COMMUNITY RESPIRATION IN A LOWLAND RAIN FOREST IN PASOH, PENINSULAR MALAYSIA[1]

Kyoji YODA, *Department of Biology, Faculty of Science, Osaka City University, Osaka 558*

半島部マレーシア・パソーにある低地多雨林の群落呼吸

大阪市立大学理学部生物学教室　依　田　恭　二

Synopsis

YODA, Kyoji (Dep. Biol., Fac. Sci., Osaka City Univ., Osaka) 1983. Community respiration in a lowland rain forest in Pasoh, Peninsular Malaysia. Jap. J. Ecol., 33: 183–197.

The total community respiration rate was estimated in undisturbed stands in the Pasoh Forest Reserve, Negeri Sembilan, Malaysia. Dark respiration rates were determined with a large number of detached samples of leaves and woody parts taken from plants of various sizes ranging from a 55m-tall emergent tree to undergrowth herbs. Respiration rates in leaves tended to decrease toward the lower layers of the forest canopy, the mean leaf respiration rate per tree thus increasing with increasing tree size. Respiration rates of woody parts depended on both their diameter and the size of the tree they were taken from. Inter-species differences were relatively small in both cases. A procedure for assessing the total respiration of a tree solely from its DBH was formulated taking all these factors into consideration. Combining the formulation with a DBH census, the rate of total respiratory consumption of dry matter by the whole community was estimated at 75.2 t $ha^{-1}y^{-1}$, of which 94% was accounted for by trees (DBH≥4.5 cm). Leaf, branch, trunk, and root parts contributed, respectively, 50%, 21%, 15%, and 15% to the total tree respiration.

Indtroduction

This study's purpose was to estimate the total respiration in a lowland rain forest community in Peninsular Malaysia as part of the integrated ecosystem research project carried out by the Joint Malaysia/Japan/UK Team within the framework of the International Biological Program (IBP). Respiration rates were determined from detached samples of leaf and woody parts and integrated into the estimates of single tree and total community respiration by the aid of empirical mathematical equations.

Attempts at estimating the total respiratory consumption of assimilated organic matter by a forest community have been limited in number. Various methods were employed to overcome the difficulty of directly measuring gas exchange with intact trees of enormous size. When respiration of a single tree is estimated from the observed respiration rates of detached wood samples, a serious difficulty arose from the dependence of the rates on the size of the woody parts. Boysen Jensen (1932) and others (MÖLLER et al., 1954; MÜLLER & NIELSEN, 1965; etc.) summed up respiration rates of detached samples, taking into account the distribution of biomass in different size classes of woody parts that constitute a tree. This procedure was letter elaborated by YODA (YODA et al., 1965; YODA, 1967; KIRA, 1968; YODA, 1978), who formulated the steps necessary for summation in terms of a series of quantitative equations.

Various factors other than diameter are, however, responsible for the wide variability of respiration rates in woody parts (NEGISI, 1977). The effect of severing is important in determining respiration of detached wood samples (ZELAWSKI, 1960; OOHATA et al., 1967; NEGISI, 1974, 1977) and should be given proper attention. The position of branches in a tree crown also affects their respiratory activity.

Leaf respiration is also affected by the position of leaves in a tree. The rate of leaf respiration

---

Table 1. List of sample plants and their dimensions.

Sample No.	Species etc.	DBH [cm]	Height [m]	Respiration measured in			
				Leaf	Stem	Branch	Root
T11	*Koompassia malaccensis*	100.0	55	×			
T10	*Shorea globifera*	32.4	30	×	×	×	
T9	*Mangifera foetida*	23.2	24	×	×	×	
T8	*Calophyllum* sp.	21.6	22	×	×	×	
T7	*Saurauja tristyla*	15.6	18	×	×	×	
T6	*Lansium domesticum*	13.1	15	×	×	×	
T5	*Coelostegia griffithii*	12.3	14	×	×	×	
T4	*Hopea* sp.	4.2	8	×	×	×	×
T3	*Ochanostachys amentacea*	3.5	7	×	×	×	×
T2	*Shorea pauciflora*	3.1	7	×	×	×	×
T1	*Shorea macroptera*	3.2	5	×	×	×	×
MT1	Mixed small trees	ca. 2	2–4	×	×	×	×
MT2	Mixed tree saplings	ca. 1	0.5–2	×	×	×	×
P1	*Licuala* sp. (palm)	—	0.5–2	×			
MT3	Mixed tree seedlings	—	<0.5	×	×	×	×
H1	Mixed herbs and ferns	—	<0.5	×			
P2	*Zalacca* sp. (palm)	—	<0.5	×			
MP1	Mixed small palms	—	<0.5	×			

based on the leaf area is often several times larger for sun leaves on the crown surface than shade leaves growing in deep shade near the forest floor (HOZUMI et al., 1972, 1973; NISHIOKA et al., 1978). HOZUMI (KIRA et al., 1968; HOZUMI et al., 1972, 1973) proposed a mathematical model for estimating the total respiration by a forest canopy taking into account the vertical gradient of leaf respiration rate along a forest profile.

Besides micrometeorological methods (AOKI et al., 1975; KIRA & YABUKI, 1978) which are quite promising provided that a good observation tower and adequate instruments are available, combining of HOZUMI's and YODA's methods is probably the most reasonable for the assessment of community respiration by forest, if the avobe-mentioned factors are properly taken into consideration in the field measurements.

Study Site

The study site for the IBP rain forest research project as about 650 ha wide and situated in the central part of the Pasoh Forest Reserve, Negeri Sembilan, Peninsular Malaysia, at about 5°29'N and 102°18'E. An undisturbed lowland rain forest, *Shorea-Dipterocarpus* type, covered low undulating hills between 75 m and 150 m avobe the mean sea level. Although the annual amount of

rainfall is relatively small (about 2,000 mm y^{-1}), it is distributed evenly throughout the year and is enough to support dense forests with typical rain forest physiognomy. Trees of the topmost layer reach a height level of 50 m–55 m. The aboveground biomass of tree was estimated at about 470 t ha^{-1} in dry weight (KATO et al., 1978). General descriptions of the forest have been given by SOEPADMO (1973), SOEPADMO & KIRA (1977), YODA (1974), and KIRA (1976).

Respiration measurements were made near the southeastern end of the IBP Research Area from 18 to 31 July 1971. The site was close to Plot 1, one of the five permanent plots (each 100 m × 200 m) for the IBP studies, where most primary production studies by the Japanese staff were carried out.

Material and Methods

Eleven sample trees of 11 species were chosen to represent the most common species from different layers of the forest. The biggest was an emergent tree, *Koompassia malaccensis* (T11 in Table 1), in Plot 1, from which leaf samples were collected at 2 m hight intervals from the top to the base of its crown. The other 10 trees (T1–T10) were felled from a small plot adjacent to the preliminary destructive samplng plot (KATO et al., 1978) clear-fel-

led in the spring of 1971. Leaf, branch, trunk, and root samples were taken from the felled trees for respiration measurements. Undergrowth samples consisted of 14 species in the 2 m–4 m height class (MT1), 18 species in the 0.5 m–2 m class (MT2), seedlings of trees and lianas less than 0.5 m in height (MT3), *Licuala* sp. (palm) 0.5 m–2 m in height (Pl), *Zalacca* sp. (palm) less than 0.5 m high (P2), herbaceous plants less than 0.5 m high (Hl), and small palms also less than 0.5 m high (MP1).

The following dimensions were measured immediately after felling the trees; stem diameter at breast height (130 cm above the ground) or DBH (hearafter represented by the symbol D), stem diameter at ground level (D_0), stem diameter at 30 cm above the ground (D_{30}), stem diameter at a height equal to 1/10 of tree height ($D_{0.1}$), above-ground height of the tree (H), and the height of the lowest live branch (H_B). Fresh weight of leaves, branches, and main stem were measured using the stratified clip technique; whole shoots were separated into horizontal layers of 2 m deep, 0 m–0.3 m, 0.3 m–1.3 m, 1.3 m–3.3 m, 3.3 m–5.3 m, etc., and each layer was weighed. Leaves from a layer were then thoroughly mixed to take a small sample irrespective of leaf age. Roots of trees and herbs less than 10 m high were dug out and weighed.

Respiration measurements were started within 30 minutes of felling, since severing is known to effect respiration three hours after cutting (OOHATA et al., 1976). When a tree was too big to permit simultaneous measurements of all parts, branches in each layer were first cut and treated, followed by trunk and roots in turn.

