Construction and Maintenance Respiration Related to the Aboveground Growth of a Hinoki Tree

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Abstract

Carbon dioxide exchange rates were continuously measured on the aboveground parts of a hinoki (*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.) tree in the field over a 5-year period, though there was one growing season during which the data were not successfully collected. During the study period, the specific respiration rate decreased linearly with decreasing relative growth rate of the aboveground phytomass. Coefficients for the construction and maintenance respiration were about 1.4 and 0.19 yr^{-1}, respectively, *i.e.*, the construction respiration was about 1.4 times as much as the annual phytomass increment and the maintenance respiration was annually 19% of the phytomass. The growth process of the phytomass was approximately expressed by a simple logistic equation. Combining the logistic equation with the growth-respiration relationship gave an equation which predicted a proportional relationship between the total respiration and phytomass in the younger stages, where a maximum total respiration was realized. It was estimated that the construction respiration accounted for at most 80% of the total respiration in the younger stages, whereas in the mature stages the maintenance respiration dominated the total respiration, with the construction and maintenance respiration being equal at a tree age.

Key words: carbon dioxide exchange, construction respiration, field conditions, growth process, maintenance respiration

Ⅰ. Introduction

Formulae for partitioning respiration into components associated with construction and maintenance have been presented by McCREE (1970), THORNLEY (1970) and HESKETH *et al.* (1971). In herbaceous plants the formulae have been proved useful to distinguish between respiration associated with the synthesis of new tissues and respiration associated with the maintenance of existing tissues (ROBSON, 1982; van der WERF *et al.*, 1988; AMTHOR, 1989). However, little attention has been given to their application to large woody perennials (HAGIHARA and HOZUMI, 1983, 1991; SPRUGEL, 1990; RYAN, 1990; PAEMBONAN *et al.*, 1992).

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McCree (1970) described respiration with two terms, one of which is proportional to photosynthesis and the other to accumulated dry matter. Hesketh *et al*. (1971) proposed a model in which construction respiration is proportional to growth rate, and maintenance respiration is proportional to phytomass. In this model, total respiration R is given by

$$R = c\frac{\mathrm{d}w}{\mathrm{d}t} + mw, \tag{1}$$

where w represents the phytomass at time t, and c and m are, respectively, coefficients for the construction and maintenance respiration. Dividing both sides of Eq. 1 by w yields

$$R/w = \frac{c}{w}\frac{\mathrm{d}w}{\mathrm{d}t} + m. \tag{2}$$

This model states that the specific respiration rate $SRR(=R/w)$ is a linear function of the relative growth rate $RGR(=(1/w)(\mathrm{d}w/\mathrm{d}t))$. The regression of SRR on RGR in actively growing plants is thus expected to be a straight line with a slope c, a dimensionless coefficient for the construction respiration, and an intercept m, a coefficient for the maintenance respiration which has the dimension of time^{-1} (Kimura *et al*., 1978).

In this study, we applied Eq. 2 to analyze the interrelationship between respiration, phytomass and phytomass increment of the aboveground parts of a hinoki (*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.) forest tree. Respiration rates of the aboveground parts were continuously measured in the field with an open CO_2 exchange system (Hagihara *et al*., 1987) and the phytomass was nondestructively assessed over a 5-year period.

II. Materials and methods

1. Sample tree

A representative tree was selected as the sample tree within a 12-year-old plantation of hinoki (*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.) growing in an experimental field of the School of Agricultural Sciences, Nagoya University. The stand density was 15000 trees ha^{-1}.

Tree height, stem girth at 1.0 m height above ground and stem volume of the sample tree were, respectively, 3.6 m, 11.8 cm and 2.6 dm^3 at the beginning (in March 1986) and 6.1 m, 23.4 cm and 14.6 dm^3 at the end (in March 1991) of the experiment. Average annual increments in tree height, stem girth at 1.0 m height above ground and stem volume were 50 cm yr^{-1}, 2.3 cm yr^{-1} and 2.4 dm^3 yr^{-1}, respectively.

