

論 文

Diurnal and Seasonal Fluctuations in the Bark Respiration of Standing *Fagus sylvatica* Trees at Solling, West Germany*

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KAKUBARI, Yoshitaka: **Diurnal and Seasonal Fluctuations in the Bark Respiration of Standing *Fagus sylvatica* Trees at Solling, West Germany** *J. Jpn. For. Soc.* **70**: 64~70, 1988 The diurnal and seasonal fluctuations of bark respiration for a 180-day period from mid-May to late-November 1985 in standing *Fagus sylvatica* L. trees at the beech experimental area (B₁) of the Solling Project were measured with a new measuring system using an 8-bit microcomputer. Eight respiration chambers were mounted at different heights and diameters on the stems and branches of dominant and suppressed trees. Xylem temperatures in respiration chambers were measured with thermocouples inserted into an inner layer of the bark. The diurnal fluctuation in xylem temperatures differed at different heights and diameters in each tree. In the stem wood near the ground, the xylem temperature had a constant value in the daytime. In the upper part of the stem, the xylem temperature followed the air temperature after a time lag. The diurnal fluctuation of bark respiration did not parallel the air temperature changes at the different heights of the stem. The rate of bark respiration was closely dependent upon xylem temperature changes throughout the day. The abrupt depression of the respiration rate appeared at 1800 h on clear days above 20°C of xylem temperature throughout the summer season. Stem respiration rates increased quickly in May, reached a maximum in July, and then decreased gradually toward winter dormancy as a result of low temperatures and low levels of metabolic activity. The respiration rate at the same xylem temperature is obviously higher in June and July than that in September and October.

角張嘉孝：西ドイツ・ゾーリングにおけるヨーロッパブナの樹皮呼吸の日変化および季節変化 *日林誌* **70**: 64~70, 1988 西ドイツ・ゾーリングのブナ試験地 (B₁) において、ヨーロッパブナの樹皮呼吸の日変化および季節変化を調べた。測定は8ビットマイクロコンピュータを用いた新しい測定装置によって、1985年5月中旬から11月末まで、延べ180日にわたって行った。八つの樹皮呼吸室を優勢木や劣勢木の幹や枝のいろいろな高さや太さのところに設置した。樹皮呼吸室の部分の樹体に挿入した熱電対により樹体温度を調べた。樹体温度の日変化は高さや径で異なった。根元付近の樹体温度は日中一定だった。樹冠上部の樹体温度の日変化は気温の日変化と似ていたが、最大値を示す時間は気温よりも遅れた。樹皮呼吸の日変化は気温より樹体温度の変化とよく対応した。樹体温度が20°Cをこえる夏の時期の18時頃に樹皮呼吸の急激な低下がみられた。樹皮呼吸は5月に急激に上昇し、7月に最大となった。その後、低温や活性の低下などにより、冬の維持呼吸へとゆっくり減少していった。同じ樹体温度における樹皮呼吸速度を季節をとおして調べると6月や7月に高く、9月や10月では明らかに低くなった。

I. Introduction

Forest ecosystems have greater plant biomass than other terrestrial systems because of the huge accumulation of dry matter as woody stems, branches, and roots of trees. The respiration rates of woody organs are much smaller than those in leaves; however, the dry matter budget in forest ecosystems is affected remarkably by their respiratory loss since they account for the greater part of the plant biomass.

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To compare annual carbon balances among different types of forest ecosystems or to study the relationship between photosynthetic production and tree growth, the amount of carbon fixed in photosynthesis and the respiratory loss by woody organs must be known approximately.

The amount of information about bark respiration in field measurements of woody organs of trees is especially limited. *In situ* measurements of stem respiration rates in trees have been made by JOHANSSON (1933), GEURTEN (1950), NEGISI (1972, 1974, 1975, 1978, 1979, 1981), KÜNSTLE and MITSCHERLICH (1976), and LINDER and TROENG (1981). Most of these measurements covered only a short period throughout a season and a small part of the woody organs. In a climatized chamber, HAVRANEK (1985) performed *in situ* measurements of the respiration rates and radial increment of a stem on a 6.5 m high tree of larch (*Larix decidua* MILL.) at the timber line on Mt. Patscherkofel near Innsbruck, Austria.

Most of bark respiration data have been obtained from detached samples with sawn-off branches and sections of stems. This method has been questioned because the respiration rates from cut surfaces might give a wound reaction resulting in increased respiration rates (JOHANSSON, 1933; JAKŠINA, 1966).