Seventy-four plastic containers of four different sizes (7, 22, 88, and 120 litres) were prepared to enclose samples of various sizes with KOH solution kept in petri dishes. Different concentrations (0.05–2 N) and amounts (10–100 ml) of KOH solution were used according to the expected rates of CO_2 evolution from the samples following KIRITA & HOZUMI's (1966) suggestion. The containers were placed on the forest floor under dense forest canopy with a canvas cover for three hours. The maximum and minimum temperature for each series of measurements were recorded. The mean temperature inside the containers ranged between 23.5°C and 28.8°C with an overall average of 26.5°C.

The cut surfaces of fresh samples of woody parts were sealed with vaseline paste and put in containers of appropriate sizes. A wood sample consisted of one or many pieces of stem, branch, or root of the same diameter class and of an appropriate length. To measure respiration of leaves, six samples of 5, 10, 20, 40, 80, and 160 g in fresh weight taken from each hight layer were put in small plastic mesh bags and enclosed in 7-litre containers. Care was taken to leave sufficient space around the sample bag to insure free air movement in the container.

Since leaf respiration rate is known to be closely correlated with the levels of light intensity an intensive observation of the vertical distribution of light flux density was carried out in Plot 1 (YODA, 1974). In addition, the frequency distribution of the diameter of branches and trunk was determined for T10 (*Shorea globifera*) by measuring the diameter at 10 cm intervals along every tree shoot from the trunk base to the ends of all twigs to confirm its fitness to the pipe model theory (SHINOZAKI et al., 1964; YODA, 1967).

Results and Discussions

Foliage respiration
Estimation of real respiration rate

The rate of CO_2 evolution per unit weight of leaf sample obtained from a set of simultaneous measurements differed widely depending on the amount of leaves enclosed in a container. As the sample size increased, the rate decreased as shown in Fig. 1. The relative variation of CO_2 evolution rate tended to decrease with increasing sample size. Similar results were also reported for an evergreen seasonal forest of southern Thailand (YODA, 1967) and Japanese temperate forests (YODA & SATO, 1967; YODA, 1978).

In those studies, the dependence of observed CO_2 evolution rate (r_L') on sample size (W_L) was given in the hyperbolic equation.

$$1/r_L' = A_1 W_L + B_1 \qquad (1)$$

which fitted the observed data well (Fig. 1). A_1 and B_1 are coefficients determined by tree species, leaf position in the canopy, temperature, and other environmental factors. Since the decline of r_L' with increasing sample size was most probably due to insufficient aeration in a sample bag, the expected maximum rate at $W_L \to 0$, which equaled
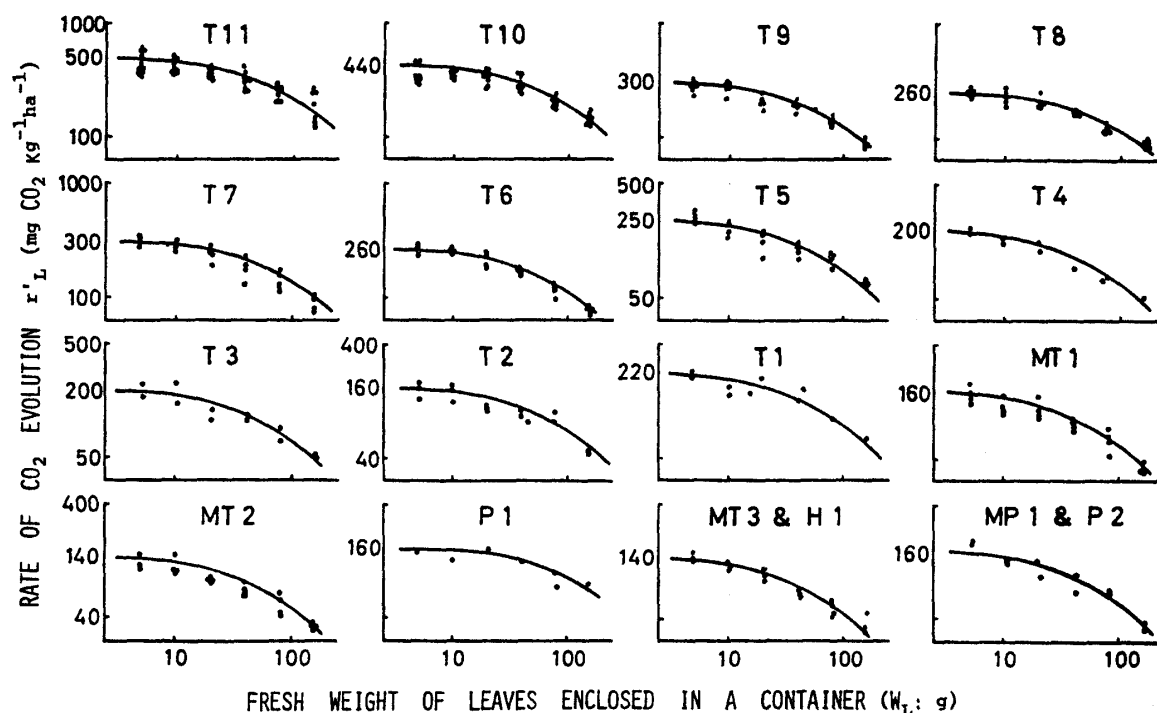
Fig. 1. Effect of sample size (fresh weight of a leaf sample enclosed in a container) on observed rates of CO_2 evolution from the samples (r_L': fresh weight).

$r_L = 1/B_1$, was assumed to be the real rate of leaf respiration in natural habitats, where the leaf density was normally small enough to insure a sufficient air supply. The real respiration rate was thus estimated for all leaf samples taken from different height levels of respective sample plants.

Factors affecting leaf respiration rate

Leaf samples taken from different height levels showed different respiration rates even when they were from the same sample tree. When respiration rate was plotted against the median height of the layer from which the leaf sample was collected, two relatively linear regressions were obtained, corresponding, respectively, to a tall emergent tree (T11) and the other samller trees (Fig. 2.) The result was somewhat different from temperate forests where the regression tended to be exponential (e.g. YODA, 1978). The linear correlation of Fig. 2 was the most apparent when the respiration rate was expressed as the fresh weight of leaves.

The mean specific leaf area (SLA) per layer increased remarkably with decreasing height as it did in temperate forests (NISHIOKA et al., 1978). Respiration rate as leaf weight (r_L) and leaf area (r_U) were found to decrease as SLA increased. The trend was more evident in r_U than in r_L, and in
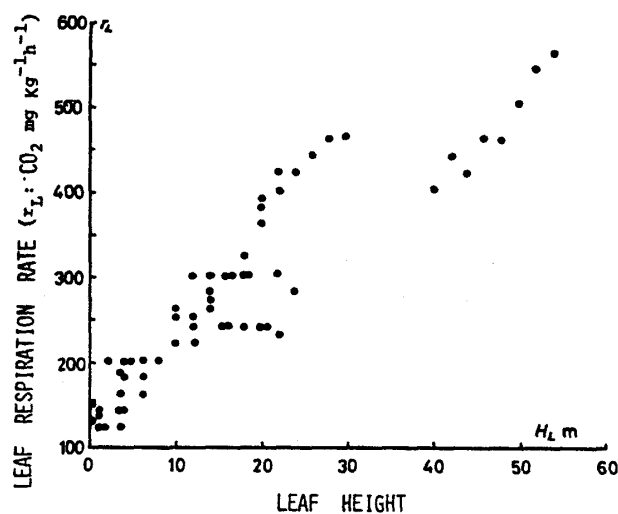

Fig. 2. Relationship between the respiration rate of a leaf sample (r_L; fresh weight) and the aboveground height where the sample was collected (H_L). Eight points on the right end represent the samples taken from a 55-m-tall emergent tree (T11).

bigger trees (T11 and T10) than smaller trees (T9–T6) (Fig. 3).

