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TOMIYASU MIYAURA[1,2] and KAZUO HOZUMI[1,3]

[1] *Nagoya University, Nagoya 464, Japan*

[2] *Present address: Forest Tree Breeding Institute, Kasahara-cho, Mito, Ibaraki 310, Japan*

[3] *Present address: 15-3, 2Cho-me, Hattori, Ikaruga-cho, Ikoma-gun, Nara 636-01, Japan*

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Summary

Growth of a single sugi (*Cryptomeria japonica* (L.f.) D. Don.) tree was analyzed on the basis of a dry matter budget. The aboveground net production rate and death rate were defined as the anabolic rate and catabolic rate, respectively. Growth rate of aboveground tree weight, v_w (kg_{dw} year^{-1}), was defined as follows:

$$v_w = v_p - v_d, \qquad (1)$$

where v_p (kg_{dw} year^{-1}) is the aboveground net production rate and v_d (kg_{dw} year^{-1}) is the aboveground death rate. The value of v_d is obtained by measuring the monthly clippings of new dead leaves and branches attached to a sample tree. The value of v_w was calculated as the annual difference in the estimated aboveground tree weight, w_T (kg_{dw}). Finally, the value of v_p was estimated as the sum of the values of v_d and v_w. The following allometric relationships were found between v_p and w_T and between v_d and w_T:

$$v_p = a\, w_T^{\alpha}, \qquad v_d = b\, w_T^{\beta}. \qquad (2)$$

Combining Equations 1 and 2 gives a growth equation, Bertalanffy's equation, of the sample tree.

$$\frac{dw_T}{dt} = v_w = a\, w_T^{\alpha} - b\, w_T^{\beta}. \qquad (3)$$

Because the growth curve of w_T was derived from Equation 3, the analysis of the growth of w_T is based on direct measurement of the dry matter budget.

Keywords: anabolic rate, catabolic rate, growth rate, death rate, net production rate.

Introduction

Bertalanffy (1949) pointed out that animal growth is the net result of synthesis (anabolism) and breakdown (catabolism) of tissue components. Tree growth is also the net result of anabolic and catabolic processes. Measurement of anabolism and catabolism of a single tree would permit quantitative analysis of tree growth, but this has never been done on the basis of actual data. The aim of the present study was to undertake such an analysis.

Definition of the dry matter budget of a tree

We defined the dry matter flow of a single tree as follows: (1) net production rate (anabolism) is the rate of dry matter input to the tree, and is the difference between the rates of photosynthesis and respiration, (2) the rate of tissue death, including grazing, (catabolism) is the rate of dry matter output from the tree, and (3) the growth rate of the tree is defined as the difference between the input rate and the output rate.

Because death rates of bark and sexual organs are usually very small compared with the death rates of leaves and branches (Miyaura and Hozumi 1985, 1988, 1989), we defined the sum of death rates of leaves and branches as the aboveground death rate. Furthermore, because the grazing rate is very small compared with the death rates of leaves and branches, we regarded the death rate of leaves and branches as the catabolic rate of the aboveground part of the single tree.

Figure 1, which is based on a compartment model, shows the main flow of dry matter from the living parts of a tree to the surface of the forest floor. Because a large proportion of the dead leaves and branches remain on the tree for more than 3 months after their death (Tange et al. 1989), we were able to gather and weigh leaves and branches as they died by clipping them before they were abscised.

Materials and methods

Sample tree

The measurements were made on a young sugi plantation in the Nagoya University Forest at Inabu, about 55 km east of Nagoya, Japan. The plantation had a mean tree height of 6.84 m, mean stem-diameter at breast height (1.3 m above the ground) of 11.86 cm, tree density of 2,158 trees ha^{-1}, and stand age of 14 years in April 1984.

