier, 2001; Paebonan et al., 1991; Stockfors 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, and 1.92 in August and 2.55 in June, respectively. However, Q_{10} of stem and branches decreased with increasing diameter when respiration rate was regressed against the stem temperature at the specific position. Q_{10} ranged from 1.28 to 6.4 during the same period (September to October, 2003) (Fig. 2A). The variation was higher than the seasonal variation reported by Lavigne (1996) and Paembonan et al. (1991) with measurements throughout the year. Q_{10} values measured by Lavigne (1996) on *Pinus banksiana*, and by Paembonan et al. (1991) on *Chamaecyparis obtuse* were between ca. 1.5 and 3. Q_{10} is a very important component of the respiration rate estimate, but many previous researchers mentioned above noted only the relationship between Q_{10} and temperature, and recorded the seasonal variation in Q_{10} values. According to the results of this study, in order to estimate the total stem/branch respiration rate of an individual tree or an entire stand, it may be more important to consider the variation in Q_{10} (or temperature) within a tree than to regard the seasonal variation in its Q_{10}

values. The variation in Q_{10} within a tree can be explained by the heterogeneity of organ temperatures along height, diameter, and bark thickness, which is due to differences in response to the heat energy which has been transferred from sunlight to the stems and branches (Kakubarri, 1988; Stockfors, 2000), that is, small stems and branches gain and lose the heat energy faster than large ones. This suggestion can also explain about the positive relationship between time lag and diameter (Fig. 2B). In this case of Japanese red pine trees, the diameter represents the combination of height and bark thickness; that is, if the diameter is large, the height is lower, and the bark is thicker. Another important factor for the variation in Q_{10} and lag time was the CO_2 transported in xylem sap (Negisi, 1972, 1979; Teskey and McGuire, 2002, 2005). Some of the CO_2 respired from woody tissue is carried upward in the xylem sap rather than diffusing outward through the bark. Damesin et al. (2002) also found that Q_{10} values in the stem decreased as stem diameter increased, and that the Q_{10} values for branches were higher, although the range of Q_{10} values was smaller than the one in the present study.

The annual aboveground woody tissue maintenance respiration (R_A) calculated using ${}_{20}R_{vol}$ was $2.55 \text{ tCha}^{-1}\text{yr}^{-1}$ and the R_A calculated using ${}_{20}R_{sur}$ was $1.72 \text{ tCha}^{-1}\text{yr}^{-1}$. The result showed that branch respiration was an important component of the total aboveground woody respiration at stand level (about

45% or 34%). Our results ($2.55 \text{ tCha}^{-1}\text{yr}^{-1}$ for volume base, $1.72 \text{ tCha}^{-1}\text{yr}^{-1}$ for surface area base) for the Japanese red pine stand studied were compared with the previous studies (Table 4). Our values were close to the ones indicated by Yokota and Hagihara (1995) for a stand of 8-year-old *Chamaecyparis obtuse* ($2.4 \text{ tCha}^{-1}\text{yr}^{-1}$), by Meir and Grace (2002) for a tropical rain forest (2.06 to $2.18 \text{ tCha}^{-1}\text{yr}^{-1}$), and by Damesin et al. (2002) for a stand of 30-year-old *Fagus sylvatica* (1.54 to $1.82 \text{ tCha}^{-1}\text{yr}^{-1}$). Our values were higher than the values reported by Ryan et al. (1997) for a boreal forest (0.12 to $0.68 \text{ tCha}^{-1}\text{yr}^{-1}$), by Ryan et al. (1995) for four conifers, ponderosa pine, western hemlock, red pine, and slash pine (0.52 to $1.62 \text{ tCha}^{-1}\text{yr}^{-1}$), by Edwards and Hanson (1996) for an oak forest (0.83 to $1.10 \text{ tCha}^{-1}\text{yr}^{-1}$) and by Ryan and Waring (1992) for a stand of 40-, 65-, and 245-year-old *Pinus contorta* ssp. *latifolia* (0.61 to $0.79 \text{ tCha}^{-1}\text{yr}^{-1}$). Stand respiration values are very different among these studies and interspecies comparisons are difficult because climate, tree density, age and scaling-up methods differ among them (Damesin, 2002). However, Meir and Grace (2002) found that there was a very strong relationship between annual aboveground woody tissue respiration (combined maintenance with growth respirations) and leaf area index (LAI). According to our and previous results for annual aboveground woody tissue maintenance respiration at stand level (Table 4), the R_A (only maintenance respiration) showed a positive relationship with annual

mean temperature and LAI, and showed a negative relationship with stand age and latitude. This indicates that the woody tissue maintenance respiration will be roughly estimated by a forest stand states (location, climate, and age *etc.*) irrespective of vegetation type.

