

林木の呼吸 I

立木密閉法によるアイグロマツの呼吸測定

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inherent to trees. Since we cannot yet fully understand the complex conditions which affect the respiration rates in detached samples, a non-destructive measurement of respiration in standing trees is necessary for the accurate analysis of the dry matter budget in forest communities.

In this connection, an enclosed standing tree method with a plastic bag was adopted to measure the nighttime respiration of pine trees (*Pinus densi-thunbergii* UYEKI) growing on the campus of Nagoya University. The purpose of this study is to assess respiratory consumption of a standing tree and a forest stand, to follow their seasonal changes, and to analyze relationships among respiration rate, air temperature, and tree size.

II. Materials and Methods

The study was carried out monthly from October 1977 to March 1979 with 7 to 11 year-old (as of 1978) trees of *Pinus densi-thunbergii* UYEKI, a natural hybrid of *P. densiflora* SIEB. et ZUCC. and *P. thunbergii* PARL., planted on the campus of Nagoya University. The general features of study site are as follows: the area, tree density, mean tree height, and mean diameter at breast height (d.b.h.) are 178 m², 0.64 trees/m², 3.25 m, and 3.75 cm (as of 1978), respectively. From the study site, four trees were chosen as sample trees. *H* (tree height), *D*₀ (diameter at ground surface), *D*₃₀ (diameter at 30 cm above ground), *D* (d.b.h.), *D*_B (diameter at top of clear length) of them in October 1978 were as follows: Tree 1: 3.98 m, 12.64 cm, 9.07 cm, and 7.51 cm. Tree 2: 3.43 m, 8.20 cm, 5.80 cm, 4.20 cm, and 5.20 cm. Tree 3: 2.11 m, 5.90 cm, 4.00 cm, 2.10 cm, and 4.13 cm. Tree 4: 1.43 m, 2.90 cm, 2.00 cm, 0.90 cm, and 2.30 cm.

Figure 1 shows the enclosed standing tree method used in this study. The above-ground part of the sample tree was enclosed by a plastic bag made of thick laminated nylon film (Toyo-gosei-film, polypropylene 30 μ /nylon 40 μ /polyethylene 70 μ). The bag was prepared by welding the film according to tree size. In order to keep airtightness, the chink between the bag and tree was filled with potter's clay. It was confirmed from a preliminary experiment that the leak of air from the bag was negligible during the measurement.

A thermometer was hung from a low frame (Fig. 1) to follow changes in the air temperature (*T'*) in each bag, and the monthly mean air temperature (*T*) was calculated for each bag and month. Furthermore, monthly mean air temperatures in the four bags for each month ($\bar{T}$) were calculated from *T*.

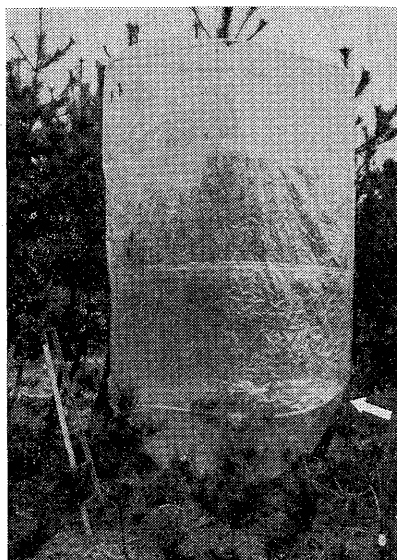


Fig. 1. Enclosed standing tree method
The arrow indicates a low frame.

The volume of a bag was calculated from its diameter and height by assuming that its shape consisted of a cone and a cylinder. The volume of the four bags were as follows: Tree 1, 10472 liters; Tree 2, 3844 l; Tree 3, 955 l; and Tree 4, 79 l.

The respiration measurement started at sunset. Through vinyl pipes ($\phi=4$ mm), whose mouths were placed at three different levels above ground, three gas samples were taken respectively from the upper, middle, and bottom parts of the bags by using plastic injectors (TERUMO) after removing the gas which remained in the pipe. The volume of a sample of gas was 20 cm³. The sampling was conducted at one hour intervals.

The CO₂ concentration of each gas sample was measured by an apparatus with an infrared gas analyser (URAS-1, HARTMANN and BRAUN). For the determination of the CO₂ concentration of a gas sample, the preliminarily obtained relationship between the areas recorded on the chart and CO₂ concentration of standard gases was used.

An F-test was conducted to detect the significant differences of the CO₂ concentration among sampling times, the upper, middle, and bottom parts of the bag, and their interactions at each measurement. Least significant differences (L.S.D.s) were calculated for the differences of CO₂ concentration among sampling times and the three parts of the bag.

