

PRIMARY PRODUCTION AND TURNOVER OF ORGANIC MATTER IN DIFFERENT FOREST ECOSYSTEMS OF THE WESTERN PACIFIC*

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This review is intended to introduce an outline of the results of community metabolism studies on various forest ecosystems of the Western Pacific area made by Japanese investigators in these past ten years.

In 1955, SATOO opened this line of research by publishing his first report (65) on the productivity of artificial plantations in this country. A few years later, in 1957 and 1958, four groups of ecologists and forest scientists including ourselves began almost simultaneously to follow him, and the fields of study were expanded to include various types of natural and artificial vegetation ranging from subarctic conifer forests of Hokkaidô to the tropical jungle of Southeast Asia. Since that time, more than one hundred stands belonging to some forty different forest types have been investigated, of course mostly within Japan Proper, but also in the Ryukyus (40), Thailand (21, 22, 24, 42, 44-47, 93, 100) and Cambodia (23).

Steady progress has been made in the methodology for analysing the metabolism of forest community. These studies were, therefore, not always based on one and the same method, making it difficult to compare the results obtained by different authors. Thus the contents of this review are more or less tentative; yet we hope, this may well be a useful starting point for more advanced studies to be made under the framework of the International Biological Programme.

*Contributions from JIBP-PT No. 1

This paper, excluding the last two sections, was read at the 11th Pacific Science Congress, Tokyo, on August 25, 1966 in the Symposium No. 26, 'Ecosystem metabolism and biological productivity in the Pacific land area'. This publication is partly supported by the special project research, 'Studies on the dynamic status of biosphere', sponsored by the Ministry of Education.

Estimation of biomass

Any kind of productivity study must start with the exact estimation of biomass, an especially troublesome task in the study of forest vegetation. Direct measurement or weighing of forest biomass of a reasonably wide area is quite unrealistic and impracticable. A noteworthy contribution by the Japanese was the elaboration of the technique of estimating tree biomass on the basis of the correlation between the amount of stem, branch, root, leaf, etc. of a tree and its stem diameter.

It is now widely accepted that the weight (w) of a tree stem, for instance, is given by a function of dbh as follows, or by a linear regression on the logarithmic coordinates (Fig. 1).

$$w = AD^h \quad (1)$$

D : dbh. A, h : constants.

This regression can cover a fairly wide range of stem diameter, and is easily obtainable

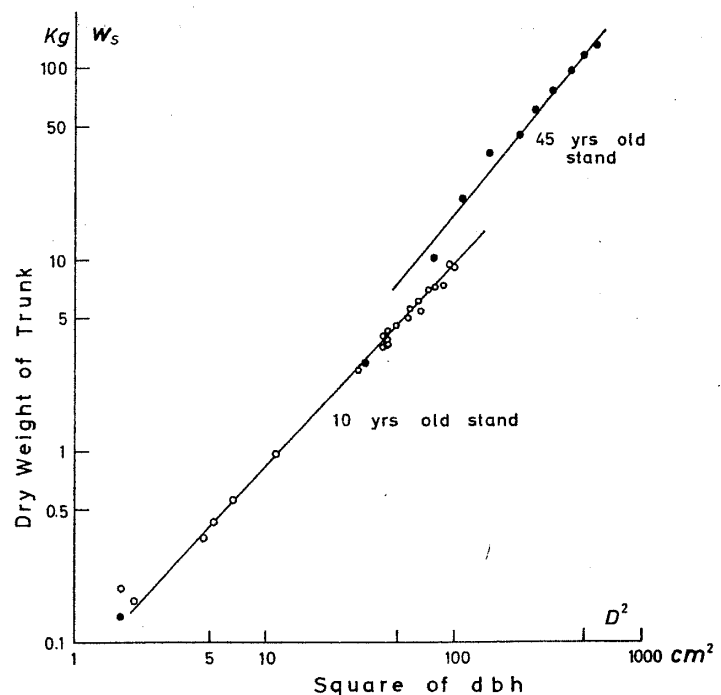


Fig. 1. Trunk weight—dbh allometry in *Cryptomeria japonica* plantations of Kikuti, central Kyûsyû (53)

Different regressions are obtained from stands of different ages.

by felling an appropriate number of sample trees of different sizes from the study area. Once it is established, the total biomass of stems on the area may easily be estimated by simply recording the dbh of all existing trees. This empirical formula is nothing but an example of

the law of allometry well known to biologists since the classical study of J. S. HUXLEY and G. TEISSIER, so that we often call this method as *the allometric method* (5, 11, 51). It is theoretically superior to the traditional method of stock estimation, in which the weight of an average-sized tree is multiplied by tree number (29, 51).