2. Estimate of aboveground biomass

Stem volume of the sample tree was estimated monthly from the tree height and stem girths at 50-cm intervals. On the basis of an allometric relationship between aboveground phytomass w (kg d. wt) and stem volume v (dm^3) ($w = 0.501\,v$; number of

observations=17 trees; coefficient of determination=0.998), the stem volume was converted into the aboveground phytomass.

3. Climatic conditions

Radiation was measured above the crown of the sample tree with a photometric sensor (IKS-15; Koito Ind., Ltd.). The photometric units were converted to quantum units: 1 klx=18 μ mol m^{-2} s^{-1} (McCREE, 1981). Other climatic factors, such as rainfall and relative humidity, were obtained from Nagoya Meteorological Station in the immediate vicinity of the experimental field. Annual total radiation, annual mean air temperature, annual total rainfall and annual mean relative humidity during the experimental period were respectively 7300±146 (SE) mol m^{-2} yr^{-1}, 15.0±0.2°C, 1522±67 mm yr^{-1} and 65.2±0.4%. There were no clear differences in climatic conditions among years over the 5-year period.

4. Respiration measurement

The installation was an open system for determining the carbon dioxide exchange of a forest tree under field conditions (HAGIHARA et al., 1987). Aboveground parts of the sample tree were covered with a chamber, which was cylindrical, except for a conical upper part, with some small ventilators. The chamber was made of transparent polyvinyl chloride films (Takafuji Chem. & Syn. Co., Ltd.) 0.2 mm thick. The skirt of the chamber was tied around the base of the tree stem.

Ambient air was mixed in 4 m^3 buffer tanks with fans to minimize short-term fluctuation in CO_2 concentration before being pumped into the chamber. The flow rate of air introduced into the bottom of the chamber was adjusted in such a way that the difference between CO_2 content in air outside and inside the chamber was less than 10 -15%: approx. 50 m^3 h^{-1} in summer and approx. 15 m^3 h^{-1} in winter, as measured with a thermal flow meter (TH-1200; Tokyo Keiso Co., Ltd.). Air inside the chamber was stirred with an air mixing fan at a flow rate of 480 m^3 h^{-1}.

Sample air at the inlet and outlet of the chamber was sucked through vinyl tubes into an infrared gas analyzer (IR21; Yokogawa Elect. Works, Ltd.). In order to avoid the condensation of water vapor inside the vinyl tubes, they were heated with aerial frame heating wires.

Air temperature was detected both inside and outside the chamber by platinum resistance thermometers (SHT-01; Koito Ind., Ltd.). The air temperature inside the chamber was adjusted to that outside the chamber through a temperature controller (MC-A3KW; Koito Ind., Ltd.).

Carbon dioxide exchange rates were recorded at 3-minute intervals throughout the experimental period. However, we were unable to obtain data from April 1989 to March 1990 because of system failure.

5. Data analysis

Aerial dark respiration in the daytime was estimated hourly from the observed daytime temperature, on the basis of the relationship between nighttime respiration rate and air temperature (PAEMBONAN et al., 1991). The nighttime respiration was measured

from dusk to dawn. Daily dark respiration rate was obtained by combining the estimated daytime respiration with the observed nighttime respiration. Annual respiration was obtained by summing the daily dark respiration rates over a year from April to March.

Annual respiration rates were expressed as the loss of dry matter assuming a conversion factor of 0.614 g d. wt (g CO_2)$^{-1}$ (Mariko and Koizumi, 1993).

III. Results

1. Growth of aboveground phytomass

To pursue the growth of aboveground phytomass, we examined the relationship between relative growth rate RGR (yr^{-1}) and mean phytomass $\bar{w}$ (kg d. wt), in which RGR and $\bar{w}$ were calculated from the following equations:

$$RGR = \frac{\ln w_2 - \ln w_1}{t_2 - t_1}, \tag{3}$$

$$\bar{w} = \frac{w_2 - w_1}{\ln w_2 - \ln w_1}, \tag{4}$$

where w_1 and w_2 stand for the aboveground phytomass in March in a given year t_1 and in March in the subsequent year t_2, respectively.