The dimensions of the sample tree chosen from the plantation are shown in Table 1. Tree height and diameter at breast height of the sample tree were close to

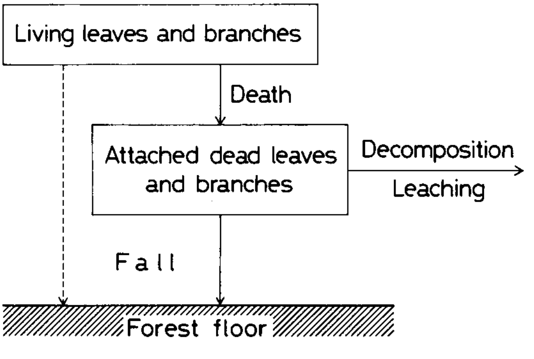

Figure 1. A compartment model showing dry matter flow from living leaves and branches to the surface of the forest floor. Leaves and branches of a sugi tree tend to remain on the tree for a long time after death. Thus, the death rate for leaves and branches can be measured by clipping the currently attached dead leaves and branches immediately after their death. Direct fall of living leaves and branches (dashed line) is small compared with the fall of dead leaves and branches.

Table 1. Tree size, aboveground growth rate, aboveground death rate and aboveground net production rate of the sample tree. Abbreviations: t = time after observation of initial tree sizes, D = stem diameter at breast height, D_B = stem diameter at the height just below the lowest living branch, H = tree height, w_T = estimated aboveground tree weight, $\overline{w_T}$ = approximated mean value of w_T during the period from t_1 to t_2, v_w = aboveground growth rate, v_d = aboveground death rate, v_p = aboveground net production rate.[1]

Year observed	Tree age	t (year)	D (cm)	D_B (cm)	H (m)	w_T (kg)	$\overline{w_T}$ (kg)	v_w (kg year^{-1})	v_d (kg year^{-1})	v_p (kg year^{-1})
1982	12	0	7.70	6.75	5.89	7.992				
							9.756	3.770	0.102[1]	3.872
1983	13	1	8.94	8.05	6.60	11.762				
							14.027	4.803	0.223[1]	5.026
1984	14	2	10.25	9.29	7.36	16.565				
							18.123	3.210	0.346	3.556
1985	15	3	10.73	9.99	8.20	19.775				
							22.290	5.235	0.643	5.878
1986	16	4	11.62	10.92	9.23	25.010				
							27.429	4.989	1.058	6.047
1987	17	5	12.38	11.78	9.95	29.999				
							32.690	5.538	1.388	6.926
1988	18	6	13.21	12.73	10.40	35.537				
							38.811	6.744	2.157	8.901
1989	19	7	14.07	13.62	11.21	42.281				
							45.570	6.745	2.527	9.272
1990	20	8	14.90	14.48	11.77	49.026				

[1] v_d was not measured during the periods from 1982 to 1983 and from 1983 to 1984, so that the values of v_d during these periods were estimated by using the $v_d - w_T$ relationship shown in Figure 3 and Equation 6.

the mean values of trees on the plantation.

Death rate

All attached dead leaves and branches of the sample tree were removed in July 1984. After that, currently attached dead leaves and branches were clipped at monthly intervals from August 1984 to June 1990. The dry weight of currently attached dead leaves and branches was defined as the death rate of leaves and branches during the clipping interval. Annual death rate of leaves and branches was calculated as the sum of the monthly death rate from July to June in the following year.

The annual aboveground death rate, v_d, was assumed to be the sum of the annual death rates of leaves and branches. The death rates of bark, cones and male flowers were ignored because they were very small compared with those of leaves and branches.

Tree size

Four dimensions of the sample tree were measured annually in April from 1982 to 1990. The dimensions were tree height (H, m), stem diameter at breast height (D, cm), height of trunk at which the lowest living branch was attached (H_B, m), and stem diameter (D_B, cm) at H_B.

In the sugi plantation, six trees of different sizes were felled, and the dry weights of foliage (w_L kg), branches (w_B kg) and stem (w_S kg), were measured between August 5 and August 10, 1985 and used to estimate the weight of the corresponding organs of the sample tree.

Based on the destructive measurement in August 1985, allometric relationships between w_L and D_B, between w_B and D_B, and between w_S and D^2H were determined by the least squares method. They were given by

$$w_L = 0.0202 D_B^{2.45} \text{ (kg, cm)}, \quad r^2 = 0.98,$$

$$w_B = 0.00108 D_B^{3.18} \text{ (kg, cm)}, \quad r^2 = 0.96,$$

$$w_S = 0.0369\,(D^2H)^{0.850} \text{ (kg, cm}^2\text{ m)}, \quad r^2 = 0.99, \tag{1}$$

where r^2 is the coefficient of determination.