This basic principle of the allometric method needs certain modifications to assure a high degree of estimating accuracy and wide applicability. For instance, as seen in Fig. 1, the allometric correlation between trunk weight and dbh sometimes differs in different stands of the same species according to their age and habitat. This confusion can be avoided by simply introducing tree height (H) as the second parameter (51). The regression of trunk weight on D^2H is the same for both stands as shown in Fig. 2, and indeed it can be applied to almost all *Cryptomeria* plantations throughout Japan (53). In addition, the adoption of this two parameter

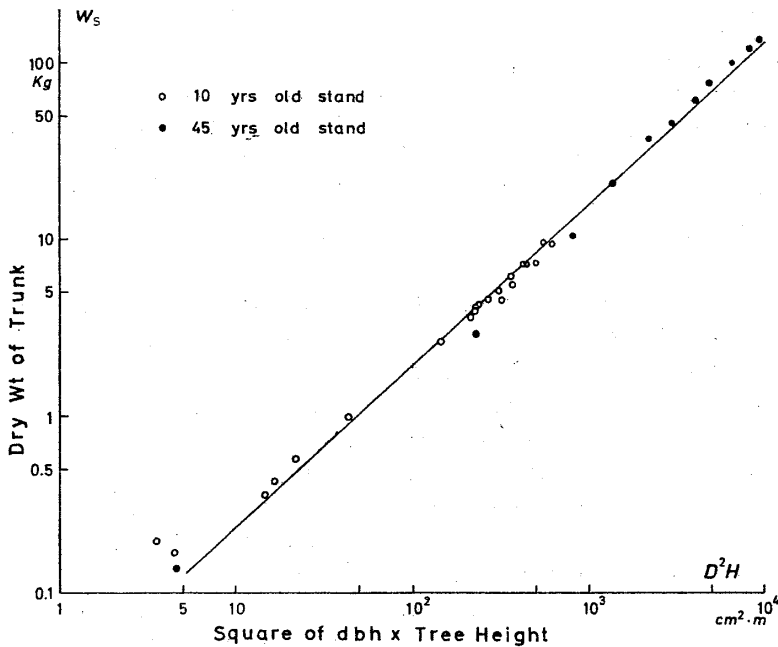


Fig. 2. Weight of a trunk as the allometric function of D^2H , where D and H are dbh and height of aboveground shoot. The source of data is the same as in Fig. 1.

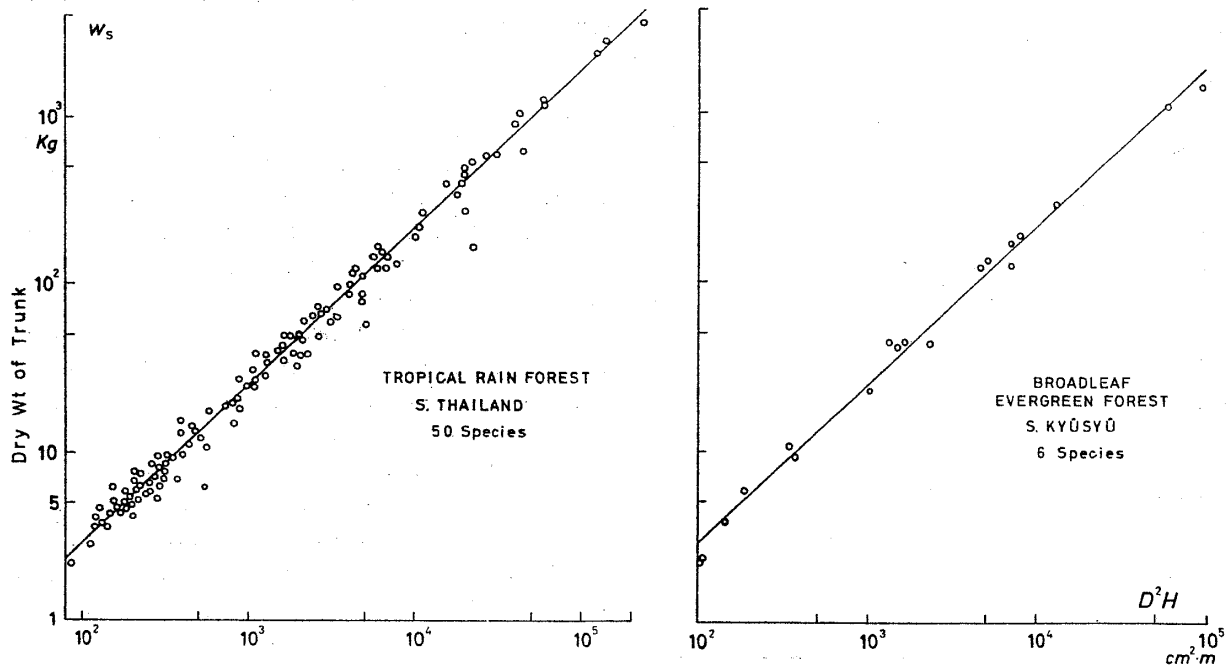


Fig. 3. Trunk weight— D^2H allometry in two different forest types of the Western Pacific (45, 43). Where a stand is composed of many tree species of similar life form, one and the same allometric regression can cover the trunk weight— D^2H relations in every species. The regression is exactly the same in these two forests.

system can improve the accuracy of biomass estimation to a considerable extent, as easily recognized in the comparison between Fig. 1 and Fig. 2. The regression line on the latter diagram is apparently better fitted to individual tree data.

