Chapter 15
Respiration of Larch trees

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15.1   Introduction

Modeling of trees based on whole-plant physiology is a powerful tool to understand function and structure of forest ecosystems (Yoda et al. 1963; Hozumi and Shinozaki 1974; McCree 1983; Sievänen et al. 1988; Hagihara and Hozumi 1991; Mori and Hagihara 1991; Shugart et al. 1992; Watanabe et al. 2004). In particular, whole-plant carbon budget is a sensitive and biologically meaningful indicator to understand plant responses to environmental changes (McCree 1986, 1987; Adams et al. 1990; Gonzàlez-meler and Siedow 1999; Tjokelker et al., 1999). Single-leaf physiology does not predict plant growth and productivity, since individual leaves do not always reflect the physiological behavior of the whole-plant (Sims et al. 1994; Hikosaka et al. 1999). Nevertheless, whole-plant physiological characteristics have been measured only in crops, grasses, horticultural crops, and juvenile trees, whose body sizes are relatively small compared to mature forest trees (Geis 1971; Peters et al. 1974; Reicosky and Peters 1977; Garrity et al. 1984; Meyer et al. 1987; Dutton et al. 1988; Graham 1989; Berard and Thurtell 1990; Bower et al. 1998; Nogués et al., 2001). Because measurement of mature trees requires extensive set-up for controlling temperature and gas exchange, air conditioning units (Meyer et al. 1987) with supply of alternating current are commonly required. However, such a system is generally unavailable in the field in remote areas. In particular, boreal and tropical forests are usually located at remote sites, where elaborate measurement set-up cannot be operated. Therefore, a new system is necessary for measuring the whole-tree respiration with relatively simple equipment.

   Respiratory consumption in forest ecosystems is thought to be the main parameter determining CO_2 budget (Valetini et al. 2000). Plant respiration is generally affected by a small number of environmental factors (mainly temperature) in contrast to photosynthesis (light, temperature, and other factors) (e.g., Sprugel et al. 1995). Therefore, plant respiration would be a good indicator to evaluate the carbon budget. Particularly, temperature dependency of whole-tree respiration will be an important information in predicting response of a given forest ecosystem to warming temperature. However, previous studies on whole-tree respiration have been generally

restricted to night measurements without temperature controls (Ninomiya and Hozumi 1981, 1983a; Adu-bredu et al. 1996a, 1996b; Yokota and Hagihara 1996, 1998). Therefore, improvements are required of such methods in order to estimate both daytime and night respiration rates more accurately.

Such a system for whole-tree respiration measurement was developed for use in intact trees in the field, under regulated air-temperature. It uses a closed air-circulation system that does not require constant supply of alternating electric current. This method was then applied for trees in an old stand of *Larix gmelinii* (Rupr.) Rupr in Central Siberia. This species is distributed widely in the continuous permafrost region, often as monospecific stands (see Chap. 1), and seems to play a key role in terrestrial carbon cycling of boreal forests. Extent of annual carbon fixation and release by heterotrophic soil respiration in old larch forests in Siberia appears small (see Chaps. 6, 9, and 10), but the process of CO_2 consumption by autotrophic respiration still remains unclear.

In this chapter, we first introduce the new system for measuring whole-tree respiration, and discuss its methodological advantages and limitations. Second, we examine temperature dependency of *L. gmelinii* tree respiration and its variation in relation to individual size. Third, we estimate stand-level aboveground total respiration rate during a growing season, then discuss how the respiratory CO_2 release is associated with aboveground net primary production (ANPP) and net ecosystem production (NEP) in the permafrost larch forest.

15.2 Approaches and Measurement System

15.2.1 Study Site

Whole-tree aboveground respiration was measured in an old multiaged *L. gmelinii* stand (>220 years-old; plot C1) of Site 2 located near the settlement of Tura, Central Siberia (64°N, 100°E) (location see Fig. 1.3). Detailed characteristics of this stand are summarized in Fig. 6.1 and Table 6.1, and climate, and geological and floristic conditions of the study area are described elsewhere (Chaps. 1 and 2).

Measurement of whole-tree aboveground respiration was conducted during two summers (from July to August in 1997–1998). During the periods, thickness of soil active layer (i.e., depth from the ground surface to permafrost table) was about 30 cm.