If the growth of phytomass follows a simple logistic curve, there is a linear relationship between RGR and $\bar{w}$ (Nishiwaki and Shinozaki, 1952; Charles-Edwards et al., 1986). Figure 1 shows a negative linear relationship between RGR and $\bar{w}$ over an experimental period of 5-year (coefficient of determination=0.941). Therefore the growth process of the aboveground phytomass w (kg d. wt) may be expressed in the following differential equation:
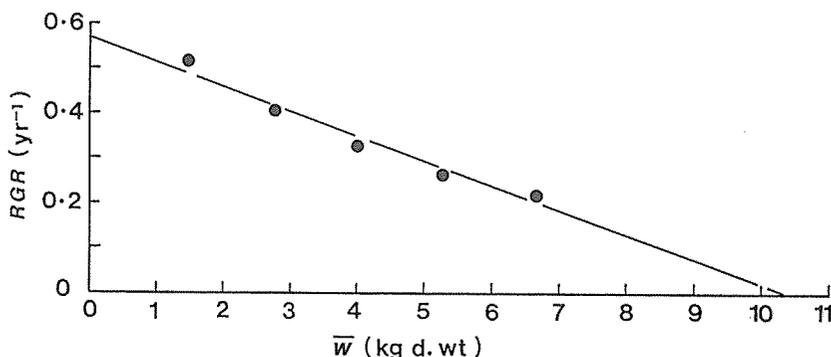

Fig. 1. Linear relationship of the relative growth rate RGR and mean phytomass $\bar{w}$ of aboveground parts. The straight line corresponds to Eq. 5, where the growth coefficient λ and maximum aboveground phytomass W are respectively 0.56 yr^{-1} and 10.3 kg d. wt.

$$\frac{1}{w}\frac{\mathrm{d}w}{\mathrm{d}t} = \lambda\left(1 - \frac{w}{W}\right). \tag{5}$$

Here t is the time (yr), λ is a growth coefficient and W is a maximum aboveground phytomass. The values of λ and W in the equation can be assessed from intercepts on the ordinate and abscissa, respectively. The observed values of λ and W were 0.56 ± 0.06 (SE) yr^{-1} and 10.3 kg d. wt ($\lambda/W = 0.0544\pm0.0037$). The relatively low value of W may be due to the dense planting of this stand, $i.e.$, 15000 trees ha^{-1}.

The solution of Eq. 5 is

$$w = \frac{W}{1 + k\exp(-\lambda t)}, \tag{6}$$

where k is a constant specific to W and w at $t=0$, and was determined to be 5000.

2. Respiration, phytomass and phytomass increment

The annual respiration R (kg d. wt yr^{-1}) tended to increase with increasing phytomass throughout the experimental period. Figure 2 shows the relationship between the specific respiration rate SRR ($= R/\bar{w}$) and relative growth rate RGR of the aboveground phytomass. It appears from the figure that SRR decreased linearly with decreases in RGR (coefficient of determination $= 0.960$). As expected from Eq. 1, this relation suggests
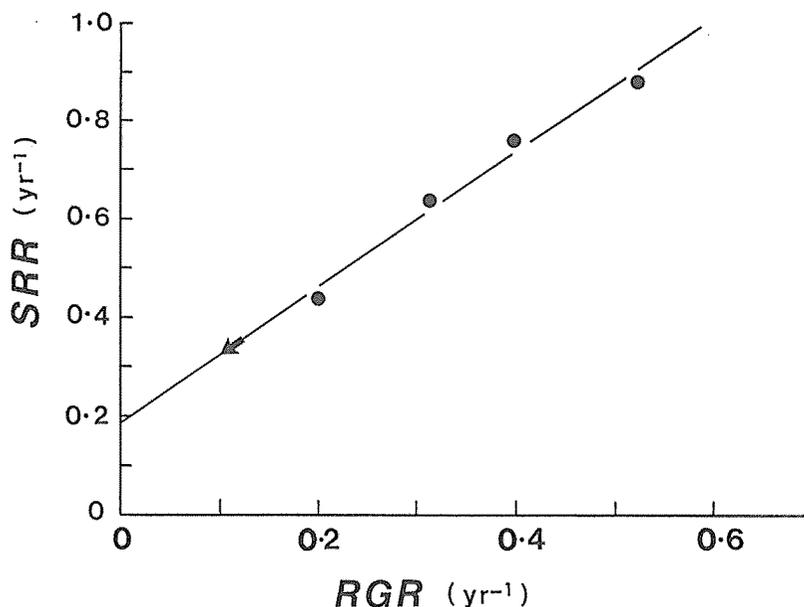