Incidentally, such an allometric function is not necessarily specific to a single tree species, but may be common to several or more species growing together in the same community and having a similar life form. Fig. 3 presents two striking examples of such cases. The left-hand diagram illustrates the trunk weight— D^2H allometry in a tropical rain forest of Thailand in which 50 different species are involved. The one on the right hand shows the same relation in an evergreen broadleaf forest of southern Kyûsyû that covers 6 species. Most noteworthy is that the two regressions are exactly the same in spite of the wide difference of climate and a great geographical distance between the two forests concerned. Similar relations have been found in several groups of tree species in tropical deciduous forests of Thailand (42), an evergreen broadleaf forest of southernmost Kyûsyû (26), a subalpine conifer forest of central Japan (29), subarctic conifer forests of Hokkaidô (51), a deciduous broadleaf forest of

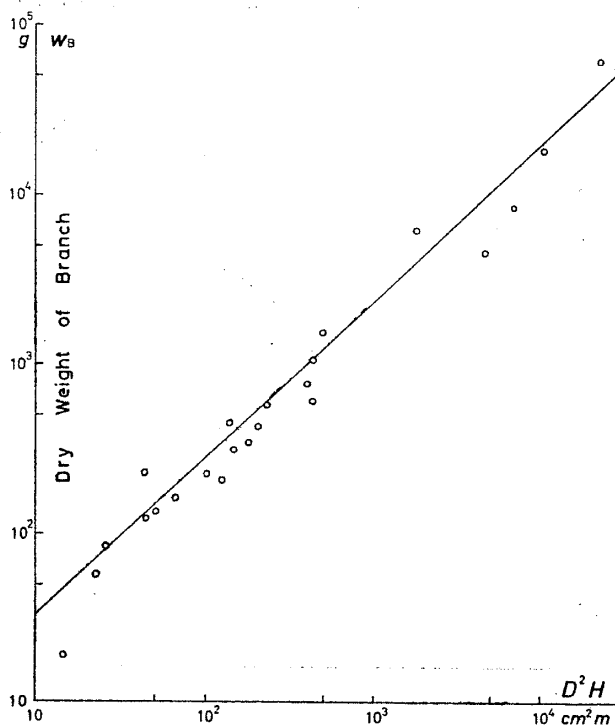


Fig. 4. Branch weight— D^2H allometry in subarctic conifer forests of eastern Hokkaidô, including *Abies sachalinensis*, *Picea jezoensis* and *Picea glehnii* (51)

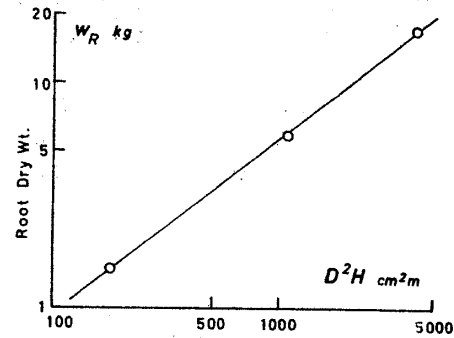


Fig. 5. Root weight— D^2H allometry in trees of a tropical rain forest of southern Thailand (45)

The allometry constant, h in Eq. (1), was equal to 0.775 in this case.

central Japan (12), and so forth. The practical significance of this interesting fact may need no further explanation.

We can also estimate the biomass of branch or root by essentially the same procedure, although the branch weight— D^2H relations (33, 51–53, 66–68, etc) in individual trees tend to fit with the allometric function less faithfully when compared to the case of trunk (Fig. 4). Root biomass data (1, 16, 28, 44, 96) are, on the other hand, very scarce at present (Fig. 5), but it is worth while mentioning that the allometric constant h in root weight— D^2H functions tends to be considerably smaller than 1, indicating that the top/root ratio is likely to increase with increasing tree size.

Leaf biomass

The biomass of leaves of a tree has somewhat different characteristics, and is more difficult to estimate than wood biomass. Not only is it correlated with dbh and tree height, but it also varies according to stand age, community structure and other factors. Fig. 6 shows an example of birch stands in Hokkaidô, where the regression of foliage amount on dbh differs markedly among the stands of different ages (69, 70). The difference remains as it is even if dbh is substituted by D^2H . SHINOZAKI et al. (1964) developed a new theory that successfully explained the quantitative correlation between foliage and woody organs in a tree, and expected that the amount of leaves should have the closest correlation not with dbh but with the diameter of bole at the joint of the lowest living branch (Fig. 7) which we may designate as D_B . Indeed Fig. 7 well demonstrates that the foliage biomass of the birch trees is pro-

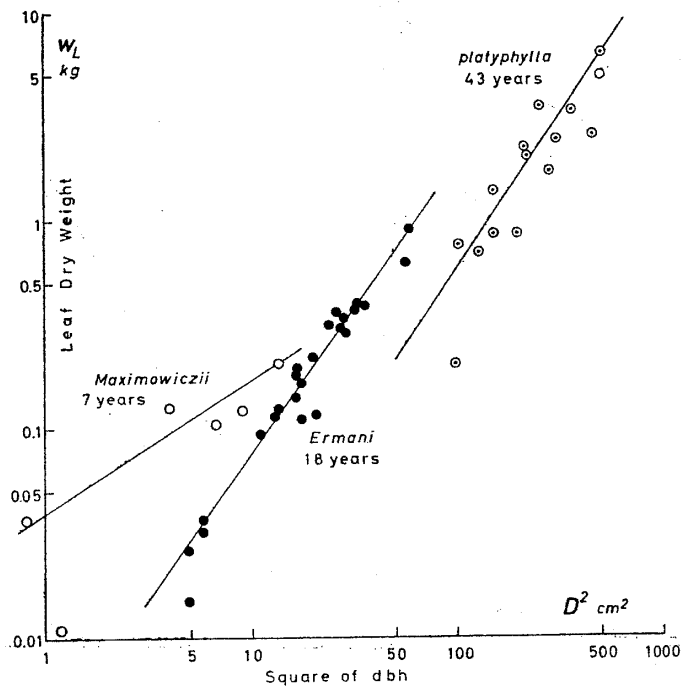


Fig. 6. Leaf weight—dbh allometry in birch stands of Hokkaido

The three stands, 43-year-old stand of *Betula platyphylla japonica* at Asyoro, *B. Ermani* stand at Simizu, and *B. Maximowiczii* stand at Nipesotu, have respectively different regressions (10).