The values of w_L, w_B and w_S of the sample tree were estimated by substituting values of D, D_B and H for the sample tree (measured annually in April) into these allometric equations. We assumed that the allometric relationships did not change during the measurement period between 1982 and 1990. The value of the aboveground tree weight, w_T, was estimated from the sum of the estimated values of w_L, w_B and w_S:

$$w_T = w_L + w_B + w_S. \tag{2}$$

Estimated values of w_L, w_B, w_S and w_T are listed in Table 1.

In the following analysis, we used the value of w_T as a measure of tree size. In addition, we used the estimated mean value of w_T, $\overline{w}_T$, in the period from t_1 to t_2.

$$\overline{w}_T = \frac{w_{T2} - w_{T1}}{\log w_{T2} - \log w_{T1}}, \tag{3}$$

where t_1 is the year after the beginning of the observation in 1982, $t_2 = t_1 + 1$ year, and w_{T1} and w_{T2} are aboveground tree weights estimated at year t_1 and t_2.

Growth rate and net production rate of the sample tree

Growth rate of the aboveground weight of the sample tree was calculated as

$$v_w = \frac{w_{T2} - w_{T1}}{t_2 - t_1}. \tag{4}$$

The aboveground net production rate, v_p, was estimated as the sum of aboveground death rate and aboveground growth rate:

$$v_p = v_w + v_d, \tag{5}$$

where we assume that both v_w and v_d are measured on an annual basis. Values of v_p, v_w and v_d of the sample tree are listed in Table 1.

We did not measure the death rate during the period from July 1982 to June 1984, but we estimated the death rate of the sample tree during this period using the v_d – w_T relationship (Equation 6) and the w_T value of the sample tree. Estimated v_d values were small compared with the estimated v_w values between July 1982 and June 1984 (Table 1).

Results

Seasonal change in the death rate of leaves and branches

Figure 2 shows seasonal changes in the monthly death rate of leaves and branches of the sample tree. The death rate of leaves showed a characteristic seasonal change; about 80–90% of the annual death rate was observed between August and October.

In this plantation, measurement of litterfall rate has been conducted since 1984 (Miyaura and Hozumi 1989). The litterfall rate is maximal between January and April, with very little litterfall being observed between August and December, whereas death rates of leaves and branches peak four to six months earlier than the peak of litterfall rate. Thus, most dead leaves and branches remain attached to the tree for more than three months.

Tree size dependency of v_d and v_p

Figure 3 shows the relationship between v_d, the aboveground death rate, and w_T, the aboveground tree weight. The relationship between v_d and w_T is approximately linear

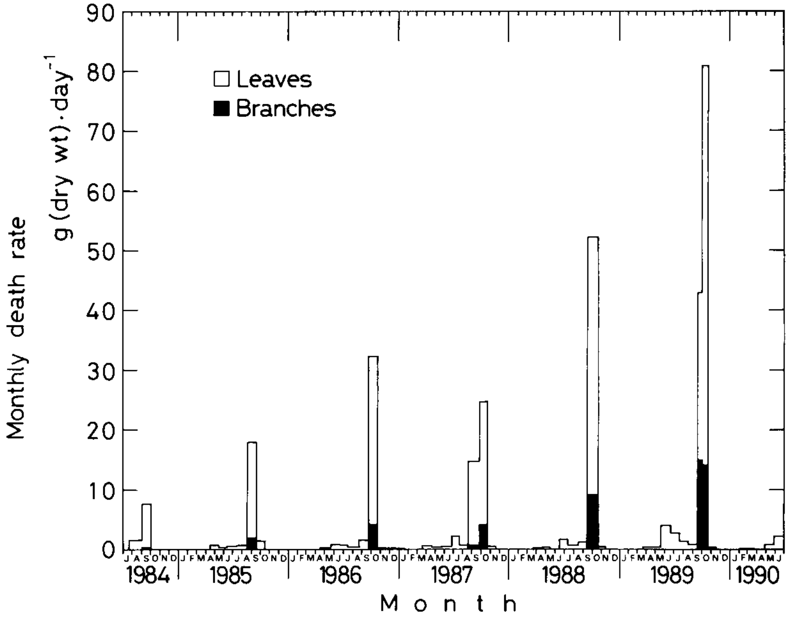

Figure 2. Seasonal trend of the monthly death rate for leaves and branches of the sample tree.