In order to assess the respiration loss of the forest stand, the following census and measure-

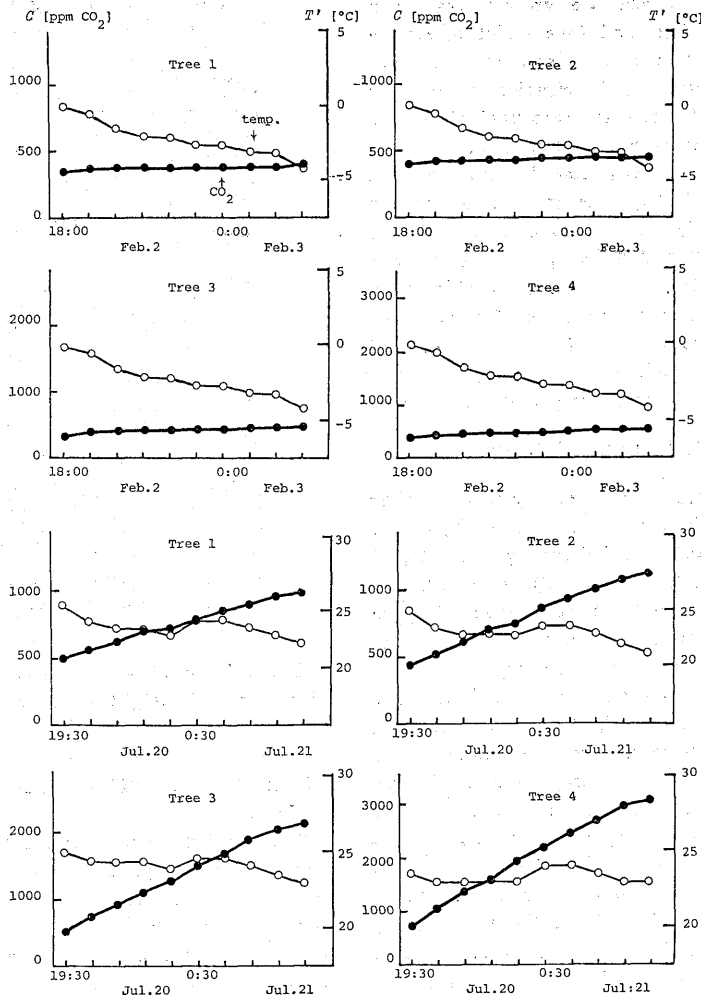


Fig. 2. Changes in CO_2 concentration (●) and air temperature (○) in the bag on February 2~3 and July 20~21, 1978

ments were made. The diameter and height of all trees on the study site were measured in April 1977 and October 1978. The biomass of the study site was estimated by an allometric method (YODA, 1971; OGAWA and KIRA, 1977) based on the data of six sample trees felled in November 1978.

III. Results

1. Changes in CO_2 concentration in the bags

The F-test showed that all the observed differences among sampling times were significant at the one percent level and that 1/5 of the observed differences among the upper, middle, and bottom parts of the bags also were significant at the one percent level. L. S. D. s among the sampling times were bigger than those among the three

parts of the bags in all observations. In the following, the mean value of CO_2 concentration of the three parts of a bag was taken for the CO_2 concentration in the bag at that time.

A few examples of time courses of CO_2 concentration in bags are shown in Fig. 2. It can be seen from the figure that the courses show some saturation curves. This indicates that the respiration rates were high at twilight and gradually declined toward midnight. These declines largely followed those of air temperatures in the bags (Fig. 2). This tendency was clearer in winter than in summer.

The average nighttime respiration rate of the above ground part of the sample trees, r_{Ti} [$\text{mg CO}_2/\text{tree hr}$], were calculated by Eq. (1):

$$r_{Ti} = \frac{1}{t_n - t_0} \cdot V \cdot \frac{44}{22.4} \left(C_n \cdot \frac{273}{273 + T_n} - C_0 \cdot \frac{273}{273 + T_0} \right) \cdot 10^{-6} \quad (1)$$

where t_0 , C_0 , and T_0 are the time [hr], CO_2 concentration [ppm CO_2], and air temperature [$^{\circ}\text{C}$] in the bag at the beginning of the experiment respectively; while t_n , C_n , and T_n are those at the end of the experiment; V is the volume of the bag [1].

2. Respiration rates of the sample trees

The seasonal changes in respiration rates of the sample trees (r_{Ti}) are illustrated in Fig. 3 together with the seasonal courses of the mean air temperature within the four bags, $\bar{T}$. The seasonal trend of r_{Ti} largely followed that of the air temperature except during August. In general, the respiration rate increased gradually from winter to mid-summer, reaching a maximum in July, abruptly falling in August, and thereafter decreasing toward winter.

The relationships between the respiration rate (r_{Ti}) and the air temperature ($\bar{T}$) are shown in