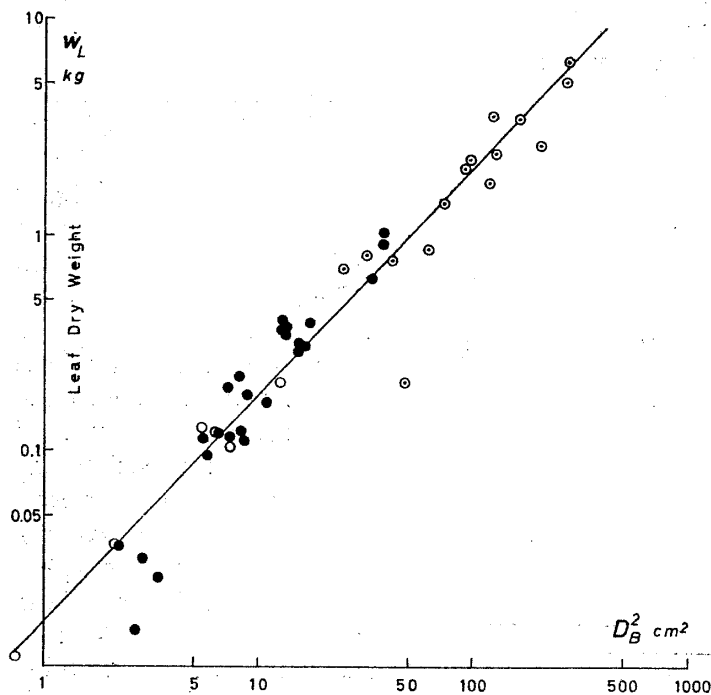


Fig. 7. Leaf weight— D_B allometry in birch stands

The leaf biomass per tree is approximately proportional to the square of D_B irrespective of the differences of species and stand age. For symbols see Fig. 6.

portional to the square of D_B or to the area of stem cross section at this specific height in every stand. This method of foliage biomass estimation proved especially useful in such sun-loving trees as birch, larch, and *Cryptomeria*.

Another very important property of leaf biomass is that a tree growing in a closed stand can not have an infinitely large amount of foliage however big the tree may be. Instead, it seems that there is a certain upper limit of foliage biomass for a tree in a given stand. When the amount of leaves is plotted against the total weight of woody shoot, one obtains a kind of ceiling curve as shown in Fig. 8. It is successfully formulated by the generalized allometric function proposed by OGAWA et al. (1965),

$$\frac{1}{w_L} = \frac{A}{(w_{TC})^h} + B, \quad (2)$$

where w_L and w_{TC} stands for the weight of leaves and that of aerial woody shoot, while A and B are coefficients specific to the stands concerned. The allometric constant h may often be close to 1 as seen in Fig. 8. This peculiar property of leaf biomass is likely to be overlooked if one is contented with the simple allometry between w_L and dbh given on the right side of the figure, where the trend of ceiling is not at all apparent. The latter way of leaf biomass estimation has long been used since its proposal by KITTREDGE (1944), but it should be emphasized that it can not be free from the danger of serious overestimation where big trees over 30–40cm dbh are concerned.

The leaf is only a minor component of total forest biomass in its absolute quantity. However, in view of its functional importance as photosynthetic apparatus, the estimation of its amount is one of the key points in the study of primary production. The behavior of leaf biomass in response to varying community structure and environment is quite different from that of total biomass. As an example, Fig. 9 shows