Acknowledgments

We would like to thank Dr H. Sakugawa for his permission to carry out this study at the ecological tower in Higashi-Hiroshima city, Japan. We also would like to thank Dr S.J. Joo and Dr M.H. Yim for their helpful discussions, and Dr J.H. Yoon, Dr S.J. Moon, and Mr T.S. Jo for fieldwork assistance.

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Explanation of Tables

Table 1. Measuring periods and characteristics of sampled stem/branch segments.

Table 2. Tree density, stem volume (V_s), and branch volume (V_b) of each D class for Japanese red pine trees in the study site.

Table 3. Annual woody tissue maintenance respiration rate for each D class of Japanese red pine trees in the study site.

Table 4. Comparison of each stand characteristic and aboveground woody tissue maintenance respiration estimated at a various forest stands.

Table 1.

Sample stems/branches	Measuring periods	Height of sampling point (m)	Diameter of sampling point (cm)
Sample 1	Sep. 27 – 29	2.5	29.6
Sample 2	Sep. 27 – 29	2.5	24.6
Sample 3	Sep. 27 - 29	2.5	24.5
Sample 4	Sep. 27 – 29	2.5	21.7
Sample 5	Sep. 27 – 29	2.5	21.5
Sample 6	Sep. 27 – 29	2.5	20.7
Sample 7	Sep. 27 – 29	2.5	17.0
Sample 8	Sep. 27 – 29	2.5	13.9
Sample 9	Sep. 27 – 29	2.5	11.7
Sample 10	Sep. 30 - Dec. 3	2.5	22.8
Sample 11	Sep. 30 - Dec. 3	1.8	34.8
Sample 12	Sep. 30 - Dec. 3	3.8	30.0
Sample 13	Sep. 30 - Dec. 3	7.2	27.1
Sample 14	Sep. 30 - Dec. 3	14.3	16.6
Sample 15	Sep. 30 - Dec. 3	9.4	25.2
Sample 16	Sep. 30 - Dec. 3	12.3	22.1
Sample 17	Sep. 30 - Dec. 3	15.4	12.5
Sample 18*	Sep. 30 - Dec. 3	13.8	8.7
Sample 19*	Sep. 30 - Dec. 3	11.4	8.0
Sample 20*	Sep. 30 - Dec. 3	14.8	4.9
Sample 21*	Sep. 30 - Dec. 3	15.9	4.8
Sample 22*	Sep. 30 - Dec. 3	15.3	3.5
Sample 23*	Sep. 30 - Dec. 3	14.2	3.1

* is branches.

Table 2.

D class (cm)	Number of trees (trees ha ⁻¹)	V_s (m ³ ha ⁻¹)	V_b (m ³ ha ⁻¹)
5~10	125	5.54	0.98
10~15	250	21.49	3.77
15~20	225	37.31	6.47
20~25	125	36.71	6.29
25~30	200	89.59	15.23
35~40	75	46.24	7.82
Total	1000	236.88	40.56

Table 3.

D class (cm)	Respiratory consumption (t C ha ⁻¹ yr ⁻¹)			Relative respiration of D class (%)
	Stem	Branch	Stem + Branch	
5~10	0.059	0.058	0.117	4.6
10~15	0.187	0.173	0.360	14.1
15~20	0.262	0.227	0.489	19.1
20~25	0.214	0.174	0.388	15.2
25~30	0.463	0.361	0.824	32.2
35~40	0.216	0.162	0.378	14.8
Total	1.400	1.155	2.555	100

Table 4.