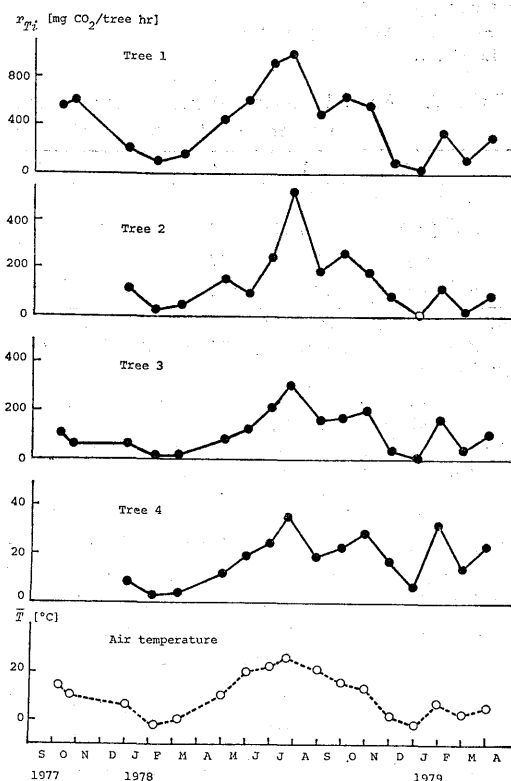


Fig. 3. Seasonal changes in r_{Ti} and T . Since the rate of Tree 2 in December 1978 was slightly negative, it was estimated by Eq. (2) and is shown by the white dot.

Fig. 4. As is widely known, the $\log r_{Ti} - T$ relationships were approximately linear, but it was recognized that the gradient varied at $10 \sim 15^{\circ}\text{C}$. Below $10 \sim 15^{\circ}\text{C}$, the gradient was steeper than the gradient above this temperature, namely, the response of the respiration rate to the seasonal changes in monthly air temperature from November to March was more sensitive. The thermal coefficient (Q_{10}) of the respiration rate was estimated to be $1.14 \sim 1.79$ in the higher temperature range and $4.27 \sim 9.81$ in the lower one.

Figure 5 shows a few examples of the observed relationships between the respiration rate (r_{Ti}) and the tree diameter at the top of clear length (D_B , cm). The $\log r_{Ti} - \log D_B$ relationship was approximately linear, thus, the relationship satisfied the power function,

$$r_{Ti} = a D_B^b \quad [\text{mg CO}_2/\text{hr tree, cm}] \quad (2)$$

where a [$\text{mg CO}_2/\text{tree hr cm}^b$] and b [dimensionless] are coefficients. Seasonal changes in the coefficients, a , b , in Eq. (2), and the coefficient of determination (r^2) are given in Table 1. Similar power-form relationships were observed between r_{Ti} and D_0 , D_{30} , D , D_0^2H , D_{30}^2H , D^2H , and D_B^2H . But their goodness of fit is usually less than that of Eq. (2).

Based on the seasonal trend of r_{Ti} , the amount of annual respiration of a sample tree (ΔR_{Ti}) was estimated by assuming that the respiration rate was constant within the month for which the value was obtained, and that one month equaled 720 hours. The annual amount of respiration and the tree size are given in Table 2 for each sample.

To make clear the size dependency of ΔR_{Ti} on the dry weight of the sample tree (above ground

Table 1. Seasonal changes in the coefficients, a , b , in Eq. (2) and the coefficient of determination, r^2

			a	b	r^2
			mg CO_2/tree hr cm^b	Dimen- sionless	Dimen- sionless
1977	Dec.	29	2.63	2.29	0.97
1978	Feb.	2	0.31	2.76	0.98
	Mar.	6	0.56	2.72	0.97
	Apr.	29	1.88	2.80	1.00
	May.	29	3.42	2.36	0.92
	Jun.	26	3.73	2.65	0.99
	Jul.	20	6.41	2.52	0.99
	Aug.	28	3.33	2.41	1.00
	Sept.	27	3.51	2.50	1.00
	Oct.	26	5.38	2.18	0.98
	Nov.	29	6.43	1.21	0.71
	Dec.	30	1.45	1.09	0.35
1979	Jan.	30	6.74	1.95	0.90
	Feb.	28	3.84	1.37	0.53
	Mar.	27	4.12	2.05	0.93

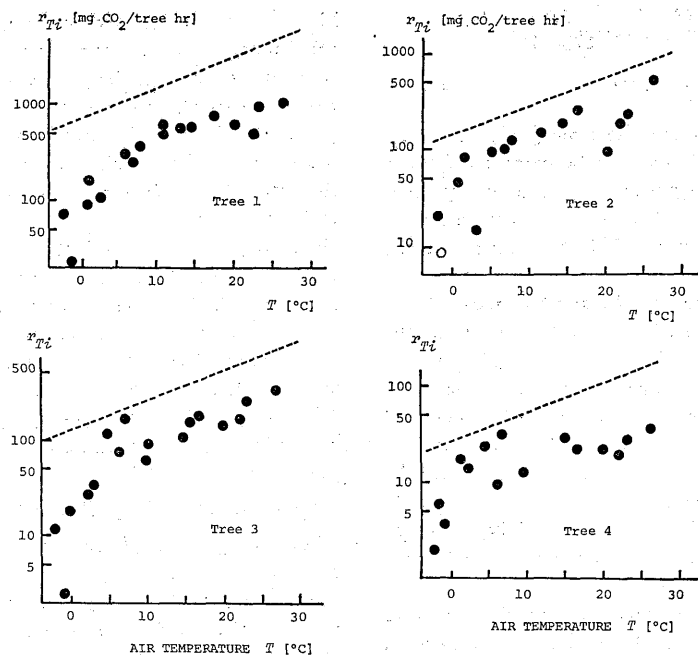


Fig. 4. Relationship between r_{Ti} and T
The dotted lines show the lines whose thermal coefficient (Q_{10})=2.00.
For the white dot, see the explanation in Fig. 3.