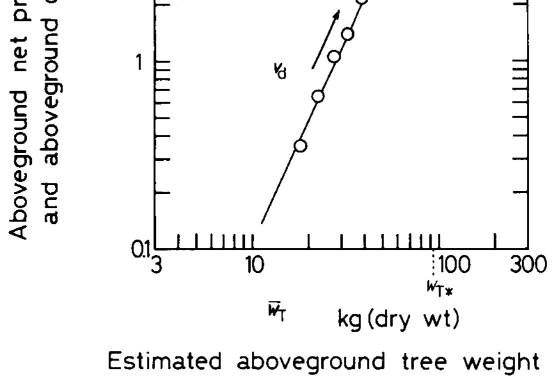

Figure 3. Relationships between aboveground net production rate (v_p) and estimated aboveground tree weight ($\overline{w}_T$) and between aboveground death rate (v_d) and $\overline{w}_T$ of the sample tree. The lines in the diagram are obtained by Equations 6 and 7, and the arrows indicate the progress of time, w_{T*} = the asymptotic value of w_T.

on logarithmic coordinates. Thus, we have the following power-form equation,

$$v_d = b w_T^{\beta}, \tag{6}$$

where the constant b = 0.000744 ($kg^{1-\beta}$ $year^{-1}$), the constant β = 2.16, and the coefficient of determination (r^2) = 0.98.

The power-form relationship between v_p (the aboveground net production rate) and w_T is also shown in Figure 3;

$$v_p = a w_T^{\alpha}, \tag{7}$$

where a = 0.905 ($kg^{1-\alpha}$ $year^{-1}$), α = 0.594, and r^2 = 0.79.

The constants, a, α, b and β in Equations 6 and 7 were determined by an ordinary least square method.

Growth rate as expressed by the function of tree size

Figure 4 shows the relationship between v_w, the aboveground growth rate, and w_T. From Equations 5, 6 and 7, we obtain the $v_w - w_T$ relationship,

$$v_w = v_p - v_d = a w_T^{\alpha} - b w_T^{\beta}. \tag{8}$$

We defined w_{T*} as the value of w_T at the intersecting point of two lines in Figure 3. From Equation 8, w_{T*} is represented by

$$w_{T*} = \left(\frac{a}{b}\right)^{\frac{1}{\beta - \alpha}}. \tag{9}$$

The value of v_p tends to equal the value of v_d when w_T approaches w_{T*}. This means that v_w approaches 0 (kg $year^{-1}$) when w_T approaches w_{T*}.

The growth curve of w_T

Converting the symbol of growth rate of the aboveground tree weight from v_w to dw_T/dt, we obtain the differential equation for the growth of aboveground tree weight:

$$v_w = \frac{dw_T}{dt} = a w_T^{\alpha} - b w_T^{\beta}$$

$$= a w_T^{\alpha}\left[1 - \left(\frac{w_T}{w_{T*}}\right)^{\beta - \alpha}\right]. \tag{10}$$

This equation is equivalent to Bertalanffy's equation.

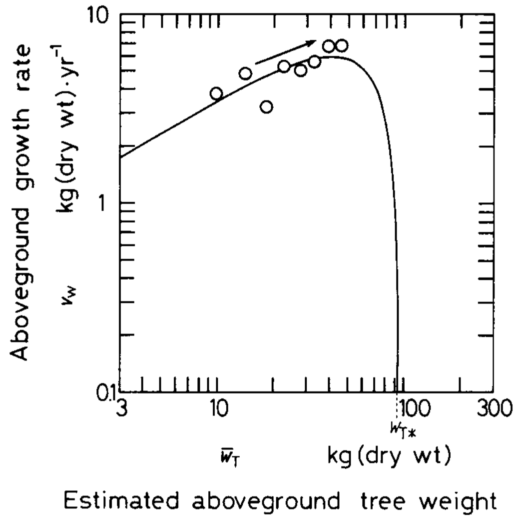

Figure 4. Relationship between aboveground growth rate (v_w) and estimated aboveground tree weight ($\overline{w}_T$) of the sample tree. The smooth curve in the diagram is obtained by Equation 8, and the arrow indicates the progress of time, w_{T*} = the asymptotic value of w_T.