Dominant species	Stand age (yr)	Latitude (°)	Temp. ()	Prec. (mm yr ⁻¹)	BA	LAI	R _A	Base	References
<i>Pinus contorta</i> ssp. <i>latifolia</i>	40	39	2	740	35.2	12.3	0.61	Sapwood volume	Ryan and Waring (1992)
<i>Pinus contorta</i> ssp. <i>Latifolia</i>	65	39	2	740	40.4	12.1	0.74	Sapwood volume	Ryan and Waring (1992)
<i>Pinus contorta</i> ssp. <i>Latifolia</i>	245	39	2	740	44.7	7.7	0.79	Sapwood volume	Ryan and Waring (1992)
<i>Chamaecyparis obtuse</i>	8	35	15	1543	-	-	2.4	Dry weight	Yokota and Hagihara (1995)
<i>Pinus resinosa</i>	31	46	3	804	42.4	6.2	0.7	Sapwood volume	Ryan et al. (1995)
<i>Tsuga heterophylla</i> , <i>Pseudotsuga menziesii</i>	39	45	9	1320	67	8.7	1.62	Sapwood volume	Ryan et al. (1995)
<i>Pseudotsuga elliotii</i> var. <i>elliotii</i>	24	29	22	1180	26.1	2.2	1.46	Sapwood volume	Ryan et al. (1995)
<i>Quercus alba</i> , <i>Q. prinus</i> , <i>Acer rubrum</i>	40-75	35	13.3	1400	21.5	5	0.83- 1.10	Sapwood volume	Edward & Hanson (1996)
<i>Picea mariana</i>	150	55	-	542	32	4.9	0.57	Surface area	Ryan et al. (1997)
<i>Pinus banksiana</i>	63	55	-	542	17	2.2	0.12	Surface area	Ryan et al. (1997)
<i>Populus tremuloides</i>	53	55	-	542	34	2.2	0.42	Surface area	Ryan et al. (1997)
<i>Picea mariana</i>	115	53	-	390	36	5.6	0.48	Surface area	Ryan et al. (1997)

<i>Pinus banksiana</i>	63	53	-	390	13	2.5	0.17	Surface area	Ryan et al. (1997)
<i>Populus tremuloides</i>	68	55	-	390	27	3.3	0.68	Surface area	Ryan et al. (1997)
<i>Pinus banksiana</i>	14	53	-	390	9.1	2.8	0.21	Surface area	Ryan et al. (1997)
<i>Fagus sylvatica</i>	25-35	48	9.2	820	17.5	5.6	1.54	Volume	Damesin et al. (2002)
<i>Fagus sylvatica</i>	25-35	48	9.2	820	17.5	5.6	1.82	Surface area	Damesin et al. (2002)
Sterculiaceae, Ulmaceae,	-	3	23-26	1520	-	4.4	2.06-	Surface area,	Meir and Grace (2002)
Leguminosae							2.18	Volume	
<i>Pinus densiflora</i>	40	34	13.5	1494	29.54	-	2.55	Volume	This study
<i>Pinus densiflora</i>	40	34	13.5	1494	29.54	-	1.72	Surface area	This study

Note: Basal area ($\text{m}^2 \text{ ha}^{-1}$); LAI: Leaf area index ($\text{m}^2 \text{ m}^{-2}$); R_A : annual aboveground woody tissue maintenance respiration rate ($\text{tCh}^{-1} \text{ yr}^{-1}$).

Explanation of Figures

Figure 1. Relationships between respiration rates per unit of surface area (A) or per unit of volume (B) and stem/branch diameter at 20°C. The fitted line corresponds to the function described in equation 10.

Figure 2. Relationships between Q_{10} (A) or time lag (B) and diameter of stems/branches. The regression lines: $y = 5.8023x^{-0.4516}$ ($R^2 = 0.75$) for Q_{10} , and $y = 1.8109\ln(x) - 1.333$ ($R^2 = 0.73$) for time lag.

Figure 3. Seasonal changes in stem and branch respiration rates per ground surface calculated using $_{20}R_{vol}$, and in stem temperature for Japanese red pine trees.

Figure 4. Relationships between annual amount of maintenance respiration of individual trees and D^2H . The lines correspond to the relationships given by equations 23 for stems and 24 for branches.