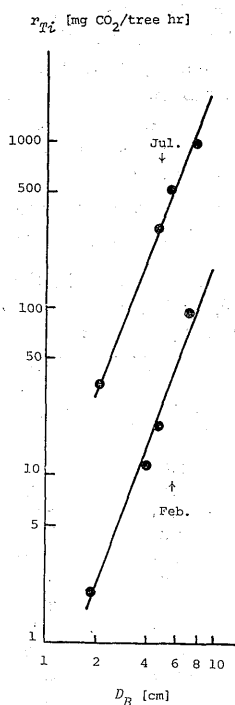


Fig. 5 Relationship between r_{Ti} and D_B in February and July 1978

The solid lines are given by Eq. (2): $r_{Ti}=0.31 D_B^{2.76}$ (Feb.), $r_{Ti}=6.41 D_B^{2.29}$ (Jul.).

Table 2. Annual amount of respiration in the sample trees in relation to their size

Tree No.	1	2	3	4
Mean tree size				
$D_B^{\#}$ [cm]	7.71	5.25	4.48	2.00
$H^{\#}$ [cm]	378	297	188	130
$w_T^{\dagger}$ [g]	9470	3838	2644	397
Annual amount of respiration				
ΔR_{Ti}	4031	1451	1041	148
[g CO ₂ /tree yr]				

$\#$ shows that D_B and H are mean values of D_B and H in Dec. 1977 and Nov. 1978.

$\dagger$ shows that w_T are mean values of w_T in Dec. 1977 and Nov. 1978 by assuming allometry.

portion, w_T) given in Table 2, the ΔR_{Ti} - w_T relationship was examined with log-log coordinates. Here w_T was estimated from the allometric relationship between D_B and w_T determined for several trees other than the sample trees, or

$$w_T = 77.94 D_B^{2.35} \text{ [g d. w./tree, cm]}$$

The relationship between ΔR_{Ti} and w_T shown in Fig. 6 satisfied the power function,

$$\Delta R_{Ti} = 0.34 w_T^{1.03} \text{ [g CO}_2\text{/tree yr, g d. w./tree]} \quad (3)$$

It can be concluded that ΔR_{Ti} is almost directly proportional to w_T , since the exponent of Eq. (3) approximates unity.

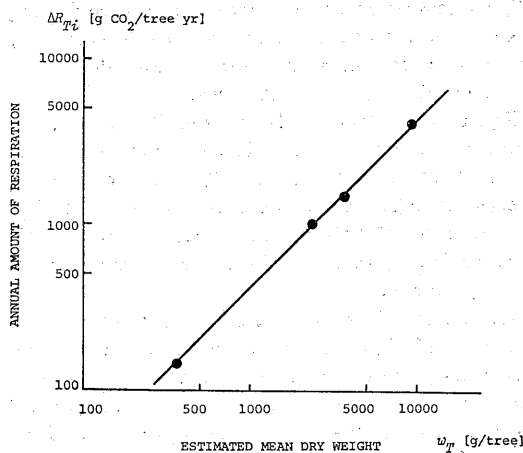


Fig. 6. Relationship between ΔR_{T_i} and w_T
The relationship is given by Eq. (3).

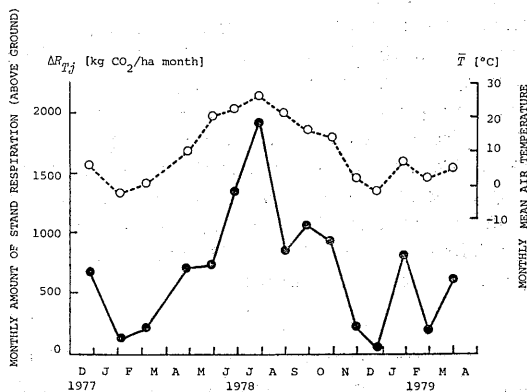


Fig. 7. Seasonal changes of ΔR_{T_j} and $\bar{T}$
The depression of ΔR_{T_j} in August was noticeable.

3. Respiration of the entire stand

Using the relationship of Eq. (2), the monthly amount of respiration of the entire stand (above ground portion) ΔR_{T_j} [kg CO₂/ha month], can be calculated by the following equation:

$$\Delta R_{T_j} = \sum_{i=1}^N a_j D_{B_{ij}} b_j 720 \frac{1}{Q} 10^{-2} \quad (4)$$

where the subscripts i and j denote tree number and month respectively, a_j and b_j are coefficients specific to each month, $D_{B_{ij}}$ is the stem diameter at the top of the clear length calculated by the assumption of linear growth of D_B with time, N is the number of trees in the stand, and Q [m²] is the area of the study site. In Eq. (4), it is assumed that the relationship of Eq. (2) applies to all trees in the stand.