The vertical distribution of relative illuminance along the big tree, *Koompassia malaccensis* (T11), observed by YODA (1974) is compared with the corresponding vertical gradient of leaf respiration

186

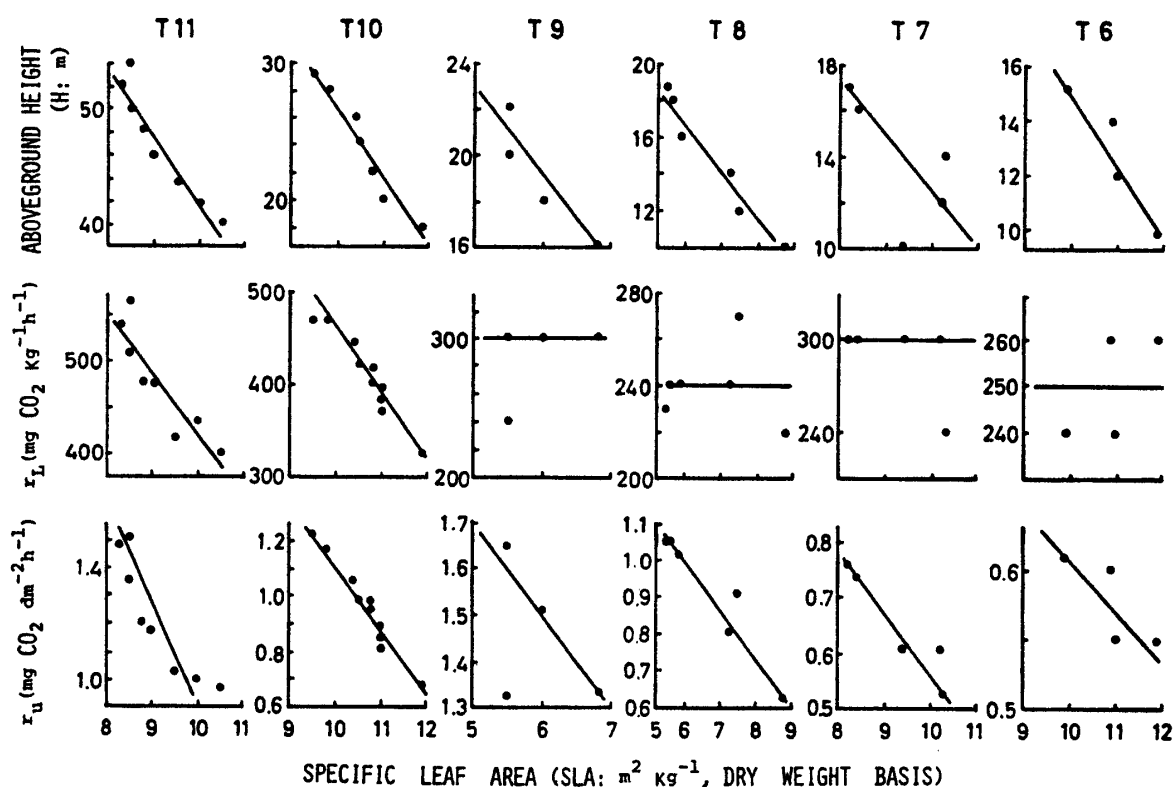SPECIFIC LEAF AREA (SLA: $m^2 \ kg^{-1}$, DRY WEIGHT BASIS)

Fig. 3. Correlations between specific leaf area (SLA) and leaf height [above], and between leaf respiration rate and SLA.

Respiration rates are expressed as fresh weight (r_L) [middle] and as leaf area (r_U) [bottom].

rate in Fig. 4, A & B to show the close resemblance between the two. The correlation between r_L (dry wight) or r_U at a given height level and the mean relative illuminance at the corresponding height was linear on logarithmic coordinates (Fig. 4C) and could be approximated by

$$r_L = A_2(I'/I_0)^b \qquad (2)$$

in which I_0 and I' stand for the illuminance values simultaneously observed over the tree top and at a height level in the canopy. A_2 and b are empirically derermined coefficients.

The same relation was also reported for certain temperate forests by YODA (1971), while HOZUMI (KIRA et al., 1969; HOZUMI et al., 1972, 1973) NISHIOKA et al. (1978) and YODA (1978) adopted a hyperbolic approximation,

$$\frac{1}{r_L} = \frac{A_3}{I'/I_0} + B_3 \qquad (3)$$

instead of Eq. (2). However, Eq. (2) resulted in a closer fit than Eq. (3) for the data obtained for this paper.

Mean respiration rate per tree as affected by tree size

To facilitate the estimation of total canopy respiration, the mean leaf respiration rate per tree ($\bar{r}_L$) was calculated by

$$\bar{r}_L = (r_L L)/L ,$$

where r_L and L refer to leaf respiration rate and leaf weight in a given 2 m layer. All layers of a tree crown were summed. Table 2 shows the results for all sample trees and plants, together with the mean SLA (leaf area/leaf dry weight) and the mean dry weight/fresh weight ratio.

Mean leaf respiration rate per tree as leaf weight tended to become smaller with decreasing tree size. As dry weight, it ranged from 500 $mgCO_2kg^{-1}h^{-1}$ in the 55 m-tall *Koompassia* tree to 140 $mgCO_2kg^{-1}h^{-1}$ in herbaceous plants and mixed tree seedlings on the forest floor. Compared to leaf area, it was largest for a *Mangifera foetida* tree (T9) (1.65 $mgCO_2dm^{-2}h^{-1}$), followed by *Koompassia* (T11) (1.34 $mgCO_2dm^{-2}h^{-1}$), *Calophyllum* (T8) (1.10 $mgCO_2dm^{-2}h^{-1}$), *Shorea globifera* (T10) (1.06
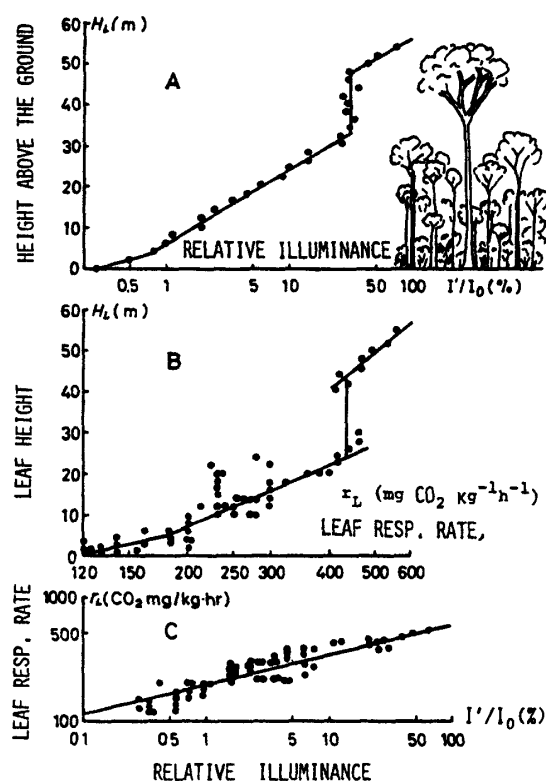
187

Fig. 4. Vertical gradient of mean relative illuminance (I'/I_0) in Stand 1 of the Pasoh forest [A] (YODA, 1974) and the dependence of leaf respiration rate, (r_L: fresh weight) on leaf height [B] and corresponding relative illuminance [C].

$mgCO_2dm^{-2}h^{-1}$), etc. These values fall within the same range as the respiration rates for sun leaves of tall trees observed by KOYAMA (1982) in Pasoh (1.2–2.2 $mgCO_2dm^{-2}h^{-1}$).

The regression of mean leaf respiration rate ($\bar{r}_L$) to DBH (D) was approximately linear on log-log coordinates (Fig. 5),

$$\bar{r}_L = A_4 D^a \tag{4}$$

$A_4 = 0.0460$ and $a = 0.196$ for $\bar{r}_L$ as dry weight [$mgCO_2kg^{-1}h^{-1}$], or

$A_4 = 0.140$ and $a = 0.267$ for $\bar{r}_L$ as fresh weight. D: [cm].

YODA et al. (1965) noticed the same relationship in a Japanese beech forest. As recognized in Fig.
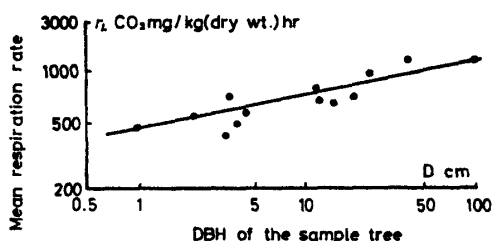

Fig. 5. Dependence of mean leaf respiration rate per tree (r_L: dry weight) on tree size indicated by DBH(D). The regression is approximately linear on log-log coordinates.