To study the forest damage by air pollution, the research project of the University of Göttingen began on July 15, 1985. The German team shared a part of the CO₂- and H₂O- gas exchange measurements as an indicator of the effects of acid rain, and the Japanese team took part of the measurements of respiratory loss from the bark respiration of trees.

As a first step, the diurnal and seasonal fluctuations in bark respiration from the stem were measured in standing trees of European beech (*Fagus sylvatica* L.) within the experimental area (B₁) at Solling, West Germany. To compare the differences of the rates of photosynthesis and transpiration at two different times, the sample trees selected included the same tree which SCHULZE (1970) used for measurements of the gas exchange of twigs in 1968, during the International Biological Program (ELLENBERG, 1971, ELLENBERG and others, 1986).

II. Materials and Methods

The measurements of bark respiration were performed in a natural 138-year-old stand of *F. sylvatica* at Solling (N51°45', E9°35', altitude 500 m), about 55 km northwest of Göttingen in northern Germany. Detailed descriptions of the stand and site are given by ELLENBERG (1971) and SEIBT (1981).

The general climate is characterized by abundant rainfall (approximately 1,100 mm annually), and the annual average air temperature 2 m above ground is only 6.5°C. The soil is drained normally and belongs to the types of acid brown-earth in loess over triassic sandstone (Bruntsandstein); its thickness varies between 50 and 80 cm (BENECKE and MAYER, 1971).

Bark respiration was measured in eight parts of stem bark at different heights of dominant and suppressed trees. The general structure and locations of the measurements on the stem, twigs, and roots are shown in

Table 1. General structure and location of bark respiration chambers

Sample tree			Respiration chambers (R. C.)						
Number	D.B.H. (cm)	Height (m)	Number	Height (m)	Diameter (cm)	Length (cm)	Surface area (cm ²)	Volume of R. C. (ml)	Depth* (cm)
67	25.5	18.0	2	0.8	25.96	18.0	1,467.0	1,523.7	1.5
89	43.0	28.5	3	1.3	43.47	12.0	1,638.0	1,676.0	2.0
68	50.0	27.7	7	26.0	0.80	10.0	25.1	183.4	0.5
68	—	—	4	24.5	6.37	23.0	460.0	1,521.7	1.0
68	—	—	5	22.0	14.97	30.0	1,410.0	1,505.4	1.5
68	—	—	6	19.5	20.54	22.0	1,419.0	1,487.9	2.0
68	—	—	1	0.8	50.96	10.0	1,600.0	1,631.3	2.0
68	—	—	8	-0.1	2.80	13.0	114.3	220.2	0.5

* Thermocouple inserted at depth from the bark surface.

Respiration chambers of numbers 7 and 8 were to measure twig- and root-respiration, respectively.