As was predictable, the seasonal trend ΔR_{T_j} was similar to that of r_{T_i} , that is, it largely followed

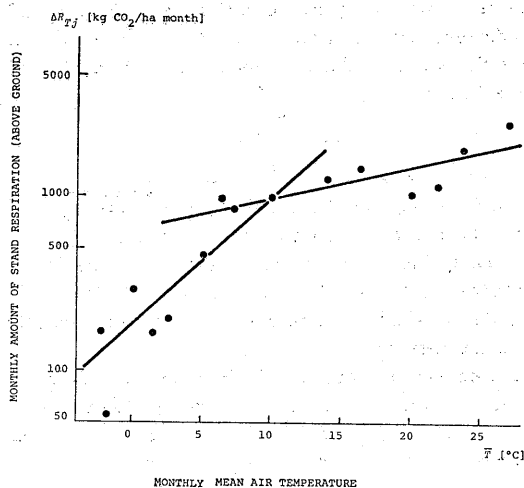


Fig. 8. Relationship between ΔR_{T_j} and $\bar{T}$
The relationship is approximated by the two heavy lines.

that of air temperature except in August (Fig. 7). Dependence of ΔR_{T_j} on $\bar{T}$ was tested by the log ΔR_{T_j} - $\bar{T}$ diagram (Fig. 8) which showed that the relationship was approximated by two straight-line segments. The thermal coefficients (Q_{10}) of ΔR_{T_j} were estimated to be 1.52 in the higher temperature range and 5.58 in the lower one. The annual amount of respiration of the entire stand (above ground portion), ΔR_T [t CO₂/ha yr, or t dry matter/ha yr] (t when referenced to weight in this paper indicates metric ton), was estimated by the following simple summation:

$$\Delta R_T = \sum_j \Delta R_{T_j} \quad (5)$$

where $\sum$ means that the summation was made from December 1977 to November 1978. From Eq. (5), ΔR_T was estimated to be 9.22 t CO₂/ha yr. If the dry matter/CO₂ conversion factor is assumed to be 0.614 (SATOO, 1973), the annual respiratory consumption amounts to 5.66 t dry matter/ha yr.

The estimate of annual respiratory loss is based on nighttime respiration. Therefore the value may be underestimated because the effect of high temperature during the daytime on the respiration rate is neglected. Taking the changes in air temperature at three hour intervals in a ten-day period observed by the Nagoya Local Meteorological Observatory into consideration, and further assuming that the thermal coefficients were 1.52 and 3.74 in the warm season (April to October, 1978) and in colder seasons (December 1977 to March 1978 and in November 1978) respectively, an estimated annual respiration amount of 7.26 t dry matter/ha yr is obtained. It should be noted that

the correction is quite tentative, and the thermal coefficients are different from the value of Q_{10} in that the latter is determined usually by short term experiments.

IV. Discussion

1. Methodological aspects

Various methods for respiration measurement of trees have been proposed but they are divided into two categories: the cutting methods and the intact methods. NEGISI (1970) and EVANS (1972) made detailed critical reviews of the merits and demerits of these methods.

An enclosure method, which belongs to the intact category, was adopted for this study to minimize the interfering effects of cutting sample trees. However this method has several problems to be considered.

First to consider is the effect of CO_2 concentration on the rate of CO_2 release from tree surfaces, this is inherent to the present experimental method and is related to the diffusion of CO_2 in the tree (EVANS, 1972) and bag, because $\dot{r}_{Ti}$ (actual respiration rate) might not be equal to r_{Ti} (apparent respiration rate which is observed in this study).

The following model of CO_2 release from the tree (Fig. 9) was assumed:

$$\left. \begin{aligned} \frac{dC}{dt} &= -\frac{\kappa}{V}(C_p - C) \\ \frac{dC_p}{dt} &= \frac{\dot{r}_{Ti}}{V_p} - \frac{\kappa}{V_p}(C_p - C) \end{aligned} \right\} \quad (6)$$

where C and V are the CO_2 concentration and the volume of the bag respectively, C_p and V_p are the

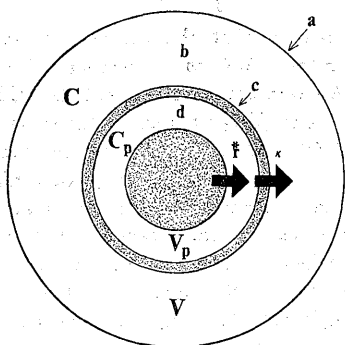


Fig. 9. A simplified diagram of the main elements involved when considering movement of CO_2 out of a respiring plant into a bag (cf. Fig. 12.5., EVANS, 1972)

a: Plastic bag, b: space in the bag, c: bark and other epidermal tissues, d: conducting system and storage space in a tree, others: see text.

CO_2 concentration and the volume of the conducting system and storage space in the tree respectively, and κ is a coefficient relating to the diffusion of CO_2 from the surface of the tree.

Equation (6) features linear simultaneous differential equations, and the solutions have been given by NINOMIYA and HOZUMI (1978). However at present it is difficult to analyze the effect of $C(t)$ on the rate of CO_2 release based on the model, because Eq. (6) includes the unknown parameters, C_p , V_p , and κ .