Fig. 2. Specific respiration rate SRR-relative growth rate RGR relationship. The straight line corresponds to Eq. 2, where coefficients for the construction c and maintenance m respiration are respectively 1.36 and 0.186 yr^{-1}. The arrow indicates the direction of time.

that the annual respiration of the aboveground parts of a hinoki tree roughly consists of one component proportional to the annual phytomass increment and another component proportional to the phytomass.

The c and m values in Eq. 1 were respectively estimated to be 1.36 ± 0.12 (SE) and 0.186 ± 0.045 yr^{-1}. This result means that the respiration consists of the construction respiration which is about 1.4 times as much as the annual phytomass increment, $\mathrm{d}w/\mathrm{d}t$, and of the maintenance respiration which is annually about 19% of the phytomass, w.

By compiling the data published for evergreen forests, Hagihara and Hozumi (1983, 1991) tentatively found the coefficients for the construction and maintenance respiration to be 1.44 and 0.0632 yr^{-1}, respectively. The present coefficient for the construction respiration was almost the same, whereas the coefficient for the maintenance respiration was three times larger.

IV. Discussion

1. R-w trajectory

The growth process of the aboveground phytomass was approximated by Eq. 5, or Eq. 6 (Fig. 1). Combining Eq. 1 with Eq. 5, we can obtain the following relationship where the total respiration R is a function of the phytomass w (Kimura et al., 1978),

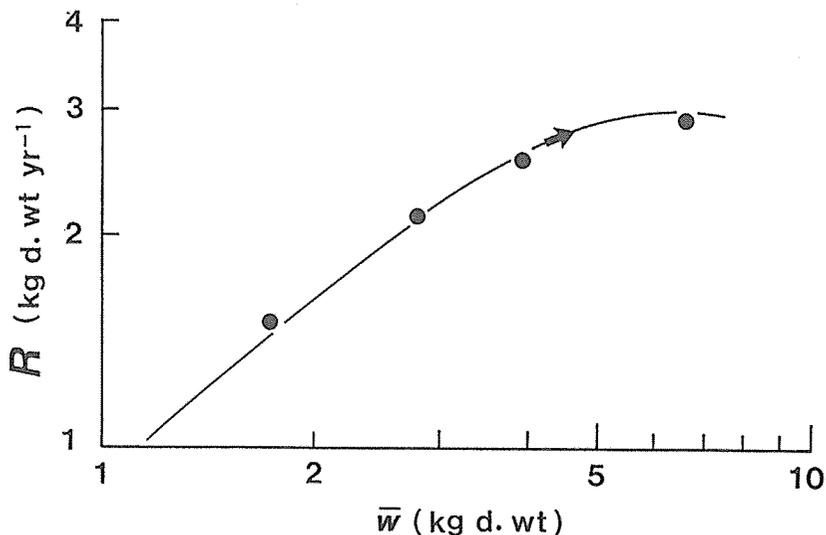$$R = c\lambda w\left(1 - \frac{w}{W}\right) + mw. \tag{7}$$

Fig. 3. Trajectory between the annual respiration R and mean phytomass $\bar{w}$ of aboveground parts. The line is based on Eq. 7. The arrow stands for the progress of years. It is expected from the equation that R shows a peak of 3.0 kg d. wt yr^{-1} at a biomass of 6.4 kg d. wt.

This equation shows that the total respiration increases roughly in proportion to the phytomass with a proportional constant of $c\lambda + m$ in younger stages when the phytomass is very small relative to W, and has its maximum value $(= w^* (c\lambda + m)/2)$ at a value of the phytomass w^* $(= W(c\lambda + m)/2c\lambda)$, for the case when $c\lambda > m$. If $m \leqq c\lambda$, then the total respiration, of which the maintenance respiration is always greater than the construction respiration, continues to increase with increasing phytomass.