15.2.2 Setting Whole-Plant Chamber

Sample trees (details see Sect. 15.2.6) were enclosed singly in a cylindrical whole-plant dark chamber. The chamber was fixed at 1.2 m in diameter, but its length was flexible from 4 to 9 m according to tree height. We framed the chamber using flexible

fiberglass rings (Fig. 15.1b), so that volume of the chamber is calculated easily. Around these sample trees, we constructed a wooden tower of about 10 m tall to hang the chamber (Figs. 15.1a and 15.2). The chamber was made of three kinds of films: 0.2 mm thick polyvinyl chloride transparent film at the very inside to keep CO_2 tightness, 0.03 mm thick polyvinyl chloride black film to achieve total darkness, and double layered 0.015 mm thick aluminum-coating films to reflect radiation.

Fig. 15.1 A chamber enclosing a standing *L gmelinii* tree (No.2). (**a**) The chamber was hanged from a mast system set at the top of a wooden tower. (**b**) Inside view of a chamber. Volume, length, and diameter of the chamber were about 9 m³, 8 m, and 1.2 m, respectively (photo: Mori)

After measuring larger trees, we cut and removed the bottom of the long chamber for enclosing smaller trees. The chamber volume ranged from 4.3 to 10 m³.

15.2.3   Closed Air-Circulation System

A closed air-circulation was achieved by connecting the whole-plant chamber to a heat exchanger with air ducts of 20 cm in diameter (Fig. 15.2). After enclosing a sample tree, we circulated the enclosed air by an electric fan equipped at the upper part of the heat exchanger. As shown in Fig. 15.1b, launched air tracked up the air duct to the top of the chamber. The air duct bore small holes on the sidewall to avoid heterogeneous CO_2 concentration within the chamber. We set a bypass to the closed air-circulation system, which acted as a transient CO_2 scrubber. This was detached from the system by two air-shutters during measurement. We kept air-tightness at the connection of the stem and the chamber by clogging clay that does not absorb CO_2. A preliminarily test of air-leakage showed no decrease in CO_2 concentration at about 900 ppm for about 30 min.
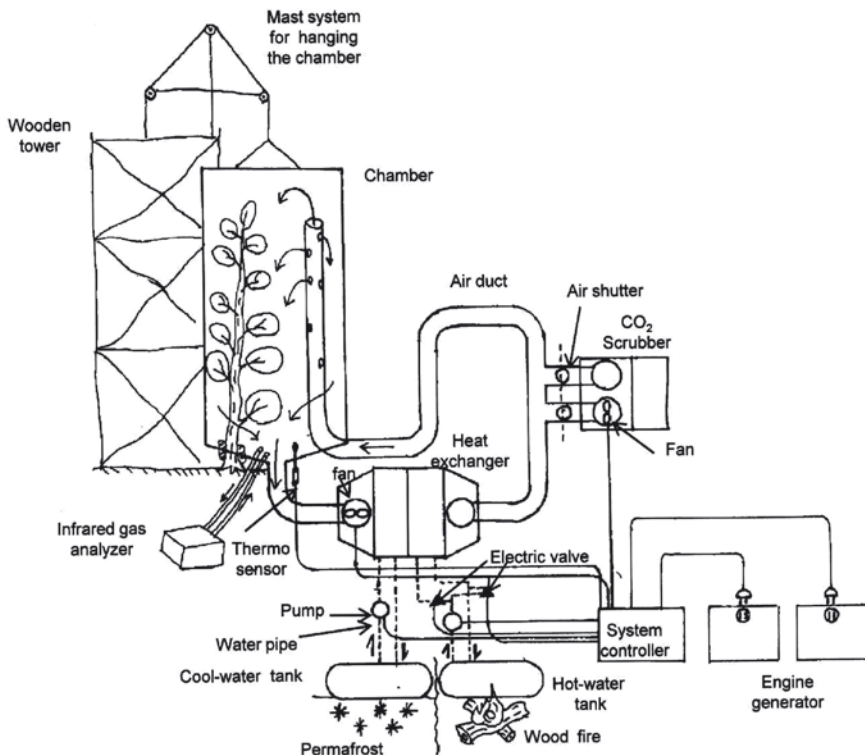