As mentioned under "Results", 20 percent of the data showed significant differences in CO_2 concentration among the upper, middle, and bottom parts of the bag. It is intended to improve on the present method to make the CO_2 concentration as uniform as possible.

2. Short term changes in the respiration rate

Discussion is directed to the overnight changes in r_{Ti} assuming $r_{Ti} = \dot{r}_{Ti}$. The respiration rate of sample trees (r_{Ti}) was high at twilight and gradually declined toward midnight (Fig. 2). This tendency was prominent during the winter season. From this phenomenon it might be considered that the respiration rate has a diurnal rhythm (BÜNNING, 1973). To explain the results shown in Fig. 2, an exogenous rhythm caused by an external factor or air temperature in the bag may be assumed. The following Eqs. (7) and (8) based on experimental results are assumed:

$$r_{Ti} = r_{Ti0} e^{kT'} \quad (7)$$

$$T' = T_0' - \alpha t \quad (8)$$

where $r_{Ti0} = r_{Ti}(T')|_{T'=0}$, T' is the air temperature in the bag, $T_0' = T'(t)|_{t=0}$, t is time, and k and α are coefficients. Equation (7) is recognized widely in a past study, and Eq. (8) is valid only from twilight to midnight.

From Eqs. (7) and (8), the rate of the changes in CO_2 concentration in the bag, dC/dt [ppm CO_2 /hr], is expressed by Eq. (9)

$$\frac{dC}{dt} = -\frac{r_{Ti0}}{V} e^{k(T_0' - \alpha t)} \quad (9)$$

Integrating Eq. (9) with respect to t gives changes in CO_2 concentration with time, Eq. (10)

$$C(t) = -\frac{r_{Ti0}}{V k \alpha} e^{k T_0'} (1 - e^{-k \alpha t}) + C_0 \quad (10)$$

where $C_0 = C(t)|_{t=t_0}$

The coefficients of Eq. (10) were determined from the finite difference curve obtained from the observed $C(t)$ - t curve, and the calculated CO_2 concentration was compared with the observed one (Fig. 10). From Fig. 10, it might be thought that Eq. (10) followed the actual changes in CO_2 con-

centration in the bag. However, the thermal coefficients of the respiration rate (Q_{10}) derived from Eq. (10) are unusually high, more than 100. Such a high value of a thermal coefficient hardly can be considered for the plant respiration rate, since the value of the thermal coefficient lies in general between 1 and 3 (KIMURA and TOTSUKA,

1973). Therefore, the respiration depression in this result might not be explained only by the exogenous rhythm caused by the air temperature in the bag.

Presumably both internal factors (endogeneous rhythm [BÜNNING, 1973] and so forth) and external factors (CO_2 concentration and air temperature in the bag, and so forth) account for the depression in the rate of CO_2 release.

3. Seasonal changes in the respiration rate

There are several reports on seasonal changes in the respiration rate of trees (NEGISI, 1966; NAKAI, 1969; OOHATA and SHIDEI, 1969; YODA, 1978; HAHARA, 1978), but there are few reports about the respiration rate of a single tree obtained by the standing tree method using constant air currents (NEGISI, 1966).

As shown in Fig. 3, the respiration rate of the sample trees reached its maximum between July and August and reached its minimum between January and February. For the most part it followed the seasonal changes in air temperature in the bag except in August when an abrupt fall was observed. This decrease presumably was caused by the dry summer of 1978 with 27 fine days and 70 mm of monthly rain fall (20 days and 143 mm are the mean values from 1941 to 1970 [Yearbook of Science, 1974]). Similar decreases have been reported also by several authors (NEGISI, 1972, 1975, 1978; OOHATA and SHIDEI, 1969; YODA, 1978).

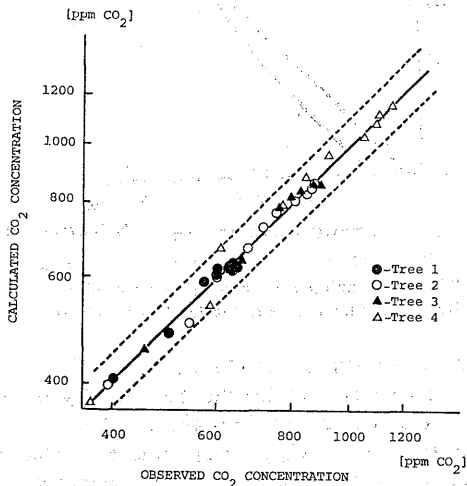


Fig. 10. Comparison of observed and calculated values (by Eq. (10)) of CO_2 concentration in the bag in April 1978

The solid line and dashed lines show 0 and ± 10 percent of the relative errors.