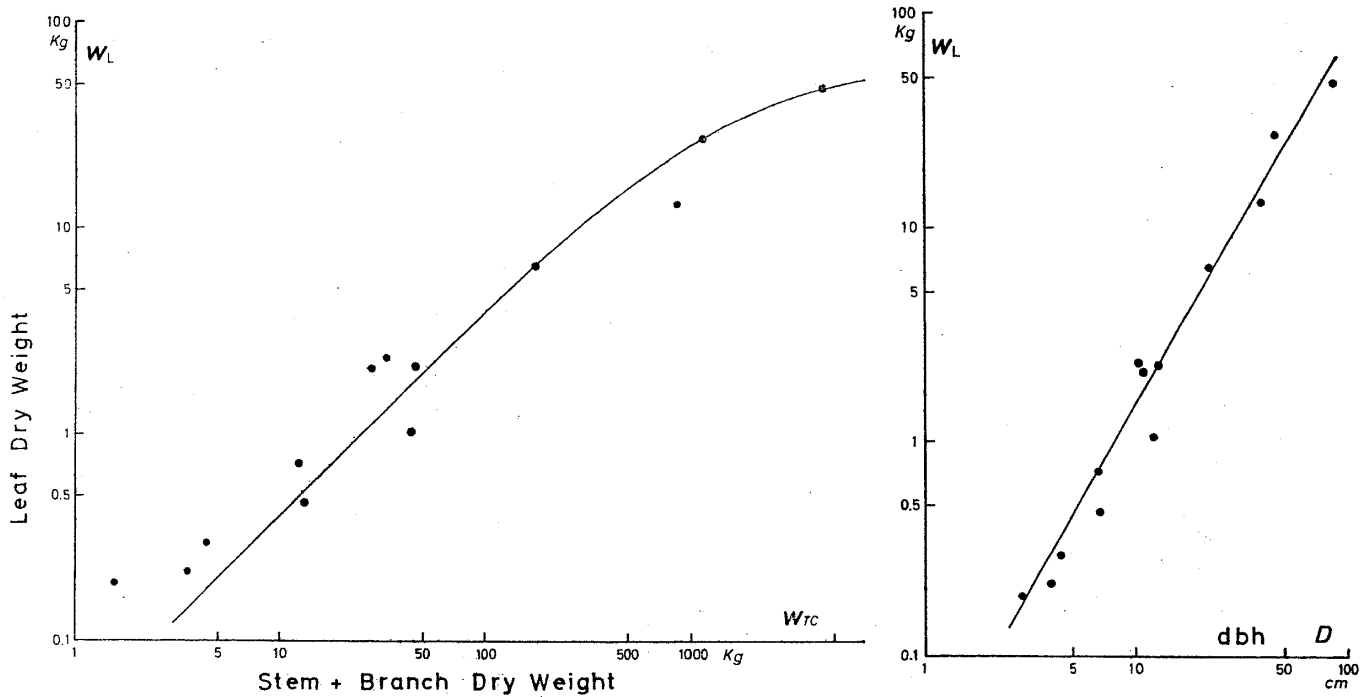


Fig. 8. Estimation of foliage amount by two different allometric functions in a cool temperate deciduous forest on Mt. Tanzawa, central Japan

Left Leaf dry weight—(trunk+branch) dry weight correlation formulated by the generalized allometric equation, $(1/W_L) = (15.435/W_{TC}) + 0.0147$. Right Simple leaf weight—dbh allometry. The amount of leaves of a tree 1 m in its dbh is expected to be ca. 80 kg according to the simple allometry, whereas it is to be ca. 60 kg on the basis of the left-hand curve. Original data including *Fagus crenata* and other 5 species were taken from IKUSIMA (1964).

the trend of leaf biomass change associated with the development of even-aged pure stands. Whereas total biomass increases monotonously with stand age, the foliage biomass on a unit

land area reaches a maximum at an early stage and then decreases somewhat to reach a more or less constant level, which is likely to be maintained for a considerably long period.

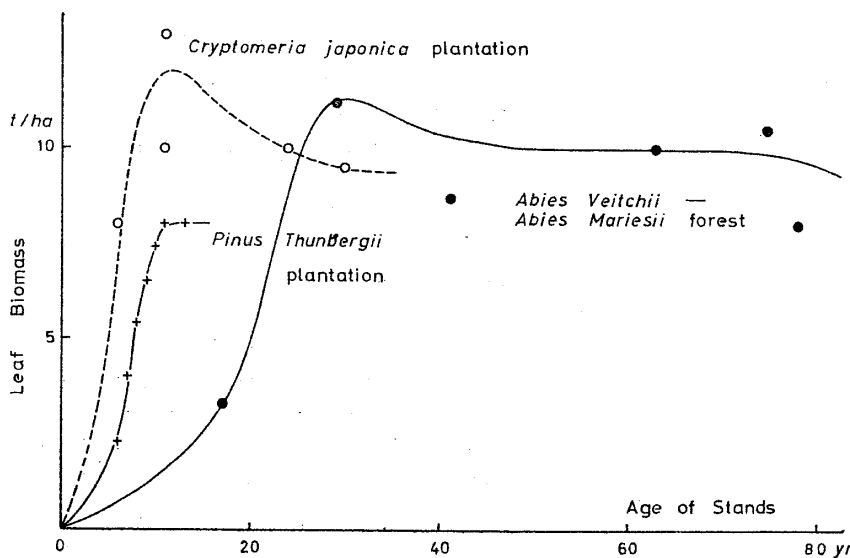


Fig. 9. Leaf biomass—age trends in some pure stands

Cryptomeria japonica plantations at Yosino, central Honsyū (53). *Abies Veitchii*—*A. Mariesii* forests on Mt. Simagare, central Honsyū (50). *Pinus Thunbergii* plantations, Tiba near Tokyo (14).

Biomass of leaves differs significantly among different forest types and different geographical regions. Fig. 10 summarizes the results of leaf biomass estimation in different forest types of the Western Pacific area. Deciduous hardwood forests of the temperate zone tend to have the least amount of leaves, mostly within the range of 2 to 4 metric tons per hectare in oven-dry weight. Forests of broadleaf evergreens and pines bear more leaves around 7–9 ton/ha. Subarctic or subalpine fir and spruce forests, as well as alpine dwarf pine scrubs, have the greatest amount reaching 20 ton/ha or even