As shown in Fig. 3, the observed annual respiration was plotted against the corresponding mean phytomass on log-log coordinates. The observed $c\lambda$-value was 0.76 yr^{-1} which was larger than the observed m-value of 0.186 yr^{-1}. It seems that Eq. 7 explains the observed R-w trajectory to some extent.

2. Time trend of the total respiration

Considering Eqs. 6 and 7, the respiration activity with the time course of growth can be written as a function of time t:

$$R = \frac{c\lambda Wk \exp(-\lambda t)}{[1 + k \exp(-\lambda t)]^2} + \frac{mW}{1 + k \exp(-\lambda t)}. \tag{8}$$

Numerical estimations based on Eq. 8 of the total, construction and maintenance respiration with the time course of growth are given in Fig. 4. As depicted in the figure, the maintenance respiration continues to increase with time until it attains to a constant rate, or the tree phytomass reaches its maximum. On the other hand, the construction respiration reaches a peak value of 2.0 $(= c\lambda W/4)$ kg d. wt yr^{-1} at a tree age of 15.2-year $(= \lambda^{-1} \ln(k))$ when the growth rate is maximum, and after that decreases with time. The total respiration shows its peak of 3.0 kg d. wt yr^{-1} after a delay of $\lambda^{-1} \ln\{(c\lambda + m)/(c\lambda - m)\}$ from the appearance of the peak of the construction respiration $(=$ tree age of 16.1-
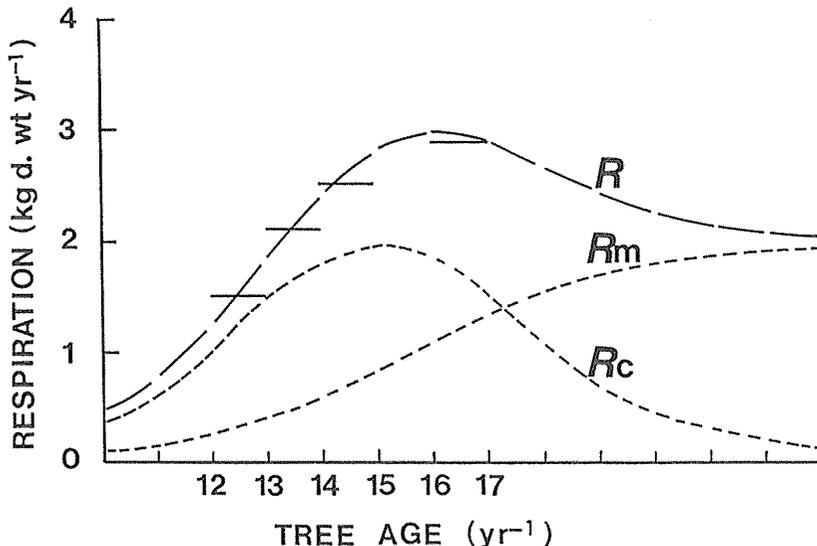

Fig. 4. Time trends of the total R, construction R_c and maintenance R_m respiration. The curves are based on Eq. 8. The horizontal lines indicate the observed values of the total respiration.

year) and then decreases to a constant value, most of which is respired for purposes of maintenance.

3. Construction-maintenance respiration ratio

It is clear from Fig. 4 that during younger stages with a pronounced increase in phytomass, the total respiration is dominated by the construction respiration which occupies at most 80% of the total respiration. With the progress of time, the construction respiration tends to decrease abruptly. Conversely, the maintenance respiration dominates over the construction respiration as the tree approaches a maximum phytomass. It is expected from Eq. 8 that the construction and maintenance respiration are equal when the tree is 17.2-year-old $(=\lambda^{-1}\ln\{k(c\lambda-m)/m\})$.

Acknowledgments

Literature cited

Amthor, J. S. (1989) Respiration and Crop Productivity. 215 pp, Springer-Verlag, New York.

Charles-Edwards, A., Doley, D. and Rimmington, G. M. (1986) Modelling Plant Growth and Development. 239 pp, Academic Press, Sydney.

Hagihara, A., Hozumi, K. and Handa, S. (1987) An apparatus for determining the CO_2 gas-exchange of a forest tree in the field. Bull. Nagoya Univ. For. **9**: 32-36.