The solution of Equation 10 under the condition of $w_T < w_{T*}$ and $\alpha < \beta$ is given by the following equation (Hozumi 1985).

$$w_T^{1-\alpha} F_1(w_T) = w_{T0}^{1-\alpha} F_1(w_{T0}) + a(1-\alpha)t,$$

$$F_1(w_T) = F\left(1, \frac{1-\alpha}{\beta-\alpha}; \frac{1-\alpha}{\beta-\alpha} + 1; \left(\frac{w_T}{w_{T*}}\right)^{\beta-\alpha}\right),$$

$$F_1(w_{T0}) = F\left(1, \frac{1-\alpha}{\beta-\alpha}; \frac{1-\alpha}{\beta-\alpha} + 1; \left(\frac{w_{T0}}{w_{T*}}\right)^{\beta-\alpha}\right), \qquad (11)$$

where F represents the Gaussian hypergeometric function (Oberhettinger 1970), and w_{T0} the initial value of w_T.

Figure 5 shows the change in w_T of the sample tree with time t. As seen in the figure, the growth curve given by Equation 11 approximates the changes in w_T of the sample tree.

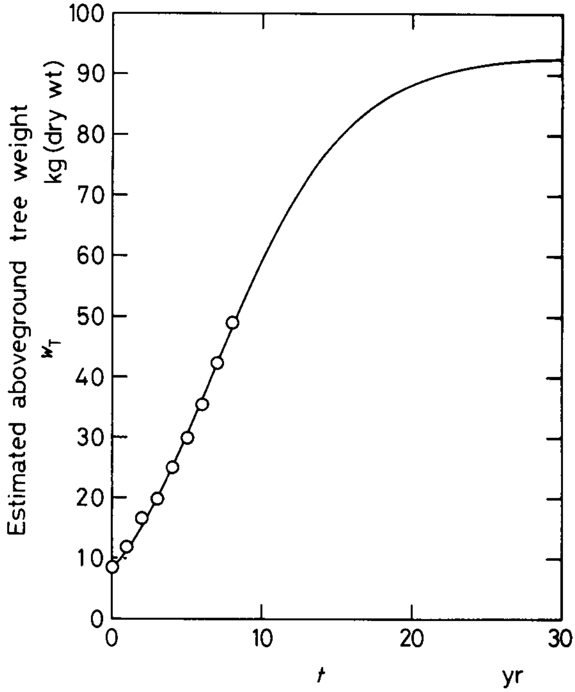

Figure 5. Growth curve of the sample tree. The smooth curve is obtained by Equation 11, t = time after observation of the initial values of tree sizes.

Time course of v_p, v_d *and* v_w

Using Equations 6, 7 and 11, we can represent v_p and v_d as a function of time t:

$$\left(\frac{v_p}{a}\right)^{\frac{1-\alpha}{\alpha}} F_2(v_p) = \left(\frac{v_{p0}}{a}\right)^{\frac{1-\alpha}{\alpha}} F_2(v_{p0}) + a(1-\alpha)\,t\,,$$

$$F_2(v_p) = F\left(1, \frac{1-\alpha}{\beta-\alpha}; \frac{1-\alpha}{\beta-\alpha}+1; \left(\frac{v_p}{v_{p*}}\right)^{\frac{\beta-\alpha}{\alpha}}\right),$$

$$F_2(v_{p0}) = F\left(1, \frac{1-\alpha}{\beta-\alpha}; \frac{1-\alpha}{\beta-\alpha}+1; \left(\frac{v_{p0}}{v_{p*}}\right)^{\frac{\beta-\alpha}{\alpha}}\right), \qquad (12)$$

and

$$\left(\frac{v_d}{a}\right)^{\frac{1-\alpha}{\beta}} F_3(v_d) = \left(\frac{v_{d0}}{a}\right)^{\frac{1-\alpha}{\beta}} F_3(v_{d0}) + a(1-\alpha)t,$$

$$F_3(v_d) = F\left(1, \frac{1-\alpha}{\beta-\alpha}; \frac{1-\alpha}{\beta-\alpha}+1; \left(\frac{v_d}{v_{d*}}\right)^{\frac{\beta-\alpha}{\beta}}\right),$$

$$F_3(v_{d0}) = F\left(1, \frac{1-\alpha}{\beta-\alpha}; \frac{1-\alpha}{\beta-\alpha}+1; \left(\frac{v_{d0}}{v_{d*}}\right)^{\frac{\beta-\alpha}{\beta}}\right), \quad (13)$$

where v_{p0} and v_{d0} are the initial values of v_p and v_d when $w_T = w_{T0}$, and v_{p*} and v_{d*} are the values of v_p and v_d when $w_T = w_{T*}$. That is,

$$v_{p0} = a\, w_{T0}{}^{\alpha}, \quad v_{p*} = a\, w_{T*}{}^{\alpha}, \quad v_{d0} = b\, w_{T0}{}^{\beta}, \quad v_{d*} = b\, w_{T*}{}^{\beta}. \quad (14)$$