Fig. 15.2 Schematic representation of the system of whole-tree respiration measurement (modified from Mori et al. 1997)

15.2.4   CO$_2$ Scrubber

The scrubber consisted of an air filter filled with soda-lime granules to absorb CO_2 (Fig. 15.2). Before the measurement, we reduced CO_2 concentration within the system to the field level to avoid CO_2 leakage from the closed system. Bouma et al. (1997) reported that high CO_2 partial pressure did not disturb respiration. Therefore, we did not eliminate high CO_2 partial pressure in the closed system.

15.2.5   Temperature Control

To control air temperature within the chamber, we utilized natural heat energy generated from wood fire and permafrost (Fig. 15.2). Natural heat energy was captured by two steel water tanks of about 40 L each. The tank for cooling was buried under ground to have a direct contact with frozen soil (i.e., permafrost table was about 30 cm deep). The tank for hot water was heated by wood fire. We circulated the hot and cool water from the tanks to a heat exchanger through water pipes (Fig. 15.2). Hot water flow was continuously regulated by two electric water valves and the cool water flow by turning the water pump on and off through the PID controlled algorithm program on a personal computer. The air circulated about 50 times per hour in the largest-sized chamber; we confirmed that this rate was enough to maintain an even CO_2 environment within the chamber. Heating and cooling ability of the heat exchanger (Hokkaido DALTON Co., Sapporo, Japan) were 1 and 0.6 kW h^{-1}, respectively, when the air temperature and relative humidity within the chamber were 20°C and 60%, respectively. We operated the system using two handy engine generators of 5 kg and 352 VA power output (KH350HA, Kokusan Electric Co. Ltd., Shizuoka, Japan).

15.2.6   Measurement of Whole-Tree Respiration

Breast-height stem diameter (DBH) and tree height of six *L. gmelinii* trees examined were as follows: 9.6 cm and 8.8 m (No.1), 8.0 cm and 7.7 m (No.2), 7.6 cm and 6.9 m (No.3), 6.3 cm and 6.4 m (No.4), 3.4 cm and 4.2 m (No.5), and 3.0 cm and 4.1 m (No.6). Among them, two individuals (No.2, 4) were selected for assessing temperature dependency of respiration by changing air-temperature within the chamber at various levels (from ca.10 to 30°C). This measurement was conducted on the same day, and $n > 20$ datasets (respiration vs. temperature) were obtained for each tree. Respiration rates of the other four trees were measured at a given level of controlled-temperature (around 20°C).

For all trees, relatively short incubation period was applied, ranging from 20 to 60 s. CO_2 concentration within the chamber was measured every 2 s by the portable gas analyzer (LI-6200, LI-COR, Lincoln, USA). A whole-tree aboveground

respiration R (expressed by μmole mole^{-1} tree^{-1} s^{-1}) was calculated with the following equation:

$$R = V(273.2 / (273.2 + \theta))(10^3 / 22.4)\, dC / dt, \tag{15.1}$$

where V is chamber volume (m^3), θ is air-temperature inside chamber (°C), and dC is increment of CO_2 concentration during incubation time of dt. The term dC/dt indicates a mean increment rate of CO_2 concentration (μmole mole^{-1} tree^{-1} s^{-1}). The (15.1) assumes that respiration is measured under standard barometric pressure and the volume of enclosed tree was negligible compared to the chamber volume (Yokota et al. 1994).

15.3   System Response and Estimated Tree Respiration

15.3.1   Temperature Control of the System

For the sample trees No. 2 and No. 4, air temperature within the chamber was increased step by step according to the program. In the case of tree No.2 (Fig. 15.3), for example, we regulated air-temperature inside the chamber (shown by closed squares; chamber volume 8 m^3) to closely follow the programmed course of temperature (open squares) from 15 to 27°C. We also minimized overshooting of air temperature by the PID algorithm for realizing respiration measurement under stable air temperature. The temperature within this large chamber was efficiently controlled, even if the programmed temperature was about 10°C higher than the ambient air temperature (closed squares in Fig.15.3). Similar result was obtained for the other tree (No.4) (Mori et al., unpublished data). Thus, the temperature could be adjusted to a target value with good accuracy; however, temperature inside the chamber was affected slightly by the ambient temperature when the difference became greater than 10°C (see diversion of filled circles and open circles between 14:50 and 15:50 in Fig. 15.3).