Hagihara, A. and Hozumi, K. (1983) Studies on the primary production in a *Chamaecyparis obtusa* plantation. J. Jpn. For. Soc. **65**: 357-365.

Hagihara, A. and Hozumi, K. (1991) Respiration. *In* Physiology of Trees (Raghavendra, A. S., ed.). pp. 87-110, John Wiley & Sons, Inc., New York.

Hesketh, J. D., Baker, D. N. and Duncan, W. G. (1971) Simulation of growth and yield in cotton: Respiration and the carbon balance. Crop Sci. **11**: 394-398.

Kimura, M., Yokoi, M. and Hogetsu, K. (1978) Quantitative relationships between growth and respiration. II. Evaluation of constructive and maintenance respiration in growing *Helianthus tuberosus* leaves. J. Plant Res. **91**: 43-56.

Mariko, S. and Koizumi, K. (1993) Respiration for maintenance and growth in *Reynoutria japonica* ecotypes from different altitudes on Mt. Fuji. Ecol Res. 8: 241-246.

McCree, K. J. (1970) An equation for the rate of respiration of white clover plants grown under controlled conditions. *In* Prediction and Measurement of Photosynthetic Productivity (Šetlík, I., ed.). pp. 221-229, PUDOC, Wagenigen.

McCree, K. J. (1981) Photosynthetically active radiations. *In* Physiological Plant Ecology I (Lange, O. L., Nobel, P. S., Osmond, C. B. and Ziegler, H., eds). pp. 41-55, Springer-Verlag, Berlin.

NISHIWAKI, Y. and SHINOZAKI, K. (1952) A new method of representing the population growth. J. Osaka City Med. Sch. **1**: 150-157.

PAEMBONAN, S. A., HAGIHARA, A. and HOZUMI, K. (1991) Long-term measurement of CO_2 release from the aboveground parts of a hinoki forest tree in relation to air temperature. Tree Physiol. 8: 399-405.

PAEMBONAN, S. A., HAGIHARA, A. and HOZUMI, K. (1992) Long-term respiration in relation to growth and maintenance processes of the aboveground parts of a hinoki forest tree. Tree Physiol. **10**: 101-110.

ROBSON, M. J. (1982) The growth and carbon economy of selection lines of *Lolium perenne* cv. S23 with differing rates of dark respiration. 2. Grown as young plants from seed. Ann. Bot. **49**: 331-339.

RYAN, M. G. (1990) Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmannii*. Can. J. For. Res. **20**: 48-57.

SPRUGEL, D. G. (1990) Components of woody-tissue respiration in young *Abies amabilis* (Dougl.) Forbes trees. Trees **4**: 88-98.

THORNLEY, J. H. M. (1970) Respiration, growth and maintenance in plants. Nature **227**: 304-305.

van der WERF, A., KOOIJMAN, A., WELSCHEN, R. and LAMBERS, H. (1988) Respiratory energy costs for the maintenance of biomass, for growth and for ion uptake in roots of *Carex diandra* and *Carex acutiformis*. Physiol. Plant. **72**: 483-491.

ヒノキの地上部の成長過程に伴った構成呼吸と維持呼吸

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　ヒノキの地上部の二酸化炭素ガス交換が，野外において5年間に渡って測定された（内1年間はデータ欠測）。現存量当たりの呼吸速度である比呼吸速度は，現存量の相対成長速度の減少に伴って線形に減少した。構成呼吸係数と維持呼吸係数はそれぞれ1.4と0.19 yr^{-1}であった。すなわち，年構成呼吸量は年成長量の約1.4倍に，また年維持呼吸量は現存量の約19%に相当していた。地上部の成長過程は，単純ロジスチック曲線で近似された。地上部のロジスチック成長と比呼吸速度－相対成長速度関係とから，若齢期においては呼吸速度と現存量との比例関係が成立すること，また最大呼吸速度を示す樹齢が存在することが予測された。若齢期には構成呼吸が呼吸の最大80%を占め，成長に伴い構成呼吸と維持呼吸が等しくなる樹齢を経過し，成熟期には維持呼吸が呼吸の大部分を占めることが予測された。