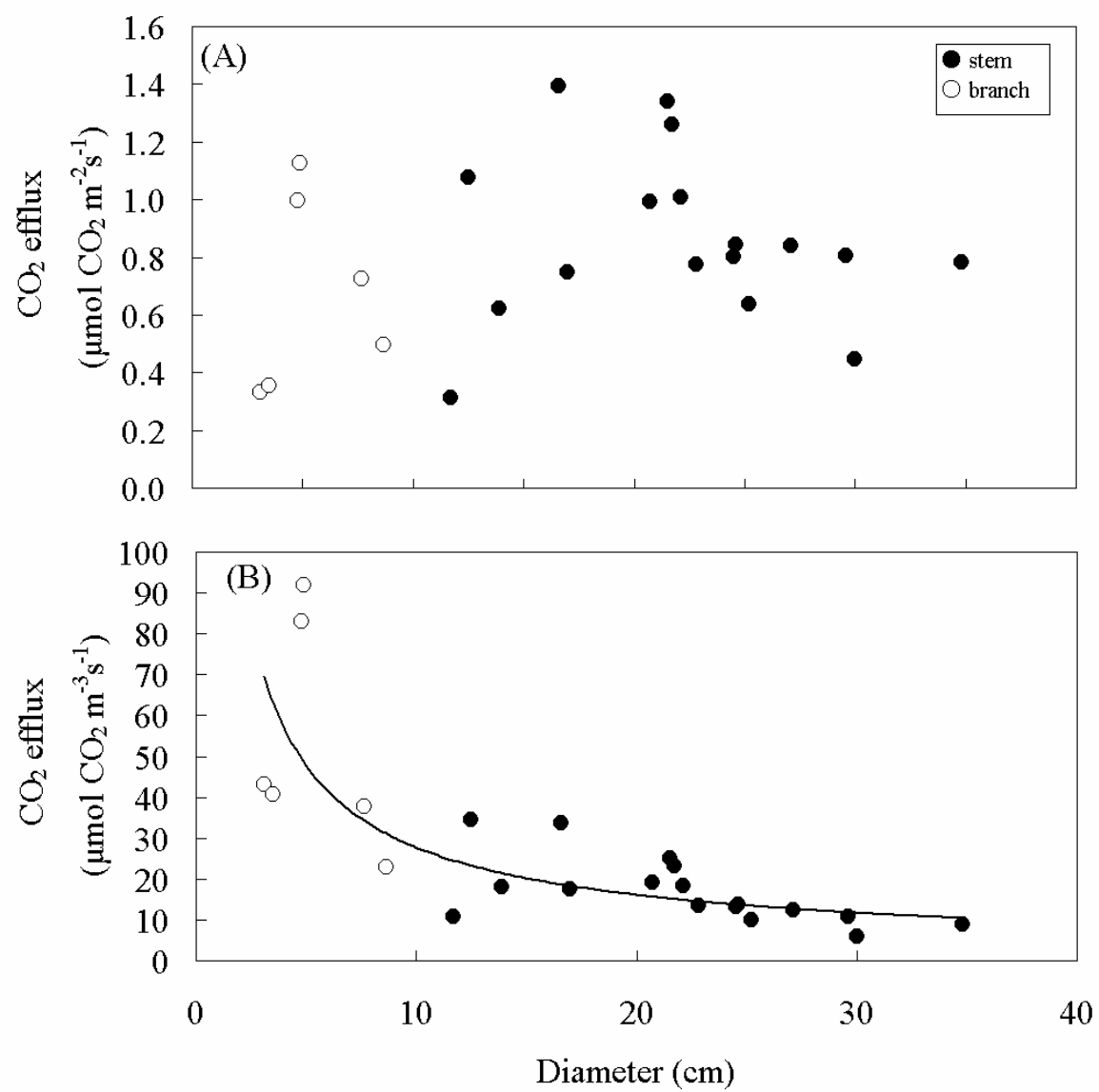


Figure 1.