15.3.2   Temperature Dependency of Whole-tree Respiration

Figure 15.4 shows an example of the relationship between incubation time and CO_2 concentration observed for a larger tree (No.2) under regulated temperature condition. The CO_2 concentration increased linearly with time, and its mean increment rate (dC/dt) was about 0.056 μmole mole^{-1} tree^{-1} s^{-1} as indicated by a linear regression (Fig. 15.4). Likewise, CO_2 emitted by respiration accumulated almost constantly within the chamber in all cases. Thus, we calculated mean CO_2 increment rate (dC/dt) at each controlled-temperature, then determined the whole-tree respiration rate (R) using the (15.1).
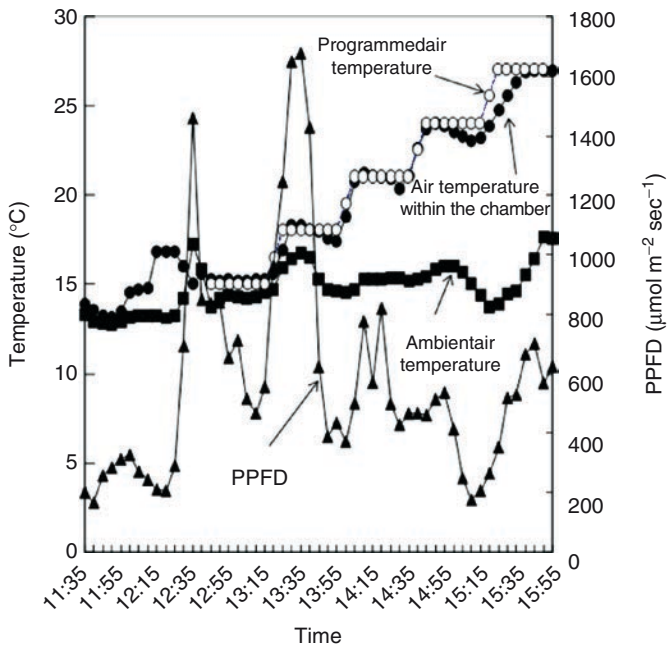
Fig. 15.3 Fluctuations in regulated air temperature within the chamber (*filled circle*), ambient air temperature (*filled square*), programmed air temperature (*open circle*), and photosynthetically active radiation (PPFD; *filled triangle*). Data were obtained from a large *L. gmelinii* tree (No.2) in mid-August (Mori et al., unpublished data)
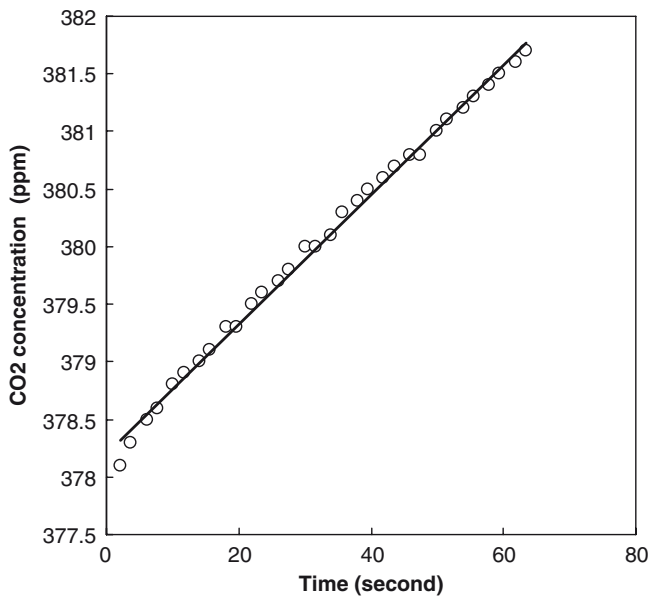