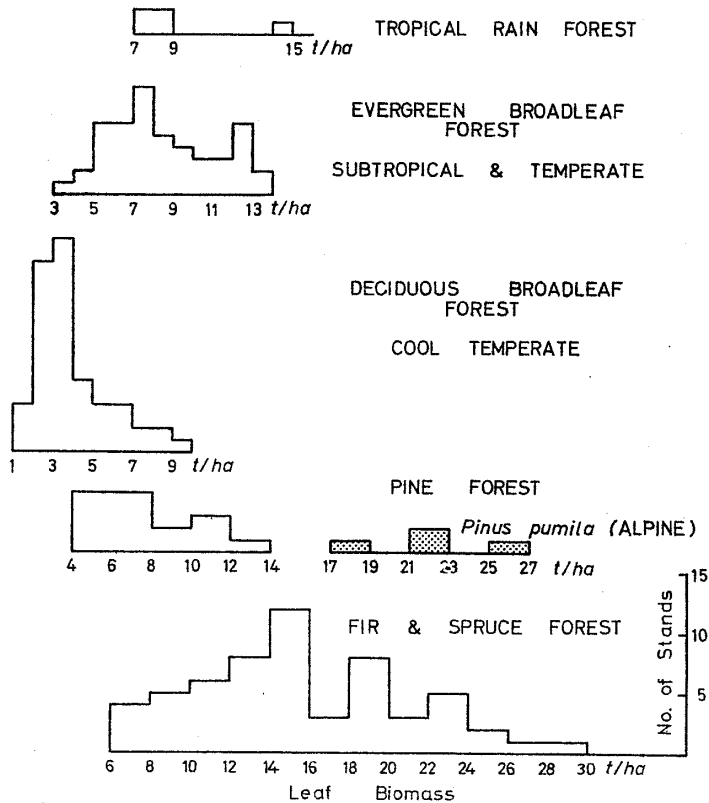


Fig. 10. Leaf biomass estimates in various forest types of the Western Pacific area

Sources of data: tropical rain forest (45, unpublished data from Cambodia by HOZUMI & YODA), evergreen broadleaf forest (15, 26, 34, 40, 43, 55, 78, 82, 86, 88-9), deciduous broadleaf forest (7, 12, 39, 76-7, 79, 86, 96), pine forest (3, 4, 9, 14, 62-3, 65, 71, 73), fir and spruce forest (6, 50-1, 64).

more. SHIDEI and TADAKI (79, 86) pointed out that the average longevity of leaves seemed to be an important factor responsible for the difference of leaf biomass so far as these temperate forests are concerned. The average life span of leaves of broadleaf deciduous trees is, of course, less than one year, while that of temperate broadleaf evergreens is usually between 1 and 3 years. The longevity of ordinary pine needles is around 2 years, while that of fir, spruce and alpine dwarf pine is much longer (3-5 years). Apparently the longer the average life span of leaves, the greater the leaf biomass.

Another important factor related to leaf biomass is the intensity of incident solar radiation. MONSI & SAEKI (1953) reached the theoretical conclusion that the leaf area index in a fully closed plant community was likely to be proportional to the logarithm of incident light intensity, provided the properties of leaves were identical. In fact, the leaf area index in more or less stabilized natural forests of broadleaved trees was found to decrease toward higher latitudes as

shown in Fig. 11. It may be over 10 in a tropical rain forest, around 8 in subtropical and warm-temperate evergreen forests, and as small as 6 in deciduous forests of the cool temperate zone.

In this connection, it should be noted that the efficiency of light absorption by leaves in terms of the light extinction coefficient of BEER-LAMBERT's formula was more or less the same in all forests growing under different climates. This might mean that the MONSI-SAEKI's mathematical model of canopy photosynthesis is also applicable to forest communities and that the latitudinal trend of leaf area index is

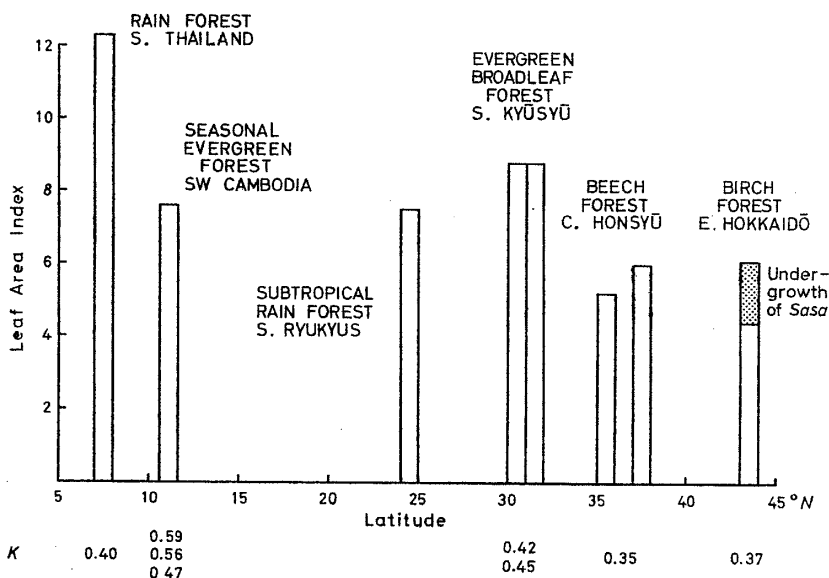


Fig. 11. Latitudinal trends of leaf area index and light extinction coefficient of canopy (K in LAMBERT-BEER's formula) in stabilized natural forests

Sources of data: rain forest of southern Thailand (45), seasonal evergreen forest of southwestern Cambodia (unpublished data by HOZUMI & YODA), subtropical rain forest of southern Ryukyus (40), evergreen broadleaf forest of southern Kyusyu (18, 26, 43), beech forest of central Honsyu (12, 39, 96), birch forest of eastern Hokkaido (10).

controlled mainly by the change of solar radiation, if there were no limitation due to the lack of water supply. The light extinction coefficient found in natural forests is generally between 0.35 and 0.55 (1/LAI) except in young sapling stands where the value is usually greater. In herbaceous communities, however, such small coefficient values are known only from grasslands (36) where the canopy is decidedly erectophile (94). Certain unknown mechanisms may exist in the light interception in broadleaf forests to account for these small extinction coefficients associated with apparently planophile (94) canopies. SHINOZAKI (1961) suggested a hypothesis based on the characteristic clumped distribution of leaves within a forest canopy, but more detailed studies seem necessary on this topic.