Table 2. Mean respiration rate of leaves per tree.

| Sample No. | Mean leaf respiration rate [r_L] | | | Mean specific leaf area [m^2 kg(D.W.)$^{-1}$] | Mean dry wt./fresh wt. ratio [kg kg^{-1}] |
	Fresh weight basis [mg CO_2kg^{-1}h^{-1}]	Dry weight basis [mg CO_2kg^{-1}h^{-1}]	Leaf area basis [mg CO_2dm^{-2}h^{-1}]		
T11	500	1136	1.34	8.5	0.44
T10	440	1100	1.06	10.4	0.40
T9	300	909	1.65	5.5	0.33
T8	260	650	1.10	5.9	0.40
T7	300	625	0.74	8.4	0.48
T6	260	650	0.60	10.9	0.40
T5	250	781	0.72	10.8	0.32
T4	200	540	0.51	10.5	0.37
T3	200	476	0.34	14.2	0.42
T2	160	364	0.30	12.0	0.44
T1	220	688	0.69	10.0	0.32
MT1	160	533	0.37	14.5	0.30
MT2	140	467	0.32	14.5	0.30
P1	160	390	0.45	8.6	0.41
MT3	140	467	0.32	14.5	0.30
H1	140	636	0.35	18.0	0.22
P2	160	444	0.27	16.6	0.36
MP1	160	444	0.27	16.6	0.36

5, the effect of tree size on the mean leaf respiration rate is apparently stronger than interspecific differences. Thus even if there are any interspecific differences, they may be neglected.

Respiration in woody parts
Respiration rates of detached samples in relation to the diameter of the samples

Observed respiration rates in wood samples depended largely on their diameter, using the hyperbolic approximation proposed by YODA (YODA et al., 1965; YODA, 1967, 1978). For branches, the respiration rate (r_B)-diameter (x_B) relation followed the equation,

$$1/r_B = A_5 x_B + B_5 . \tag{5}$$

However, the observed values of r_B varied widely over the range of x_B (Fig. 6) mainly because r_B of a given diameter tended to increase as the increased height from which branch samples were collected.

The respiration rates of stems (r_S) and roots (r_R), on the other hand, more closely fitted the following empirical equations than YODA's original equation (Fig. 7).

$$1/r_S = A_6 x_S^2 + B_6$$
$$1/r_R = A_6 x_R^2 + B_6 \tag{6}$$

The coefficients A_6 and B_6 were not significantly different from the r_S to x_S and r_R to x_R relations. Although A_6 and B_6 depended on the tree species, size, temperature and other conditions as did A_5 and B_5.

Dependence of wood respiration rate on tree size

The curves in Figs. 6 and 7 are the IIIrd type of socalled C-D curve (SHINOZAKI & KIRA, 1961). An attribute of the C-D curve is that it maintains a fixed shape on logarithmic coordinates irrespective of the values of A & B. It has a specific point called the B-point where $x = B/A$ and $r = 1/(2B)$. The B-points of the curves given by Eqs. (5) and (6) were found to have the same abscissa at $x_B = 0.5$ cm for branches (Fig. 6) and at $(x_S)^2 = (20 \text{ cm})^2$ for stems and roots (Fig. 7), except in small trees and undergrowth plants. Therefore, the different curves for different sample tree result only from differences in the value of B or the maximum respiration rate at $x \to 0$ given by $r_{max} = 1/B$.

The dependence of r_{max} on a sample tree's size or DBH proved to be approximately linear on log-log coordinates as shown in Fig. 8. Thus the respiration rate in a wood sample of a given diameter is largely determined by its diameter and
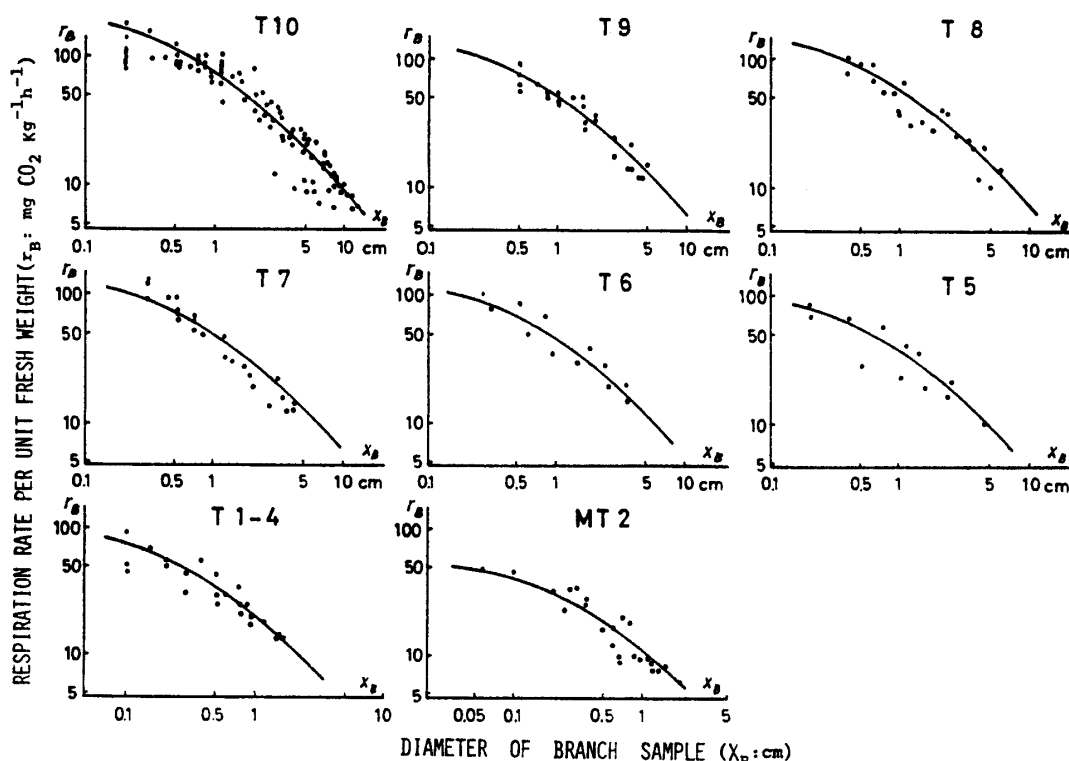

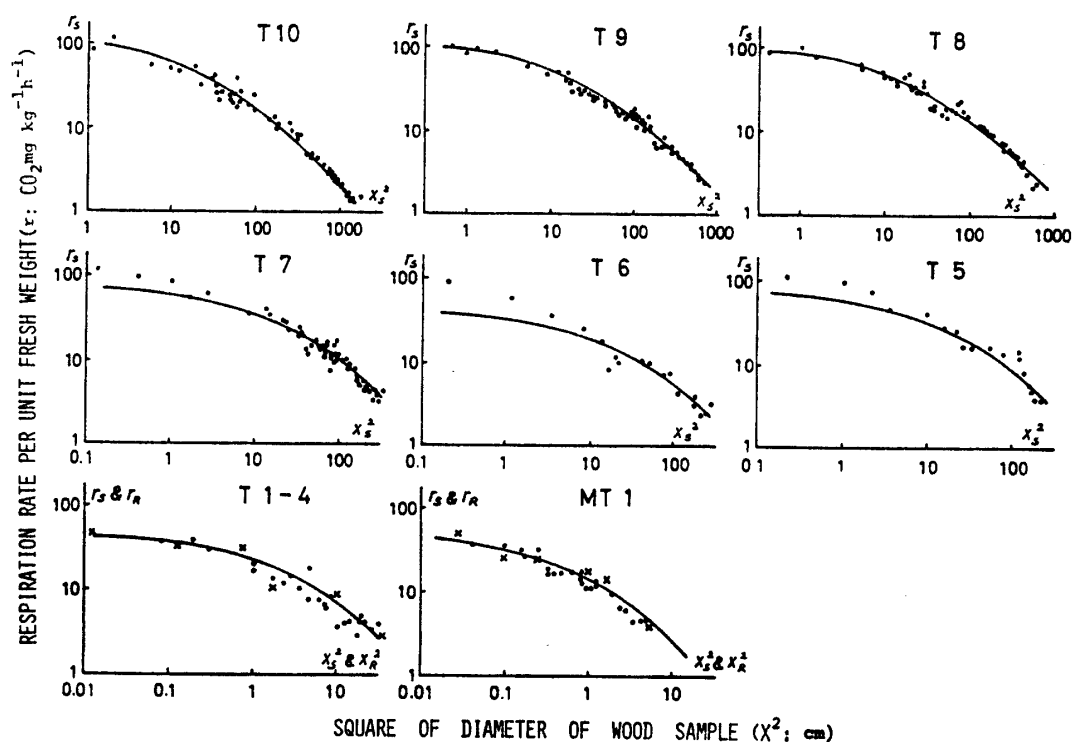Fig. 6. Respiration rates in branches $(r_B$: fresh weight) as affected by their diameter (x_B).