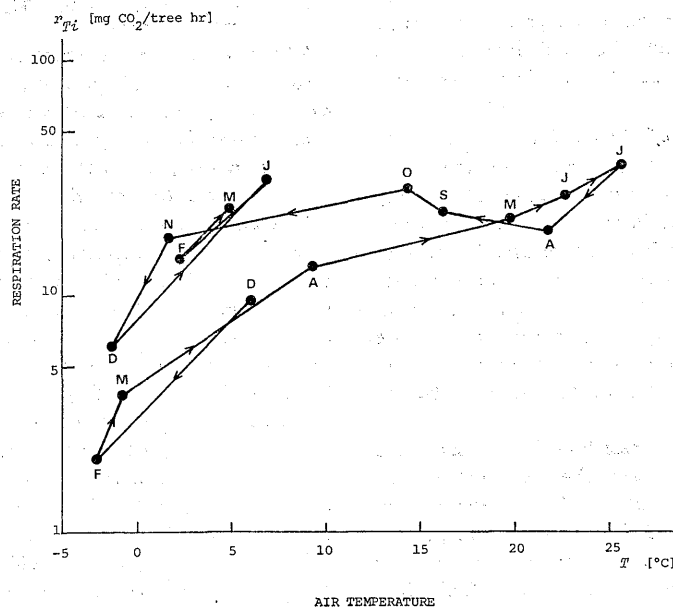


Fig. 11. Relationship between r_{Ti} and T in Tree 4. The arrows indicate progress of the season.

As mentioned before, the thermal coefficients were unusually high when calculated from the result of a short term, one night. But the thermal coefficients determined on the basis of monthly mean air temperature in the bag were appropriate when compared to other reports (Fig. 4). The thermal coefficient of the respiration rate varied between the higher temperature range and lower temperature range. Similar seasonal changes in the thermal coefficient have been reported on for the canopy respiration of *Chamaecyparis obtusa* (HAGIHARA and HOZUMI, 1977). It is said generally that the thermal coefficient of the respiration rate is high in the lower temperature range and low in the higher temperature range (KIMURA and TOTSUKA, 1973) as in the results of this study. The higher temperature season corresponded to the months with mean temperature in the bag higher than 10~15°C, namely, those from April to October. The lower temperature season corresponded to the months from November to March. In the Tokai district, the growth period extends from April to September, and the dormant period is from October to March for *P. densiflora* (NAGATA, 1968). Therefore, for present species, the dependence of the respiration rate on the monthly mean air temperature varied between the growth and dormant periods.

It should not be overlooked that the growth increment of the sample tree may affect in a complicated way the r_{Ti} - T relationship discussed above. The r_{Ti} - T diagram of sample Tree 4 (Fig. 11), whose annual growth increment is estimated to be 70 percent of the initial shoot weight, offers some suggestion on the effect of growth increment. Its further study will be useful in analyzing seasonal trends of r_{Ti} .

4. Size dependency of the respiration rate

The $\log r_{Ti}$ - $\log D_B$ relationship satisfied the power function, Eq. (2) (Fig. 5). This relationship is important for the estimation of the respiration rate of an entire stand from the respiration rate of a single tree. The relationship had a good fitness when D_B was used for the parameter. This suggests that D_B is a proper parameter whose biological meanings are stressed by the pipe model theory of tree form (SHINOZAKI *et al.*, 1964 a, 1964 b).

The $\log \Delta R_{Ti}$ - $\log w_T$ relationship satisfied the power function, Eq. (3), and the exponent of the function nearly equals unity. Thus, the annual amount of respiration of the above ground portion may be directly proportional to its dry weight as far as this experiment is concerned. This fact shows that the annual respiratory loss of the above ground portion belongs to the allometric tribe

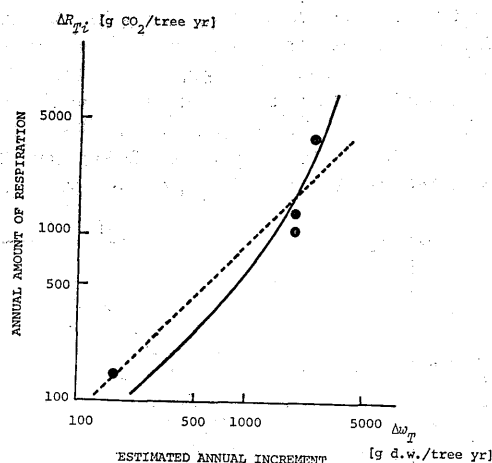


Fig. 12. Relationship between ΔR_{Ti} and Δw_T . The relationship can be roughly approximated by Eq. (1) (dashed line) and Eq. (12) (solid line).

(HOZUMI and SHINOZAKI, 1974).

The allometric relationship between D_B and w_T was presented under "Results". The annual increment of dry weight (Δw_T) was estimated by assuming that the allometry does not change during the year. As a result, the ΔR_{Ti} - Δw_T relationship can be approximated roughly by the following equations (Fig. 12):

$$\Delta R_{Ti} = 0.81 \Delta w_T^{1.01} \quad [g \text{ CO}_2/\text{tree yr}, g \text{ d.w./tree yr}] \quad (11)$$

$$\frac{1}{\Delta R_{Ti}} = \frac{2.50}{\Delta w_T} - 0.00060 \quad (12)$$

These equations suggest that ΔR_{Ti} might be directly proportional to Δw_T , and this should be examined by future experiments.