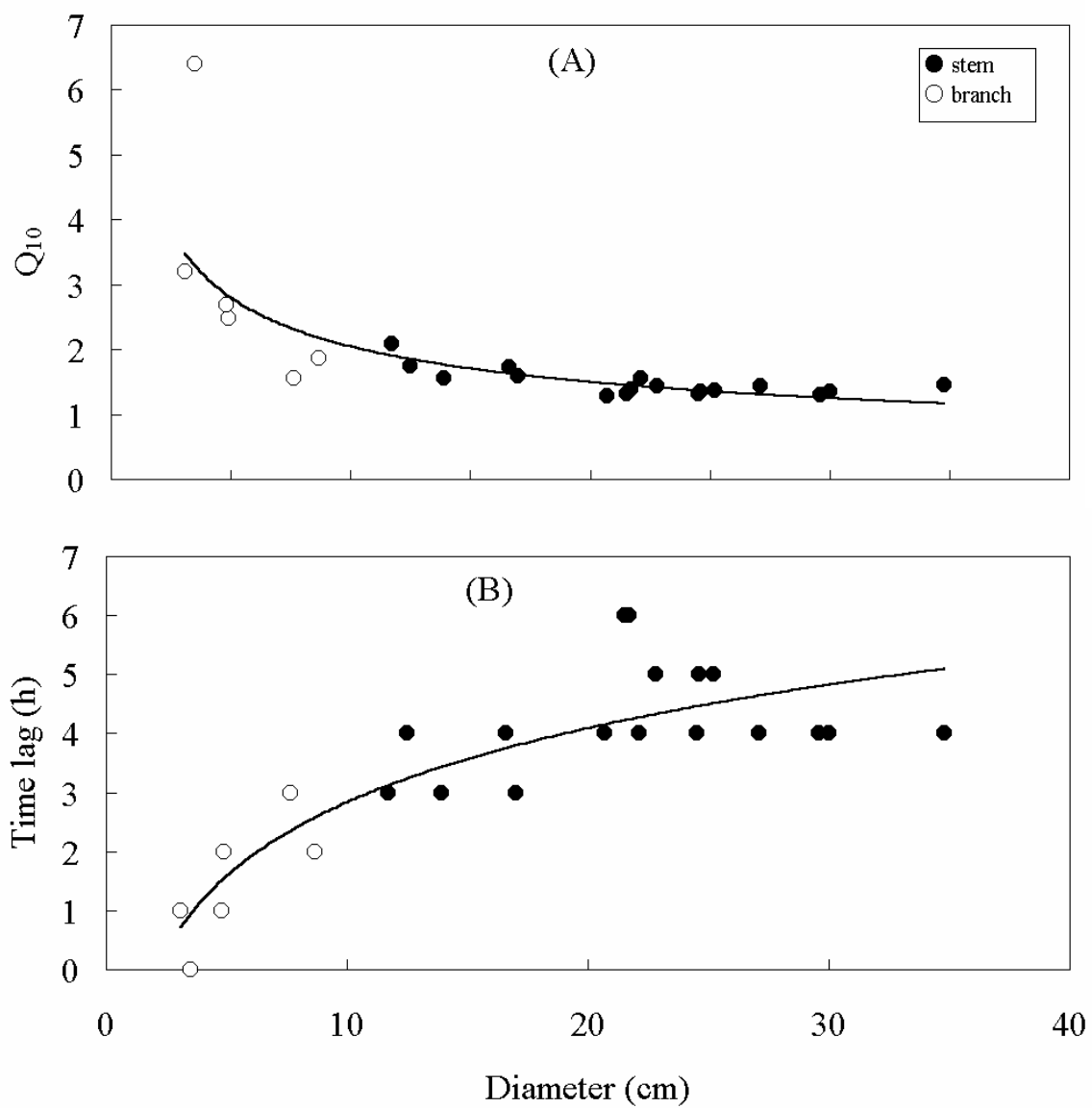


Figure 2.