Fig. 7. Respiration rates in trunks (r_S) and roots (r_R) as fresh weight as affected by their diameter (x_S and x_R).
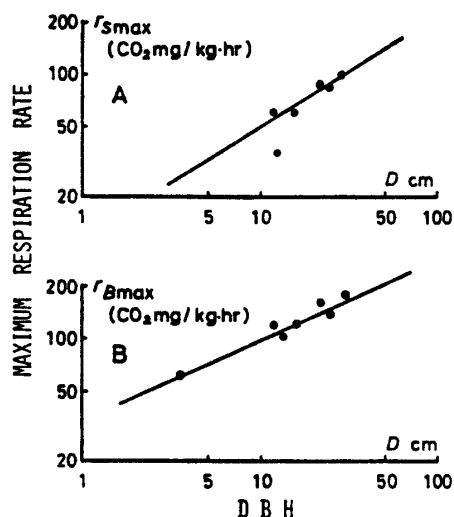

Fig. 8. Dependence of the maximum respiration rate (the rate at a very small diameter) for the trunk (r_{Smax}) and branch (r_{Bmax}) on the DBH of the tree from which samples were taken.

the size of the tree it was taken from, while interspecific differences were relatively small.

Total respiration of an individual tree

From the results described above, the total respiration of a tree of any size can be estimated by

the following procedure, if interspecific differences are disregarded as being negligibly small.

Foliage respiration

The rate of total leaf respiration per tree (R_L) was calculated as the product of the mean respiration rate ($\bar{r}_L$, dry weight) and the dry weight of leaves per tree (w_L).

$$R_L = \bar{r}_L \times w_L \tag{7}$$

The value of $\bar{r}_L$ was obtained from the DBH in Eq. (4),

$$\bar{r}_L = 460\ D^{0.196}, \tag{4}'$$
$$[mgCO_2kg^{-1}h^{-1}],\ [cm]$$

while w_L was calculated using the allometric regressions worked out by KATO et al. (1978) as follows.

$$1/H = 1/(2.0\ D) + 1/61 \tag{8}$$
$$[m],\ [cm]$$

$$w_S = 0.313\ (D^2H)^{0.973} \tag{9}$$
w_S: dry weight of stem per tree
$$[kg],\ [cm],\ [m]$$

$$1/w_L = 1/(0.124\ w_S)^{0.794} + 1/125 \tag{10}$$
$$[kg],\ [kg]$$

190

Respiration in woody parts

Provided that the respiration rates (r) of stem, branch, and root in a tree are determined solely by their diameters (x), the rate of total wood respiration per tree (R) can be calculated by the procedure formulated by Yoda (Yoda et al., 1965; Yoda, 1967, 1978), which is based on the fact that the frequency distribution of the diameters of the woody parts of a tree can be approximated by

$$f_x = K x^{-\alpha} \qquad (11)$$

Where f_x refers to the frequency of a given diameter (x) and K and α are coefficients specific to respective parts (Shinozaki et al., 1964). Denoting the weight of a part with a diameter of x by $W(x)$, the rate of total respiration of the part per tree is given by

$$R = \int_{x_{min}}^{x_{max}} r(x)\, dW(x)$$

$$= \frac{W(3-\alpha)}{x_{max}^{3-\alpha} - x_{min}^{3-\alpha}} \int_{x_{min}}^{x_{max}} \frac{x^{2-\alpha}}{Ax+B}\, dx \qquad (12)$$

in which x_{max} and x_{min} are, respectively, the maximum and the minimum diameter of the part.

Branch respiration

The coefficient α for branches is almost always equal to 2 in broadleaf as well as coniferous trees (Shinozaki et al., 1964; Yoda, 1967, 1978). The frequency distribution of branch diameter in T10 (*Shorea globifera*) in Pasoh also agreed with this general rule (Fig. 9, B).

Assuming $\alpha = 2$ in Eq. (12) and combining it with Eq. (5),

$$R_B = \frac{W_B}{x_{Bmax} - x_{Bmin}}$$

$$\left[\frac{1}{A_5} \ln(A_5 x_B + B_5)\right]_{x_{Bmin}}^{x_{Bmax}} \qquad (13)$$

where R_B is the rate of total branch respiration per tree and W_B denotes the total branch weight. The maximum and the minimum diameter were empirically determined as follows. B_5 and A_5 were obtained as functions of DBH (D) from Fig. 8. W_B could be estimated from D and tree height (H) by the empirical equation derived from results of destructing samplings (Kato et al., 1978). The calculation was made using fresh weight.
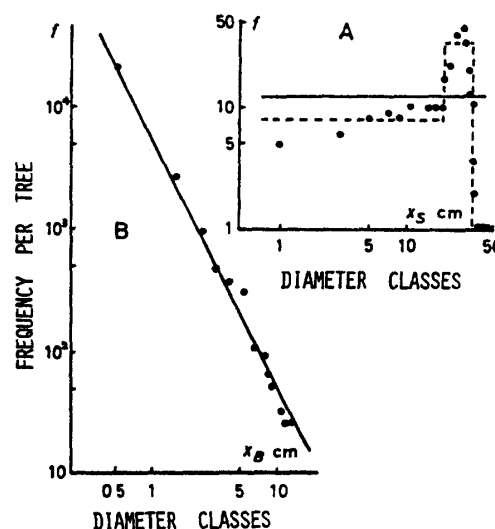

Fig. 9. Frequency distributions of trunk diameter (x_S: class interval 2 cm) and branch diameter (x_B: class interval 1 cm) for *Shorea globifera* (T10). A: trunk. B: branch.

$x_{Bmax} = 0.4\,D$ [cm], [cm]

$x_{Bmin} = 0.2$ [cm]

$B_5 = 1/(34\,D^{0.458})$

$A_5 = B_5/0.5$

$W_B = 0.0741\,(D^2 H)^{1.041}$ [kg], [dm^3]

Trunk respiration

The frequency distribution curve for stem diameter is normally approximated by three horizontal segments, each corresponding to a cone (Fig. 9, A). The right-side segment corresponds to a flat cone that represents the swollen basal part of trunk, the central one to the main bole, which is a slender cone in shape, and the left-side one to the topmost part of the trunk bearing branches, (Yoda, 1967). For the first approximation, however, the whole trunk may be assumed to be a single cone or a single horizontal line (continuous line on Fig. 9, A). We may then assume $\alpha = 0$ in Eq. (11). Then we have

$$R_S = \frac{3W_S}{x_{Smax} - x_{Smin}} \frac{1}{A_6}$$

$$\left[x_S - \frac{B_6}{\sqrt{A_6 B_6}} \arctan \frac{x_S \sqrt{A_6 B_6}}{B_6}\right]_{x_{Smin}}^{x_{Smax}} \qquad (14)$$

from Eqs. (6) and (12). R_S and W_S refer to the respiration rate and the total fresh weight of the trunk per tree. Values were empirically estimated from the following equations.

$x_{Smax} = 1.14\,D$ [cm], [cm] (Fig. 8)

$x_{Smin} = 0$

$B_6 = 1/(11.6\,D^{0.633})$ (Fig. 8)

$A_6 = B_6/20$ (Fig. 8)

$W_S = 0.547\,(D^2H)^{0.973}$ [kg], [dm^3]

(KATO et al., 1978).

Root respiration

The diameter of roots were not actually measured in Pasoh, but α for roots was tentatively assumed to be 2.0, following the general rule obtained by preceding studies. The rate of total root respiration per tree (R_R) is then obtained as follows.

$$R_R = \frac{W_R}{x_{Rmax} - x_{Rmin}}\,\frac{1}{\sqrt{A_6 B_6}}$$
$$\left[\arctan\frac{x_R\sqrt{A_6 B_6}}{B6}\right]_{x_{Rmin}}^{x_{Rmax}} \qquad (15)$$

Here it was assumed that Eq. (6) was valid for trees bigger than the sample tree used for the root respiration measurements.