Fig. 15.4 An example of CO_2 increment (μmole mole^{-1} tree^{-1} s^{-1}) within the chamber. Data were obtained from a *L. gmelinii* tree No.4. Regression line was approximated by CO_2 [ppm] $= 0.0562\,t + 378.2$ ($r^2 = 1.00$) (Mori et al. unpublished data)

Exponential relationships were found between whole-tree aboveground respiration (R) and air-temperature inside chamber for two sample trees (Fig. 15.5). The value of R for a given temperature was much higher in the larger individual (No.2; closed circles) than in the smaller one (No.4; open circles). However, temperature dependency of R did not differ significantly between these trees ($p > 0.05$), though the regression slope appeared somewhat larger in No.2 (0.074) than that in No.4 (0.054). According to each regression, the extent of respiration increase per temperature increase of 10°C (i.e., Q_{10} value) was calculated to be 2.1 (No.2) and 1.7 (No.4).

15.3.3 Size Dependency of Whole-tree Respiration

Whole-tree respiration rate at 20°C (R^*) was positively correlated with stem diameter (DBH) among the six trees examined. Here, R^* was the corrected respiration value by assuming $Q_{10} = 2$ in all examined trees; the assumption was based on the similarity of temperature dependency of whole-tree aboveground respiration in the two sample trees (Fig. 15.5). The difference of R^* reached nearly tenfold between the smallest (DBH = 3 cm) and the largest (10 cm) individuals.
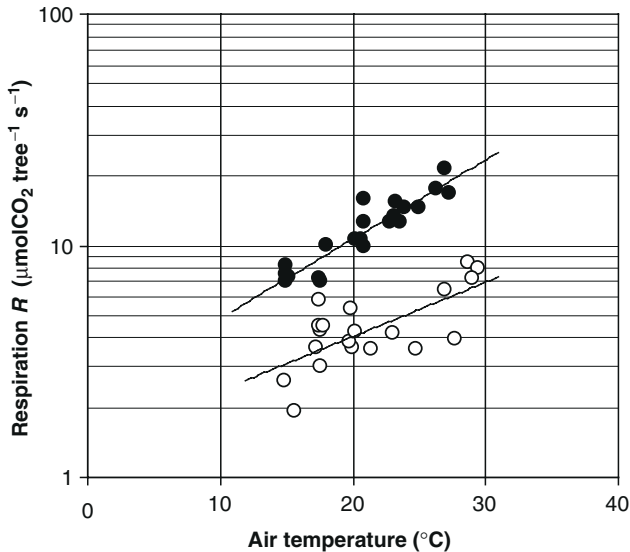

Fig. 15.5 Dependence of whole-plant respiration (R) on air-temperature (θ) for two *L. gmelinii* trees. Regression lines and symbols are as follows: $R = 2.22e^{0.074\theta}$ ($R^2 = 0.858$) for tree No.2 (*filled circle*), and $R = 1.38e^{0.054\theta}$ ($R^2 = 0.494$) for tree No.4 (*open circle*). Slopes of two regressions did not differ significantly ($F_{[1, 39]} = 2.54$, $p = 0.12$; ANCOVA) (Mori et al., unpublished data)

15.3.4 Estimation of Stand-Level Aboveground Respiration

We estimated stand-level respiration rate of the old multiaged *L. gmelinii* forest by applying the mean-sized method proposed by Ninomiya and Hozumi (1983b). Stand-level respiration is obtained by multiplying a respiration rate of the mean-sized tree by tree density of the forest. The estimate by this approach was reported to be similar to those estimated by two other methods (Ninomiya and Hozumi 1983b). Tree No.4 was selected as the mean tree, since its size was the closest to the mean DBH (6.3 vs. 6.8 cm) of the study stand.

Daily whole-tree aboveground respiration rate was calculated as the value at daily mean air-temperature by using the coefficients of regression between temperature and *R* for the sample tree (Fig. 15.5), and stand-level respiration was obtained by multiplying it by tree density (1,910 ha^{-1}). We assumed that respiration occurred potentially during four summer months (from early June to late September) when daily mean air-temperature generally exceeded 0°C. Then, annual stand-level aboveground respiration (R_{AT}) was estimated by summing up the daily respiration during this period. For evaluating the extent of year-to-year fluctuation of the estimates, we used air-temperature data that were recorded in the stand during four consecutive years (2001–2004) (see Fig. 16.7a, Chap. 16).