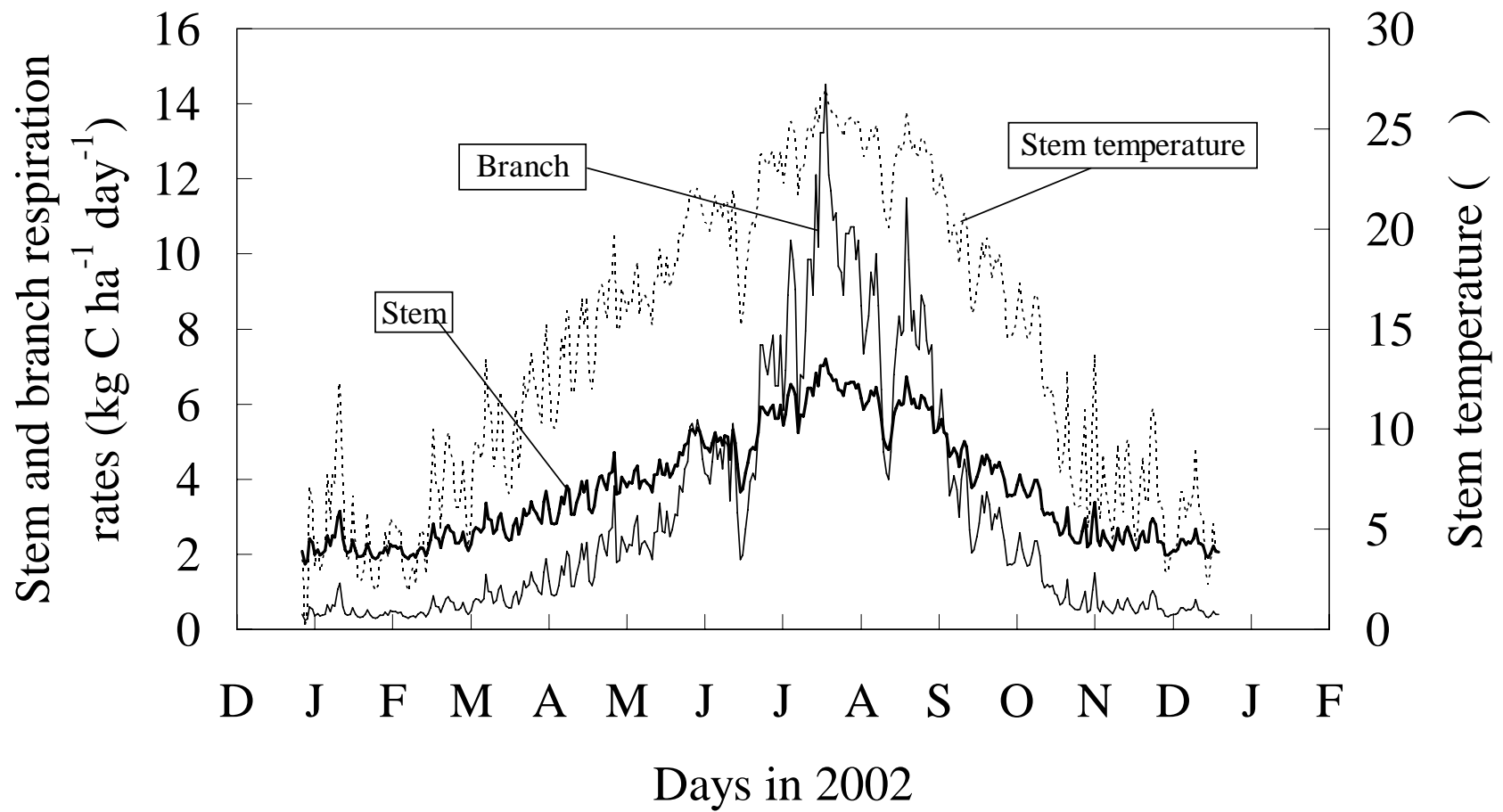


Figure 3.

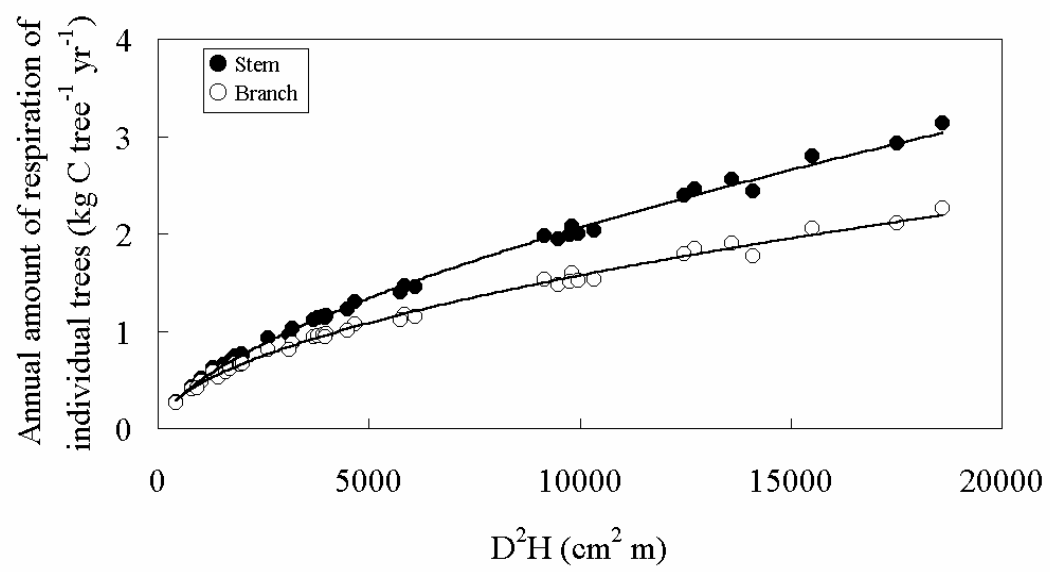


Figure 4.