The basis for the calculations folllow.

$x_{Rmax} = D$ [cm] [cm]

$x_{Rmin} = 0$

$W_R = 0.489\,(D^2H)^{0.775}$ [kg], [dm^3]

Since W_R-tree size regression was not obtained in Pasoh, the empirical allometric equation for an evergreen seasonal forest of southern Thailand. (OGAWA et al., 1965) was tentatively adopted. The relation of A_6 and B_6 for roots is similar to their relation for trunks.

Relative contribution of different parts to total tree respiration

From the procedure described above, the respiration rate of a tree could be estimated solely from its stem diameter at breast height (D). Calculated values of R_L, R_B, R_S, R_R, and their sum (R) for a range of diameters up to 100 cm are illustrated in Fig. 10. The contribution of respective parts to the total tree respiration is also shown. These curves represent the process associated with the growth of trees under natural conditions in the Pasoh forest, since the effect of tree size or the degree of shading to which trees were exposed was taken into consideration in estimating their respiration rate.

The contributions of trunk and root respiration decreased with the growth of tree. The trunk's contribution decreased more rapidly than the roots, 27% at $D = 5$ cm to 7% at $D = 100$ cm. The relative contribution of branches, on the other hand, increased remarkably from 6% at $D=5$ cm to 37% at $D = 100$ cm. The sum of respiration of all woody parts exceeded foliage respiration in small trees with DBHs less than 15 cm as well as in big trees with DBHs over 60 cm, while folliage respi-
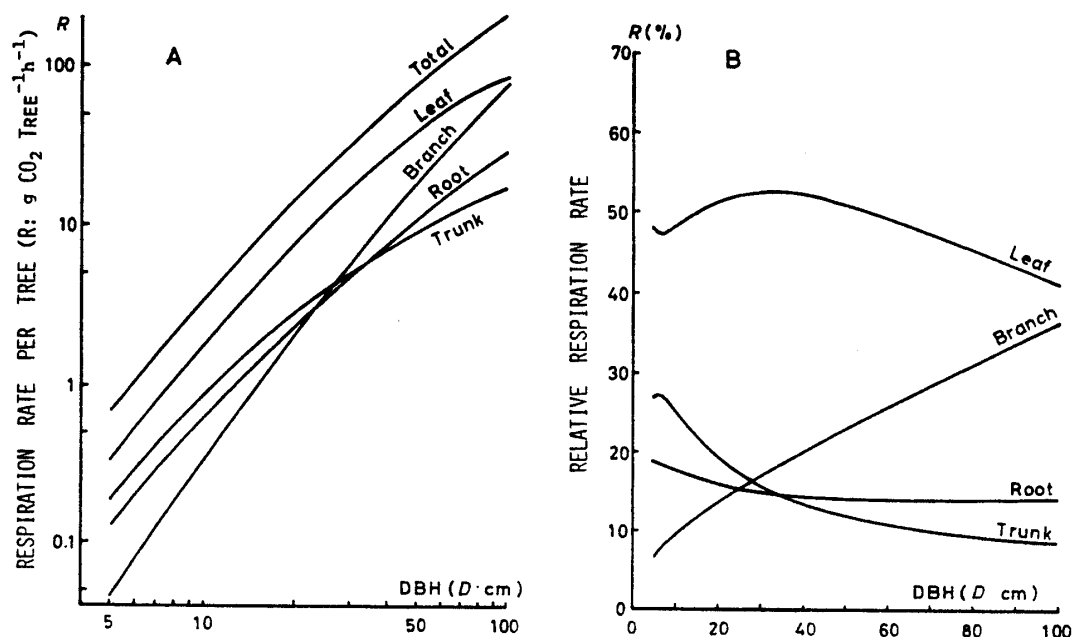

Fig. 10. Changes of tree respiration rate in its components. A: absolute changes per tree. B: relative contributions of different parts to the total tree respiration.

192

ration was greater than the woody parts respiration in medium-sized trees (15 cm $<D<$ 60 cm). This may account for the fast growth of medium-sized trees observed in Pasoh by KATO et al., (1978).

Generally, the curves in Fig. 10, A are similar to those previously reported for an evergreen seasonal forest in southern Thailand (YODA, 1967) and a warm-temperate evergreen oak forest in Kyushu, Japan (YODA, 1978). In absolute terms, however, the respiration rate per tree in the Pasoh forest at 25°C is much greater than for temperate evergreen oaks at the same temperature, if similar tree sizes are compared. This difference is mainly caused by the higher respiration rate and greater number of leaves in the rain forest trees.

When the Pasoh forest trees are compared with Thailand trees, the respiration rate of small trees tend to be less in the former than in the latter, whereas the relation is reversed for big trees. The following reasons may be reasonable for these differences; i) Pasoh forest trees tend to have greater leaf biomass per tree for larger ranges of DBH; ii) the decline of leaf and branch respiration rates in shaded small trees was not taken into consideration in the Thailand study; iii) an equation similar to Eq. (5) was adopted to approximate the dependence of trunk respiration rate on DBH in the Thailand study, while the substitution of Eq. (5) with Eq. (6) in the present study is expected to result in a more rapid decrease in trunk respiration with increasing tree size. Considering the more elaborate procedure used in the present estimation, the results obtained here are more reliable than the results from the study in Thailand.

Total community respiration
Procedure of estimation

Hourly respiration rates at 25°C of leaves, branches, trunk, and roots were calculated for all live trees with DBHs larger than 9.5 cm in the five permanent plots (Plots 1, 3, 4, 6 and 7; each 2 ha wide) by the procedure stated above, based on the tree census made by the UK team (Ashton, 1971). For smaller trees with DBHs between 4.5 cm and 9.5 cm, similar calculations were made only for Plot 1, where DBH data for trees of this size classs was available (OGAWA, unpublished data).

For tree saplings ($D<$ 4.5 cm and $H>$ 1.3 m), the respiration rates of leaves and woody parts were determined separately, and the mean rates at 25°C were estimated by taking the frequency distribution of diameter of woody parts into consideration; 16.6 $mgCO_2kg^{-1}$ (dry weight) h^{-1} for stems, 35.3 $mgCO_2kg^{-1}h^{-1}$ for branches, 26.8 $mgCO_2 kg^{-1}h^{-1}$ for roots, and 517 $mgCO_2kg^{-1}h^{-1}$ for leaves. The stand respiration rate was obtained by multiplying the rates by the biomas of the respective parts (unpublished data by OGAWA). The mean respiration rates of undergrowth plants ($H<$ 1.3 m) calculated by the same procedure were 25 mg CO_2kg^{-1} (dry weight) h^{-1} for stems, 53 $mgCO_2 kg^{-1}h^{-1}$ for branches, 40 $mgCO_2kg^{-1}h^{-1}$ for roots, and 400 $mgCO_2kg^{-1}h^{-1}$ for leaves.

The hourly rates of respiration at 25°C were converted into annual rates by simply multiplying by 8,760 hours, disregarding daily and seasonal changes of temperature. The equivalent rates of organic matter consumption were calculated using a CO_2/dry matter conversion factor of 0.614.

Stand respiration rates

Table 3. Community respiration rates in tree components (DBH$\geq$4.5cm) of Pasoh forest stands.

| | | Rate of organic matter consumption[t ha^{-1}y^{-1}] | | | | |
		Leaf	Trunk	Branch	Root	Total
Big trees ($D\geq$9.5cm)	Plot 1	33.4	9.8	14.3	10.0	67.5
	Plot 3	34.1	10.2	14.5	10.3	69.1
	Plot 4	30.8	9.3	13.2	9.3	62.6
	Plot 6	29.5	9.0	11.5	8.8	58.8
	Plot 7	32.2	9.8	13.6	9.7	65.3
	Mean	32.0	9.6	13.4	9.6	64.6
	S. D.	1.9	0.5	1.2	0.6	4.1
Small trees (4.5$\leq D\leq$9.5 cm)	Plot 1	2.8	1.6	0.4	1.1	5.9
Tree componets total ($D\geq$4.5 cm)		34.8	11.2	13.8	10.7	70.5

Table 3 shows the estimated rates of annual organic matter consumption by tree components (DBH$\geq$9.5 cm) in the five plots. Inter-stand differences in tree respiration rates were relatively small, reflecting similar DBH distributions in all the plots. The total respiration by trees with DBHs equal to or greater than 9.5 cm was estimated at 64.6 t ha^{-1}y^{-1}, of which 50% was accounted for by the leaf canopy, 21% by the branches and 15% each by the trunks and roots.