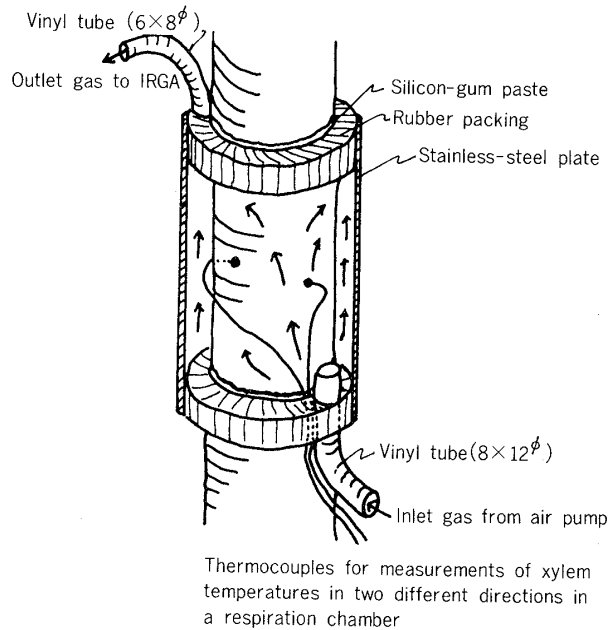


Fig. 1. Respiration chamber used for measurement of bark respiration rate

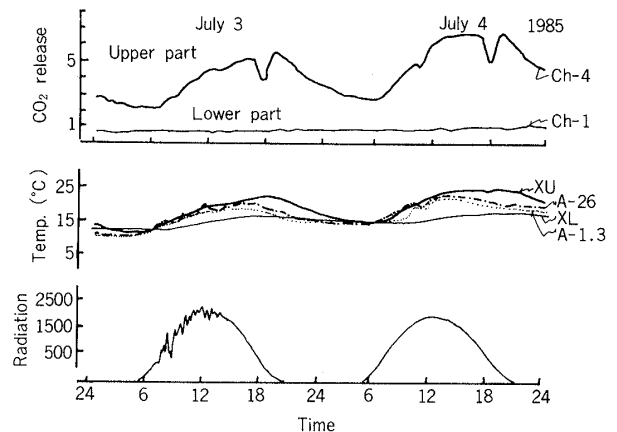


Fig. 2. Diurnal fluctuations in stem bark respiration on clear days in summer

CO₂ release: bark respiration rate ($\text{mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$) in the lower (Ch-1) and the upper part (Ch-4) in sample tree No. 68. Temp.: air temperature at the height of 26.0 m (A-26), dot-dash line) and at the height of 1.3 m (A-1.3, dotted line), xylem temperature at Ch-4 (XU, heavy solid line), xylem temperature at Ch-1 (XL, light solid line). Radiation: photon-flux density ($\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$).

Table 1. The respiration chambers described in Table 1 were enclosed with plates of stainless-steel forming cylinders. The openings between the bark and the plate at both edges of each stainless-steel cylinder were closed tightly with rubber packing and silicon-gum paste. A thin stainless-steel plate can shelter the respiration chamber from the increasing air temperature caused by solar radiation.

Air was circulated over the enclosed bark surface at a flow rate from 800 to 3,000 ml per minute through an inlet and an outlet vinyl tube attached to the respiration chamber (Fig. 1). The rate of bark respiration was estimated by measuring the rate of increase in the CO₂ concentration of the air after passing over the bark, using an infrared gas analyzer (Yokogawa, IR21, Tokyo). The temperature of the bark covered by the respiration chamber was measured with an iron-constantan thermocouple inserted into the inner layer of the bark.

The bark respiration, and air-, xylem-, and soil-temperatures were registered continuously with a new measuring system (KAKUBARI and others, 1984). A microcomputer (NEC, PC-8201, Tokyo), connected with an interface board was used as an input/output processing unit which had the functions of 32 channels of analog input for reading the output from thermocouples and the gas analyzer, and 16 channels of digital output for selecting the stream of sample gas. Each of the 8 sample gas-lines and a control gas-line was analyzed at least every 2 minutes throughout a measuring period, except during short periods when the system had to be repaired after damage caused by lightning.

Climate and phenology observed in 1985

General climatic data in Solling were given by the Grassland Experimental Station near the study area (LEUSCHNER, unpublished; NEEMANN, unpublished):

In April and early May of 1985, air temperatures were cold. Bud burst began on 14 May, and after a few fine days additional leaves developed. Weather conditions from the end of May to mid-June were bad becoming rainy days. In July the weather became fairly good for growth. The 1985 autumn was unusually warm, daily average temperature being above 15°C. Color change of leaves could be seen on 15 October, and we had hard frost and snow from late October to early November.

III. Results and Discussion

1. Diurnal fluctuations in stem bark respiration as related to temperature changes

The diurnal fluctuations of stem bark respiration at 0.8 and 24.5 m on clear summer days from July 3 to

July 4, 1985 are shown in Fig. 2 together with the air temperatures at 1.3 and 26.0 m, radiation and xylem temperatures. The daily course of bark respiration did not parallel the air temperature changes at the different heights of the stem. The rate of bark respiration was closely dependent upon xylem temperature changes throughout the day.

In the stem wood near the ground, the xylem temperature had a constant value at any time of day, perhaps because of the cooling effect of the sap flow, and had a diurnal fluctuation corresponding to the soil temperature.

With increasing heights, the xylem temperature rose quicker during the day, and the range of fluctuations of the respiration rate increased. In the upper part of the stem, the xylem temperature followed the air temperature after a time lag. The difference between the daily maximum and minimum values of respiration rates in the upper part of the stem was greater than that of the lower part of the same stem. The xylem temperature of woody organs may be affected by sap flow. The temperature of the sap near the ground might be close to the soil temperature. The xylem temperature at the base was lower than the air temperature on clear summer days.