Total biomass

An example of the accuracy of biomass estimation by the allometric method is presented in Table 1. In a tropical rain forest of Thailand, a sample area 10 m by 40 m was clear-felled, and the biomass of aboveground shoots of all trees on the area was directly weighed and also indirectly estimated by the procedures so far stated. The comparison between the measured and the estimated values showed that the relative error of estimation was usually smaller than 5%. The results seem fairly satisfactory.

The total biomass itself is not a measure of productivity in so far as forest communities are concerned, nor has it any definite correlation with the geographical situation of a forest. One sometimes speaks of the luxuriance of tropical jungle, but the biomass of a tropical rain forest is by no means greater than those of well-developed forests outside the tropics (42). YODA (1964, 1965) followed the

Table 1. Comparison of the values, determined directly and calculated, of aboveground biomass on a clear-felled plot (10 m × 40 m) in Khao Chong rain forest, southern Thailand (45)

	Stem t/ha	Branch t/ha	Total wood t/ha	Leaf t/ha	Total shoot t/ha	Leaf area index ha/ha
Directly determined	292	104	396	7.8	404	10.7
Calculated	279	116	395	8.2	403	11.2
Relative error (%)	-4.5	11.5	-0.25	5.1	-0.15	4.7

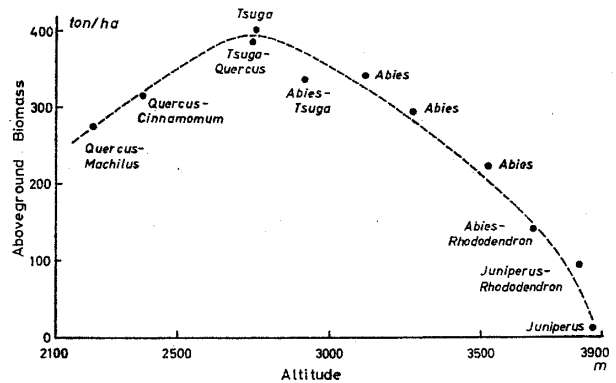


Fig. 12. Change of biomass in an altitudinal series of climax forest and scrub communities of the eastern Nepalese Himalayas (97, 98)

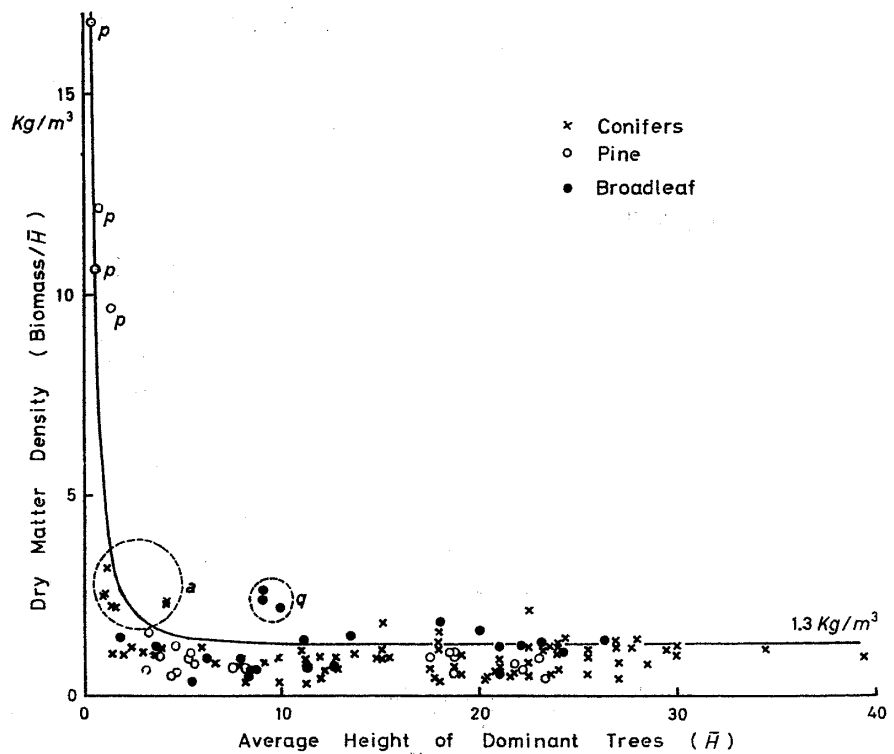


Fig. 13. Apparent density of forest biomass as related to stand height. Exceptionally high density was obtained in the alpine scrub community of *Pinus pumila* (p), dense sapling stands of *Abies sachalinensis* (a), the salt spray community of *Quercus phillyraeoides* (q), etc.

change of biomass in an altitudinal series of climax forest communities on the slopes of the eastern Nepalese Himalayas, and found the maximum in the cool temperate zone where the *Tsuga dumosa* forest thrived (Fig. 12). *Tsuga* trees were about 40 m tall. There was an apparent correlation between the biomass and the average height of the forest.