Total respiration by small trees (4.5 cm $\leq D<$ 9.5 cm) in Plot 1 was 5.9 t ha^{-1}y^{-1} or 9% of the respiration by bigger trees in the same plot. If the biomass and size distribution of small trees were the same in the other plots, the total respiration by all trees ($D>$4.5 cm) in Pasoh Forest may amount to an average of 70.5 t ha^{-1}y^{-1}.

The respiratory consumption by saplings and undergrowth were estimated, respectively, at 3.5 t ha^{-1}y^{-1} and 1.2 t ha^{-1}y^{-1}, leading to an estimate of overall community respiration rate of 75.2 t ha^{-1}y^{-1}. Big trees ($D\geq$9.5 cm), small trees (9.5 cm $> D \geq$ 4.5 cm), tree saplings ($H \geq$ 1.3 m, D < 4.5 cm), and undergrowth (H < 1.3 m) contributed 86%, 8%, 5%, and 2%, respectively, to the total community respiration. As far as big trees ($D \geq$ 9.5 cm) were concerned, about 50% of
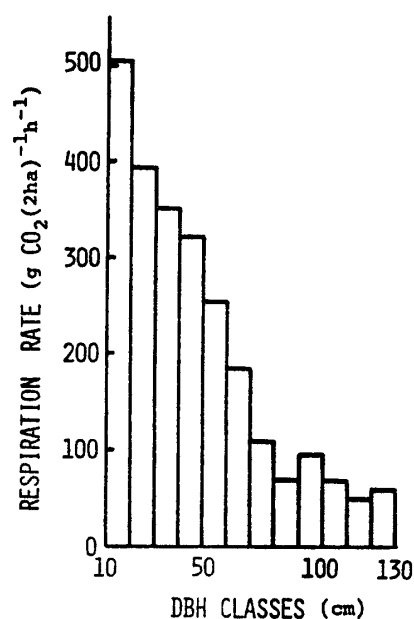

Fig. 11. Distribution of respiration of tree size classes in Plot 1.

the total tree respiration were accounted for by trees with DBHs smaller than 40 cm (Fig. 11). The share of the main canopy trees (60 cm $\leq D<$ 130 cm) was only 25%, while they were most probably responsible for more than two-thirds of the total canopy photosynthesis (Hozumi et al., 1969).

Table 4. Comparison of the estimates of community respiration rates in some tropical and temperate forests.

		Respiratory consumption [t ha^{-1}y^{-1}]					
		Leaf	Trunk	Branch	Root	Total	
Lowland	Trees[1]	34.8	11.2	13.8	10.7	70.5	
rain forest	Saplings[2]	2.3	0.6	0.2	0.4	3.5	This study
Pasoh,	Undergrowth[3]	1.0	0.1	0.0	0.1	1.2	
Malaysia	Total	38.1	11.9	14.0	11.2	75.2	
Evergreen	Trees	51.8	11.8	20.7	4.9	89.2	
seasonal forest	Saplings	2.7	0.8		0.3	3.8	Yoda, 1967
Khao Chong,	Undergrowth	5.7	11.2		8.6	25.5	
Thailand (Stand 4)	Total	60.2	44.5		13.8	118.5	
	Trees	57.4	13.1	19.0	5.6	95.1	
Ditto	Saplings	2.7	0.8		0.3	3.8	Yoda, 1967
(Stand 5)	Undergrowth	3.2	6.1		4.3	13.6	
	Total	63.3	39.0		10.2	122.5	
Warm-temperate	Trees	—	7.6	4.1	4.5	—	
evergreen oak	Saplings	—	0.1	0.9	0.3	—	Yoda, 1978
forest Minamata,	Undergrowth	—	0.1		0.0	—	
Japan	Total	19.2	12.8		4.8	36.8	

1) DBH(D)$\geq$4.5 cm. 2) Height(H)$\geq$1.3 m ,D<4.5cm. 3) H<1.3 m.

The respiration by small shaded trees thus plays a very important role in the organic matter budget of the rain forest community.

Comparison with other forest types (Table 4)

There are two estimates of community respiration by moist tropical forests available for comparison; 39 t ha^{-1}y^{-1} in a seasonal forest in Anguédédou, Côte d'Ivoire (MÜLLER & NIELSEN, 1965) and 89–95 t ha^{-1}y^{-1} in an evergreen seasonal forest in Khao Chong, southern Thailand (YODA, 1967). The aboveground biomass was about 240 t ha^{-1} in Anguédédou, about 330 t ha^{-1} in Khao Chong, and about 430 t ha^{-1} in Pasoh. Considering the differences in biomass among the forests, the community respiration in Khao Chong seems to have been over estimated, possibly due to the following reasons. i) Lower respiration rates of the leaves and woody parts in the lower strata of the forest were not taken into consideration in the estimation for the Khao Chong forest. ii) An overstimation of trunk respiration might be possible as discussed in the preceding section. iii) Sample trees were cut in the morning while respiration measurements were started in the following afternoon in Khao Chong, so that the respiration of wood samples was probably accelerated owing to the effect of severing.

The relative contribution of leaves to the total community respiration was 51 % in the Pasoh forest, 60% in Khao Chong, 43% in Anguededou, 53% in a warm-temperate evergreen oak forest in Minamata, Japan (YODA, 1978), and 46–55% in plantations of *Fagus sylvatica* in Denmark (MÖLLER et al., 1954). A tentative generalization is drawn from these figures that leaves account for nearly a half of community respiration in closed forests irrespective of forest type and climatic zones.

Summary

1. The rate of community respiration was estimated in undisturbed lowland rain forest stands in the Pasoh Forest Reserve, Negeri Sembilan, Peninsular Malaysia, based on field work done in July 1971.

2. Dark respiration rates were determined from detached samples of leaves and woody parts taken from trees of various sizes as well as from undergrowth plants immediately after the sample plants were felled.

3. The rate of CO_2 evolution from leaves decreased as the increased size of the leaf sample enclosed in the respiration chamber. The real respiration rate was estimated from the CO_2 evolution rate-sample size curve.

4. Leaf respiration rates decreased in the lower levels of the forest canopy, with increasing specific leaf area, and with decreasing relative illuminance at the height where leaf samples were collected.

5. Mean leaf respiration rate per tree was positively correlated with the DBH of the tree, the regression being approximately linear on logarithmic coordinates.

6. Respiration rates of woody parts expressed as weight decreased as the diameter of the parts increased, following hyperbolic curves.

7. The maximum respiration rates for the trunk, branches, roots of a tree were positively correlated with its DBH. The regression was also log-log linear.

8. The frequency distribution of the diameter of woody parts of a tree was found to fit the pipe model proposed by SHINOZAKI et al. (1964).

9. A procedure was developed to calculate the respiration rates in the parts of a tree solely from its DBH, using the relations of 5–8 and the allometric regressions between the weight of the parts and DBH (KATO et al., 1978).

10. Combining the above procedure with the census of trees with DBHs bigger than 9.5 cm in the five 2 ha-plots, the mean respiration rate by

the tree components of the forest was calculated at 64.6 t ha^{-1}y^{-1} in terms of annual amount of dry matter consumed by respiration. Foliage, branches, trunks, and roots, respectively, accounted for 50%, 21%, 15%, and 15% of the total respiration.

11. Smaller trees with DBHs between 4.5 cm and 9.5 cm in one of the plots were estimated to consume 5.9 t ha^{-1}y^{-1} annually by respiration. The respiratory consumption by the lower undergrowth vegetation in the same plot was 4.7 t ha^{-1}y^{-1}.

12. Thus total community respiration was estimated to be about 75 t ha^{-1}y^{-1}, which was much greater than the estimation for an evergreen oak forest of warm-temperate Japan (about 36 t ha^{-1}y^{-1}) based on a similar method of calculation (YODA, 1978).

References

AOKI, M., YABUKI, K. & KOYAMA, H. 1975. Micrometeorology and assessment of primary production of a tropical rain forest in West Malaysia. J. Agr. Met. (Tokyo), 31: 115–124.