5. Interrelationship among the annual respiration loss, biomass, and biomass increment in the entire stand

The annual shoot respiratory loss of the present stand (ΔR_T) was estimated to be 5.77 [t dry matter/ha yr]. This value was small because of the small biomass of the above ground portion, 26.36 t dry matter/ha, which represents an arithmetic mean biomass between December 1977 and November 1978. The ratio of ΔR_T to biomass, 0.21/yr, is comparable with others obtained in different forest types, 0.36/yr in a *C. obtusa* plantation (HAGIHARA, 1978), 0.22/yr in a tropical rain forest (KIRA and SHIDEI, 1967), and 0.12/yr in a warm-temperate evergreen oak forest (KIRA and YABUKI, 1978).

To express a conversion efficiency of substrate matter used for respiration into biomass, a ratio defined by $\Delta y_T / \Delta R_T$, in which Δy_T is the annual biomass increment of the above ground portion of

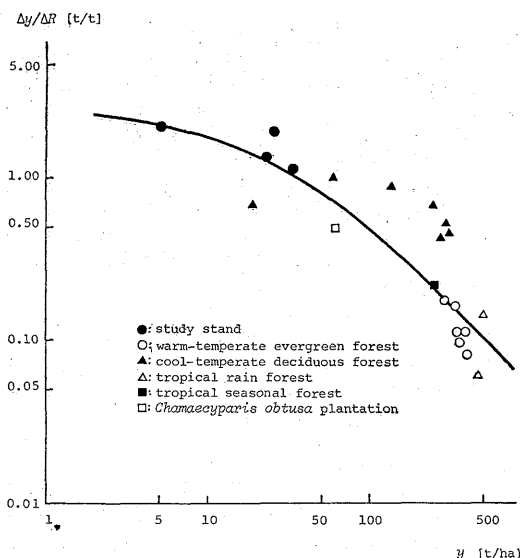


Fig. 13. Relationship between $\Delta y_T/\Delta R_T$ and y_T . The relationship is approximated roughly by Eq. (13) as shown by the curve.

Table 3. Annual respiration loss (ΔR_T), biomass (y_T), and biomass increment (Δy_T) in subplots A, B, C, and entire stand

	Subplot			Entire stand
	A	B	C	
y_T [t/ha]	25.38	5.16	31.99	22.55
Δy_T [t/ha yr]	10.95	2.40	8.87	7.62
ΔR_T [t/ha yr]	5.98	1.16	8.33	5.66
Age [yr]	7	7	11	7~11
Density [1/m ²]	1.07	0.67	0.34	0.64

the entire stand on a dry matter basis is proposed. It may be expected that the value of $\Delta y_T/\Delta R_T$ will be high in a forest which has a high degree of growth efficiency, and low in such a stand as a climax forest. The following ratio were observed: 1.33 in the study's pine stand, 0.48 in the 18 year-old *C. obtusa* plantation (HAGIHARA, 1978), 0.10 in the warm-temperate evergreen oak forest (KIRA and YABUKI, 1978), and 0.06 in the tropical rain forest (KIRA and SHIDEI, 1967).

Figure 13 illustrates the relationship between $\Delta y_T/\Delta R_T$ and y_T [t dry matter/ha] (above ground biomass) in a various forest stands (HAGIHARA, 1978; KIMURA, 1960; KIRA, 1976, KIRA and SHIDEI, 1978; TADAKI *et al.*, 1969; MÖLLER *et al.*, 1954; MÜLLER and NIELSEN, 1965). In Fig. 13, the study stand is divided into three subplots (A, B, and C) by age and density as shown in Table 3. It shows the annual respiration loss, biomass, and biomass increment in subplot A, B, and C, and entire stand. The relationship between $\Delta y_T/\Delta R_T$ and y_T is

approximated roughly by Eq. (13)

$$\frac{1}{\Delta y_T/\Delta R_T} = A y_T + B \quad (13)$$

where $A=0.22$ [ha/t] and $B=0.36$ [dimensionless].

Equation (13) is rewritten as Eq. (14)

$$\Delta R_T = A \Delta y_T y_T + B \Delta y_T \quad (14)$$

Dividing both sides of Eq. (14) by Δt , which is a time duration, results in

$$\frac{\Delta R_T}{\Delta t} = A y_T \frac{\Delta y_T}{\Delta t} + B \frac{\Delta y_T}{\Delta t} \quad (15)$$

Equation (15) shows that the respiration rate is composed of two terms; one is proportional to the product of the biomass and its growth rate, and the other is proportional to the growth rate.

It is noteworthy that Eq. (15) might be satisfied independent of the climate under which the forest stands grow. The data may suggest that $\Delta y_T/\Delta R_T$ is related to y_T by two power-form functions.

A reasonable alternative for Eq. (15) is

$$\frac{\Delta R_T}{\Delta t} = A' y_T + B' \frac{\Delta y_T}{\Delta t} \quad (16)$$

which was proposed by THORNLEY (1976). The choice between Eq. (15) and Eq. (16) should be made through future studies with more elaborate means for determining the respiration rate of standing trees.

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