At 1800 h on July 3 and at 1200 and 1800 h on July 4, the respiration rates began to fall. These decreases did not correspond to the fluctuations of xylem and air temperatures (Fig. 2) and appeared on clear days above 20°C of xylem temperature throughout the summer season. On cloudy and rainy days the decrease was not as remarkable as it was on clear days in summer. NEGISI studied the daytime depression in bark respiration in a *Magnolia obovata* THUNB. tree (NEGISI, 1972) and in young *Pinus densiflora* S. and Z. trees (NEGISI, 1974), and showed that the daytime depression in bark respiration becomes obscure after shading, defoliation, or cutting of the stem at the base level. His results suggest that the water condition in trees is an important factor relating to the daytime depression of bark respiration of the stem at the base. KÜNSTLE and MITSCHERLICH (1976) reported that stem respiration seems to be reduced during drought periods in spite of high temperatures, as it was observed in photosynthesis and respiration (BRIX, 1962), and as GUERTEN (1950) recognized, the respiration rate of bark is closely dependent on water content in the tissues. The abrupt decrease of bark respiration at the height of 24.5 m at 1200 and 1800 h on summer days may be closely dependent on the changes of water deficit in the tissues as shown in the young *P. densiflora* trees (NEGISI, 1974). However, it is still difficult to understand fully whether this decrease of respiration is connected with a reduced rate in respiration caused by a water deficit in tissues, or whether other factors play a role. The studies referenced were made on isolated individual and/or on young trees, and we have no reports about the daytime depression in the upper part of stems on clear summer days. Because the results reported were obtained from studies of young, isolated trees, further studies are needed to explain the daytime depression of stem respiration in mature trees. Especially, it seems advisable to study this decrease of respiration simultaneously with measurements of photosynthesis and transpiration of the leaves and sap-flow rate.

As shown in Fig. 3, on September 12 and 13, 1985, both autumn days, the level of respiration measured was near to the "dormant respiration" termed by JOHANSSON (1933), although the xylem temperature reached nearly 20°C. In autumn, the difference between the daily maximum and minimum respiration rates was smaller than that in summer. The wide changes of xylem temperature in autumn did not directly affect large fluctuations in the daily course of bark respiration, as was expected from the experience in summer.

Additional measurements of temperature, together with respiration at many positions, and a summation of observed values will be required for estimating reasonable respiration rate, which can be estimated from the xylem temperature, and for making clear the role that temperature plays during the daily course of bark respiration.

2. Seasonal fluctuations in bark respiration rates in relationship to xylem temperatures

In Fig. 4, the bark respiration rates measured throughout different seasons are compared with the seasonal fluctuations of xylem temperatures, photosynthetically active radiation, and rain-fall. The bark respiration rates were at low levels during the spring, during leaf coloring and winter, and at high levels from June to July, except for rainy and low-temperature days. The decrease in respiration rate during the dormant season and its increase during the growing season have been observed in many forest tree species: for example, in

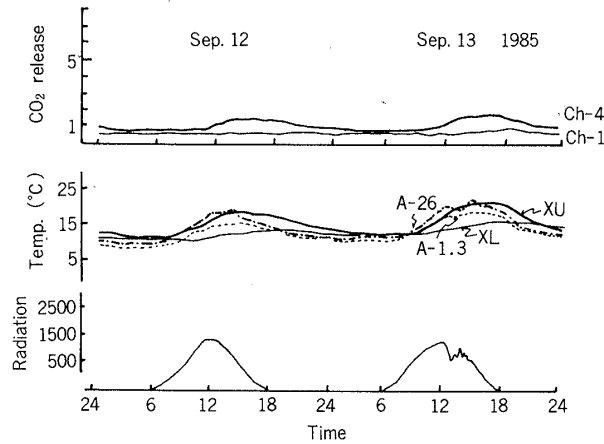


Fig. 3. Diurnal fluctuations in stem bark respiration on clear days in autumn

Note in Fig. 2 applies.