ASHTON, P. S. 1971. IBP Malayan Project: Pasoh Forest Reserve vegetation survey. (Mimeographed report)

BOYSEN JENSEN, P. 1932. Die Stoffproduktion der Pflanzen. Gustav Fischer, Jena.

HOZUMI, K., KIRITA, H. & NISHIOKA, M. 1972. Estimation of canopy photosynthesis and its seasonal change in a warm-temperate evergreen forest at Minamata (Japan). Photosynthetica, 6: 158–168.

————, NISHIOKA, M., NAGANO, M. & KIRITA, H. 1973. Estimation of the total photosynthetic production by forest canopies. Proc. East Asian Regional Seminar for IBP (ed. MORI, S. & KIRA, T.), 45–56. Japanese National Committee for IBP, Kyoto.

————, YODA, K. & KIRA, T. 1969. Production ecology of tropical rain forests in southeastern Cambodia. II. Photosynthetic production in an evergreen seasonal forest. Nature & Life in SE Asia (Tokyo), 6, 57–81.

KATO, R., TADAKI, Y. & OGAWA, H. 1978. Plant biomass and growth increment studies in Pasoh forest. Malay. Nat. J., 221–224.

KIRA, T. 1968. A rational method for estimating total respiration of trees and forest stands. "Functioning of terrestrial ecosystems at the primary production level; Proceedings of the Copenhagen Symposium, 1965" (ed. ECKARDT, F. E.), 399–407. UNESCO, Paris.

————. 1976. Pasoh Forest Reserve in Negeri Sembilan,

West Malaysia—Background information for IBP soil fauna study. Nature & Life in SE Asia (Tokyo), 7: 1–8.

————, SHINOZAKI, K. & HOZUMI, K. 1969. Structure of forest canopies as related to their primary productivity. Plant & Cell Physiol., 10: 129–142.

———— & YABUKI, K. 1978. Primary production rates in the Minamata forest. 'Biological production in a warm-temperate evergreen oak forest of Japan" (ed. KIRA, T., ONO, Y. & HOSOKAWA, T.), 131–138.

KIRITA, H. & HOZUMI, K. 1966. Re-examination of the absorption method of measuring soil respiration under field conditions. I. Effect of the amount of KOH on observed values. Physiol. & Ecol. (Osaka), 14: 23–31. In Japanese with English summary.

MÖLLER, C. M., MÜLLER, D. & NIELSEN, J. 1954. Respiration in stem and branches of beech. Forstl. Forsögsv. Danmark, 21: 273–301.

MÜLLER, D. & NIELSEN, J. 1965. Production brute, pertes par respiration et production nette dans la forêst ombrophile tropicale. Ibid., 29: 69–110.

NEGISI, K. 1974. Respiration rates in relation to diameter and age in stem or branch sections of young *Pinus densiflora* trees. Bull. Tokyo Univ. Forests, 66: 209–222.

————. 1977. Respiration in forest trees. "Primary productivity of Japanese forests; JIBP Synthesis Vol. 16" (ed. SHIDEI, T. & KIRA, T.), 86–93. Univ. of Tokyo Press, Tokyo.

NISHIOKA, M., HOZUMI, K., KIRITA, H. & NAGANO, M. 1978. Estimation of canopy photosynthesis and respiration. "Biological production in a warm-temperate evergreen oak forest of Japan; JIBP Synthesis Vol. 18" (ed. KIRA, T., ONO, Y. & HOSOKAWA, T.), 99–111. Univ. of Tokyo Press, Tokyo.

OGAWA, H., YODA, K., OGINO, K. & KIRA, T. 1965. Comparative ecological studies on three main types of forest vegetation in Thailand. II. Plant biomass. Nature & Life in SE Asia, 4: 49–80.

OOHATA, S., SHIDEI, T. & HATAKEYAMA, I. 1967. Changes in respiratory rates of excised tree organs. Bull. Kyoto Univ. Forests, 39: 100–109.

SHINOZAKI, K. & KIRA, T. 1961. The C-D rule, its theory and practical uses—Intraspecific competition among higher plants X. J. Biol. Osaka City Univ., 12: 69–82.

————, YODA, K., HOZUMI, K. & KIRA, T. 1964. A quantitative analysis of plant form—The pipe model theory. I & II. Jap. J. Ecol., 14: 97–105, 133–139.

SOEPADMO, E. 1973. Progress report (1970–1972) on IBP-PT Project at Pasoh, Negri Sembilan, Malaysia. Proc. East Asian Regional Seminar for IBP (ed. MORI, S. & KIRA, T.), 29–39. Japanese National Committee for IBP, Kyoto.

———— & KIRA, T. 1977. Contribution of the IBP-PT

Research Project to the understanding of Malaysian forest ecology. "A new era in Malaysian forestry" (ed. SASTRY, C. B., SRIVASTAVA, P. B. L. & MANAPAHMAD, ABDUL), 63–90. Universiti Pertanian Malaysia Press, Serdang (Selangor), Malaysia.

YODA, K. 1967. Comparative ecological studies on three main types of forest vegetation in Thailand. III. Community respiration. Nature & Life in SE Asia, 5: 83–148.

——— 1974. Three-dimensional distribution of light intensity in a tropical rain forest of West Malaysia. Jap. J. Ecol., 24: 247–254.

——— 1978. Estimation of community respiration. "Biological production in a warm-temperate evergreen oak forest of Japan; JIBP Synthesis Vol. 18" (ed. KIRA, T., ONO, Y. & HOSOKAWA, T.), 112–132. Univ. of Tokyo Press, Tokyo.

———, NAKAI, T. & SATO, H. 1968. Estimation of forest community respiration. "Studies on the methods for assessing primary production of forests; Progress report for 1967" (ed. KIRA, T.), 81–93. In Japanese, mimeographed.

——— & SATO, H. 1967. Re-examination of the methods for measuring respiration in forest trees. "Ibid.; Progress report for 1966" (ed. KIRA, T.), 53–60. In Japanese, mimeographed.

———, SHINOZAKI, K., OGAWA, H., HOZUMI, K. & KIRA, T. 1965. Estimation of the total amount of respiration in woody organs of trees and forest communities. J. Biol. Osaka City Univ., 16: 15–26.

ZELAWSKI, W. 1960. Changes in wood respiration during the first days after cutting. Bull. Acad. Polonaise Sci. Biol., 8: 507–513.

摘　　要

1．半島部マレーシアのネグリセンビラン州にあるパソー保護林の IBP 研究地域で，原生低地多雨林の群落呼吸速度を推定した．

2．1971年7月，巨大高木から林床植物にわたる種々の大きさの構成植物から多数の試料をとり，採取後ただちに密閉吸収法で暗呼吸を測定した．

3．葉の呼吸速度の測定値は，測定容器に入れた試料葉が多くなるほど低下したので，この関係を用いて真の呼吸速度を推定した．

4．葉の呼吸速度は，葉層の下部にゆくほど，受光量の減少と比葉面積の増大にともなって低下した．1本の木あたりの平均葉呼吸速度と，木の胸高直径 (DBH) との間には，両対数直線関係が成立した．

5．材器官の重量あたりの呼吸速度は，器官の直径が大きくなるほど双曲線的に低下した．直径がごく小さいときの枝・幹および根の最大呼吸速度は，その木の DBH と正相関をもち，やはり両対数直線関係で近似できた．

6．1本の木を構成する材器官の直径の度数分布は，既知のパイプモデル則 (Shinozaki et al., 1964) を満足した．

7．上記4～6の関係と，伐採調査よりえられた相対成長関係 (Kato et al., 1978) とを利用して，DBH のみから1本の木の各部分の呼吸量を推定する方法を開発した．

8．5か所の永久調査区 (各2 ha) の DBH 毎本調査結果から，DBH 9.5cm 以上の全樹木の呼吸速度を平均 64.6 t ha^{-1} y^{-1} (乾物消費量) と推定した．葉・枝・幹および根の寄与率は，それぞれ50%，21%，15%，15%であった．

9．1か所の調査区では，稚樹および林床植生の呼吸推定値として，5.9および 4.7 t ha^{-1} y^{-1} がえられた．

10．従って全群落の呼吸速度の推定値は，75 t ha^{-1}y^{-1} となった．この値は，日本の暖温帯照葉樹林の群落呼吸速度(36 t ha^{-1} y^{-1})(Yoda, 1978) よりはるかに大きい．