Figure 6 shows the time courses of v_p and v_d of the sample tree obtained from Equations 12 and 13.

Discussion

Hozumi (1985, 1987) analyzed the stem volume growth of some tree species by

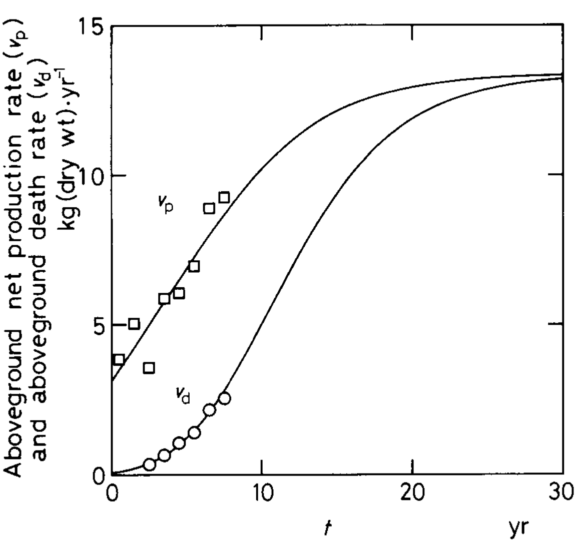

Figure 6. Changes in the value of aboveground net production rate (v_p) and aboveground death rate (v_d) of the sample tree. The smooth curves are obtained by using Equations 12 and 13, t = time after observation of the initial values of tree sizes.

using a $u - w$ diagram, and suggested that stem volume growth could be approximated by Bertalanffy's equation. We have found experimentally that the growth of aboveground tree weight was also approximated by Bertalanffy's equation.

In the past, growth analysis of forest trees has been based on growth increments, such as increases in annual ring width, annual stem diameter and tree height. Growth analysis based on the measurement of dry matter budget of a tree can provide additional information on the process of tree growth. For example, we can predict the dry matter budget of the tree by using the $v_p - w_T$ and $v_d - w_T$ relationships and the growth curve of w_T (Figures 6 and 5).

In this study, the maximum value of w_T, w_{T*}, of the sample tree was estimated to be about 93 kg. However, larger values of w_T have been reported for other sugi trees. For example, Harada et al. (1972) reported w_T values of over 700 kg. This suggests that the growth curve obtained in the present study will not cover the whole range of growth of the sample tree, which may have a higher w_{T*} value in the future (Hozumi 1987).

Allometric relationships between tree size and the rate of biological processes of forest trees, such as respiration rate and litterfall rate, have been reported for some tree species (Ninomiya and Hozumi 1981, 1983, Miyaura and Hozumi 1985, 1988, 1989). These relationships were observed among various sized trees in the same forest stand for a short period (one to several years). We have to distinguish two types of allometric relationships between tree size and the rate of biological processes of the tree. One is the relationship observed among different trees in the same forest stand, and the other is the relationship observed for a single tree with the progress of time (Paembonan et al. 1992). To determine the interrelation between the two types of allometric relationships, it is necessary to trace the relationship between tree size and the rate of a biological process over time, as was done in this study, for several trees of different initial sizes.

From a technical viewpoint, the weight of organs of a tree should be indirectly estimated in a growth analysis based on dry matter budget. Relationships between w_L and D_B, between w_B and D_B and between w_S and D^2H, respectively, of the trees of different stands and different ages are known to be represented by single allometric functions (Shinozaki et al. 1964, Kira and Shidei 1967, Causton 1985). Therefore, our assumption that weights of leaves, branches and stem of the sample tree were successfully estimated by means of allometric relationships estimated from the single destructive measurement is highly plausible.

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