The estimate of stand-level aboveground respiration (R_{AT}) during these four seasons ranged from 2.23 to 2.81 $kgCO_2$ ha^{-1} year^{-1}. On the basis of organic matter dry mass, the range corresponds to 1.37–1.73 Mg ha^{-1}y^{-1}, and is averaged 1.56 Mg ha^{-1}y^{-1}: a conversion factor = 0.614 was used (e.g., Yokota et al. 1994).

15.4 Evaluation of Measurement System

Present study applied a new closed air-circulation system to directly measure CO_2 release from aboveground parts of a whole tree. Our system has advantages compared to previous methods using a whole-tree enclosed chamber (e.g., Ninomiya and Hozumi 1981; Adu-bredu et al. 1996a; Yokota et al. 1994). First, the system enables us to determine the respiration rate at desirable and stable temperature levels in the field. Second, we do not need to consider dissolved CO_2 in water vapor which cannot be detected by infrared gas analyzer, since vapor from a plant body is considered negligible under the dark condition. Third, respiration rate is determined using one infrared gas analyzer. An open-system usually requires two analyzers to detect CO_2 concentration at both inlet and outlet of the system, and requires frequent calibration. Our closed system does not need to calibrate the CO_2 analyzer frequently. Lastly, the present system balances CO_2 concentration by attaching a CO_2 scrubber, by which leakage of CO_2 from the system can be ignored completely. Another improvement is the utilization of natural heat energy (i.e., permafrost and fire wood) for controlling air-temperature inside chamber. Although these energy sources may be applicable only in our study region, they enabled us to measure many sample trees in the field without an extensive unit of power-requiring air conditioning.

We used a dark chamber to solve problems specific to measurements of whole-plant respiration during a daytime. Because the up-streaming sap flow in the daytime cools down stem temperature near the ground, temperature of a whole plant body shows heterogeneity (Negisi 1974). Respiration rate of a lower part of the stem shows higher value than the other parts, which has a 44% share of the total stem respiration (Mori and Hagihara 1988, 1991). Sap-flow in the daytime probably interferes measurement of whole-plant respiration under a stable temperature. Hence, it was necessary to depress the sap flow of sample trees by a dark chamber. In the present system, temperature heterogeneity of the plant body was minimized. Therefore, the present set-up might serve as a better system to estimate respiratory potential of a whole-plant under a stable temperature.

However, limitations of the present system must also be considered. For example, an open system is suited to long-term monitoring of gas-exchange as demonstrated by Adu-bredu et al. (1997), while our closed system is not currently applicable to such continuous measurements. Therefore, modification of the present system to suit long-term monitoring of physiological dynamics should be considered a next challenge.

15.5 Aboveground Respiration and Production

The values of stand-level aboveground respiration (R_{AT} = 1.6 Mg ha^{-1}y^{-1}) estimated for the old *L. gmelinii* forest (plot C1) are somewhat larger than ANPP of the same stand (1.3 Mg ha^{-1} year^{-1})(Kajimoto et al. 1999), and those of other old stands (>100 years-old; 0.5–0.8 Mg ha^{-1} year^{-1})(see also Table 6.3). However, the estimate of stand-level aboveground respiration (R_{AT}) may be overestimated, because it includes respiration when *L. gmelinii* does not hold needles (i.e., early June and late September). In the study area, larch needles generally start to flush in late May or early June, but develop fully after mid-June (see Sect. 17.3). They begin to fall from early to mid-September. However, our estimate of stand-level aboveground respiration (R_{AT}) was based on the respiration rate at a whole-tree level (i.e., including needles). Individual respiration rate that was used for the present calculation of stand-level aboveground respiration (R_{AT}) was measured only for midsummer, when needles were fully developed and functioned actively. These considerations suggest that annual aboveground respiration rate of the stand and ANPP may be similar, or carbon loss due to aboveground respiratory consumption may be nearly balanced with annual net carbon gain (Fig. 15.6).