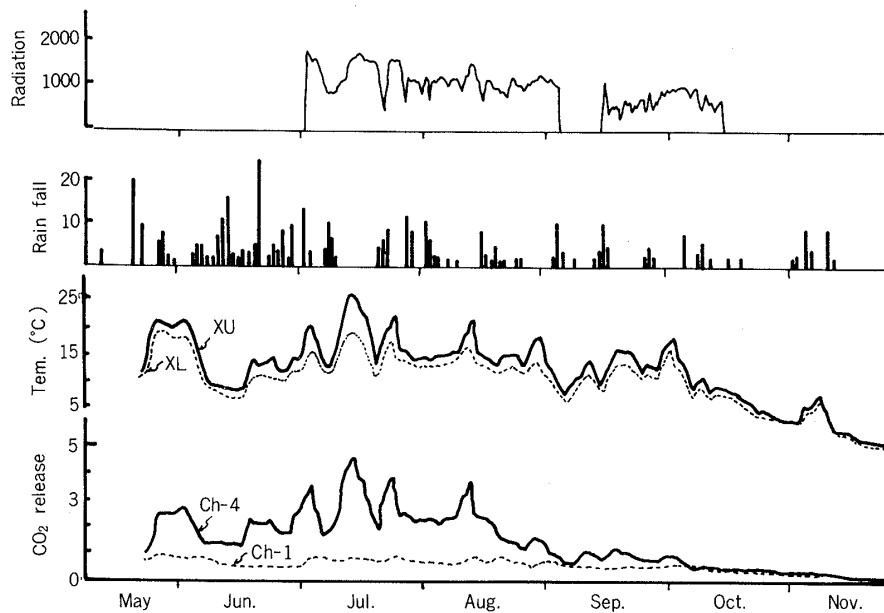


Fig. 4. Seasonal fluctuations of bark respiration rates in the upper and the lower parts of stems in relation to xylem temperatures from May to November, 1985

CO₂ release: respiration rates ($\text{mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$) in the lower (Ch-1) and the upper (Ch-4) parts in sample tree No. 68, daily mean xylem temperature of Chamber 1 (XL, dotted line) and Chamber 4 (XU, solid line), photon-flux density ($\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), and rainfall (mm day^{-1}) from unpublished data (LEUSCHNER and NEEMANN).

Chamaecyparis obtusa S. and Z. (OOHATA and SHIDEI, 1972), *P. densiflora* (NEGISI, 1974, 1975, 1978, 1979), *P. sylvestris* L. (LINDER and TROENG, 1981), *Larix decidua* and *Pinus cembra* L. (HAVRANEK, 1981), and *M. obovata* (NEGISI, 1972).

To compare the seasonal fluctuations under the same xylem temperatures, the respiration rates are shown against the temperatures in Fig. 5. In the upper part of the stem, the respiration rate reached a maximum in July, maintained a high level in June and July, and decreased to a low level in October.

The seasonal fluctuations in the lower part of the stem near the ground were different from those in the upper part, except for the decrease of respiration to the winter level in October. As shown in Fig. 5, the respiration rates at different heights and diameters on the stem and branches of same tree (Table 1) were not constant at any given xylem temperature throughout the season. The increase of respiration rates is connected with the fluctuations of xylem temperatures and the diameter growth (OOHATA and SHIDEI, 1972 ;

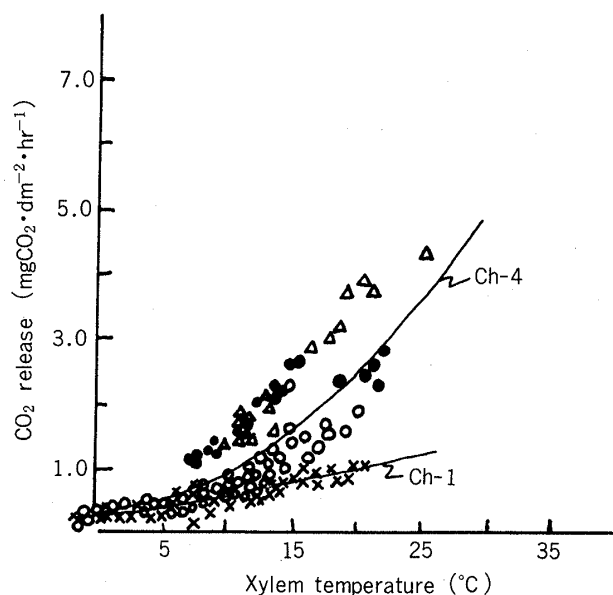


Fig. 5. The relationships between daily mean xylem temperatures and respiration rates from May to November, 1985

Respiration rates in Ch-4: triangle (July), black dots (June), white dots (other months). Respiration Ch-1: Xs. Correlation curve of Ch-4: $Y=0.218+0.032X+0.005X^2$, Correlation curve of Ch-1: $Y=0.126+0.043X+0.003X^2$.

LINDER and TROENG, 1981; NEGISI, 1981; SEIBT, 1981; HAVRANEK, 1981). A high level of bark respiration in the upper part of the stem in July may be related to the high metabolic activities during the formation of cambial tissue (HAVRANEK, 1985).

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