Present data are still limited in estimating stand-level aboveground larch respiration accurately due to both small sample size and short observation period. Nevertheless, the obtained stand-level aboveground respiration (R_{AT} = ca. 80 gC m^{-2} year^{-1} at carbon basis) falls in a value similar to net ecosystem production (NEP = 70–80 gC m^{-2} year^{-1}) estimated with the eddy covariance technique in another old stand (ca. 105 years-old) of *L. gmelinii* (plot CF in Carbon Flux Site) located in the same region (Nakai et al. 2008; details see Chap. 10).
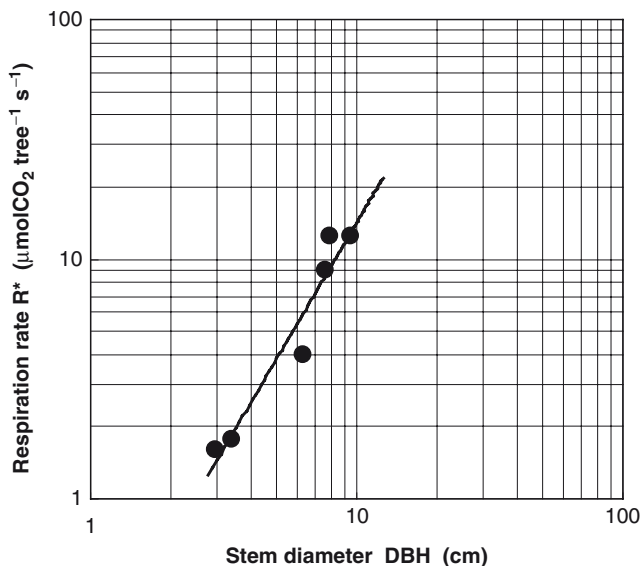
Fig. 15.6 Relationship between stem diameter at breast height (DBH) and aboveground respiration rate ($R*$) for six *L. gmelinii* sample trees. The $R*$ values were corrected for temperature at 20°C; correction was made by assuming $Q_{10}=2$ (see Fig. 14.5). Regression line was significant ($r^2=0.94$, $p<0.01$) (Mori et al., unpublished data)

Similarity of these estimates suggests that aboveground respiratory CO_2 consumption of larch trees is a major component of ecosystem carbon flow.

However, NEP is a balance between carbon gain by plant photosynthesis and carbon release due not only to autotrophic respiration, but also to heterotrophic respiration. Without data of both elements, it is not possible to determine to what extent plant (larch) respiration contributes to total ecosystem carbon flux (see Chap. 24). Particularly, root respiration must be quantified, though its measurement under field conditions is generally difficult. According to our preliminarily trial of *in situ* measurement with a small chamber attached to intact roots, temperature dependency of root respiration maybe somewhat different from that of aboveground parts (Mori et al. 1997; Mori et al., unpublished data). Thus, further examination of both aboveground and root respiration is necessary to determine components of ecosystem respiration, and whether the permafrost larch forest is functioning as a carbon sink or source.

15.6 Conclusions

A new measurement system of whole-tree aboveground dark respiration was developed using a large cylindrical dark chamber, and was applied to an old *L. gmelinii* forest in Central Siberia. We used closed air-circulation system, and determined respiration

rate on the basis of CO_2 accumulation rate within the chamber system equipped with a CO_2 scrubber. To control air temperature within the chamber, we supplied hot and cool water by either heating or cooling the tanks with wood fire or permafrost. Although the present method has limitations, it also has methodological advantages: inside-chamber temperature was controlled easily at desirable levels, and relatively short time was required for measurement.

Whole-tree aboveground respiration rate increased with temperature, and its temperature dependency was similar between two individuals examined: Q_{10} value was nearly equal to 2. Based on the measurement of a mean-sized sample tree, stand-level aboveground respiration rate was estimated to be about 1.6 Mg ha^{-1}y^{-1}, by assuming that temperature dependency of respiration was constant and growing season was 4 months (from June to September). This estimate was evaluated in relation to the estimated ANPP in an old stand, suggesting that net carbon gain was nearly balanced with respiratory carbon release. It was also indicated that CO_2 release by aboveground larch respiration was a major component of total carbon flux in the permafrost larch forest ecosystem.

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