The biomass of areal shoots divided by the height of dominant trees gives the apparent density of dry organic matter per unit space occupied by the forest. As seen in Fig. 13, this dry matter density is practically independent of stand height in ordinary forests. A fully closed stand tends to have a dry matter density of 1-1.5 kg/m³. This corresponds to the atmospheric density at the sea-level, 1.3 kg/m³. Such a small density of apparently enormous accumulation of forest biomass is rather astonishing.

However, exceptionally high dry matter density was observed in certain shrub communities and dense stands of conifer saplings. The dwarf pine (*Pinus pumila*) scrub in the alpine region of the Japanese highlands is especially noteworthy in this respect (73). Its needles and very slowly growing shoots cover the ground so densely that its dry matter density is almost 10 times as great as that of a normal forest community.

Net production

Before turning to the productivity itself, considerations should be given to the procedure of estimating net production. Fig. 14 is a diagram showing additions to and losses from the biomass of a plant community during a specified period from t_1 to t_2 . Let the biomass at the beginning of the period (t_1) be y_1 . During the period till t_2 , the net production P_n is added to y_1 , while parts of y_1 are lost by litterfall and grazing (and other consumption by heterotrophic organisms) as L_0 and G_0 . On the other hand, parts of the net production or newly formed plant tissues may also be shed as L_N and grazed away as G_N . The biomass at the end of the period (t_2) thus becomes y_2 , which is composed of the old component y_{20} formed before t_1 and the new component y_{2N} formed during the period concerned. The increment of biomass Δy is the difference between y_2 and y_1 , and is not identical with y_{2N} , but is equal to y_{2N} minus L_0 and G_0 .

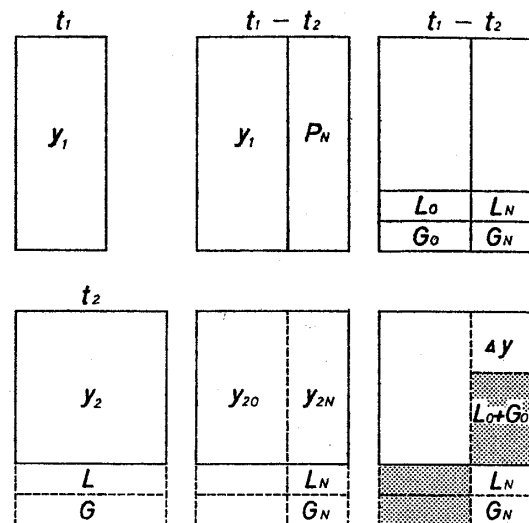


Fig. 14. A diagrammatic representation of gains and losses of biomass in a plant community during a specified period from t_1 to t_2 (24)

For further explanations see text.

This simplified analysis indicates that net production may be estimated by two different ways, either by

the sum of Δy and L and G (Method 1)

or by

the sum of y_{2N} and L_N and G_N .

(Method 2)

These two methods involve specific difficulties in practical application. In the first method, the biomass of the same community must be estimated twice at t_1 and t_2 accurately enough to assure a reliable value of the biomass increment Δy . It is a fairly difficult task especially where the biomass increment is small as in a stabilized climax forest. Besides, observations must be kept continuously for a whole year to record the amounts of litterfall and grazing consumption.

On the other hand, in the case of the second method it may suffice to measure the biomass only once, at the end of growing season. However, the amount of current-year tissues must be measured separately; for instance, current-year leaves and twigs of sample trees should be clipped and weighed, increments of wood estimated by means of stem analysis technique, and so on. The sum of current-year tissues thus obtained is evidently equivalent to y_{2N} in Fig. 14. This is the basic principle of Method 2, which has hitherto been more frequently used than Method 1. But it should again be emphasized that y_{2N} is not the net

production itself. The losses of current-year tissues due to litterfall and grazing should be added to obtain an exact estimate of net production. It is usually difficult to separate litterfall into current-year and older components, though the amount of current-year component (L_N) is not usually small enough to be negligible even in a deciduous forest as shown later. This is one of the inevitable difficulties in the application of Method 2. Furthermore, stem analysis technique is difficult to apply to branch and root, yet no reasonable alternatives have been established.

The studies of net production made so far in Japan were mostly based on Method 2. Diverse approximations were used to avoid the difficulties mentioned above. Speaking somewhat exaggerately, each study had its own methodology which differed from the others. The standardization of methodology is an urgent need which should be done as soon as possible preferably before the second phase of the IBP.

Nevertheless, the accumulation of a considerable number of net production estimates on the western coasts of the Pacific may allow certain generalizations. As summarized in Fig. 15, the annual net production of broadleaf evergreen forests in the warm temperate regions of the Japanese Archipelago, as well as those of *Cryptomeria japonica* plantations, generally range between 10 and 30 tons of dry matter per hectare with the highest frequency at 15–20 ton/ha. Pine forests have a somewhat smaller rate, having the peak at 10–15 ton/ha·yr, while deciduous broadleaf forests in the cool temperate zone have the lowest net production. Most of the deciduous forests produce only 5–10 ton/ha·yr, although the production by the whole community might be somewhat greater if the contributions of undergrowth vegetation are taken into consideration. Coniferous forests in subarctic and subalpine regions have a higher productivity with a peak of 10–15 ton/ha·yr. Evergreen forests, whether coniferous or broadleaved, apparently are more productive

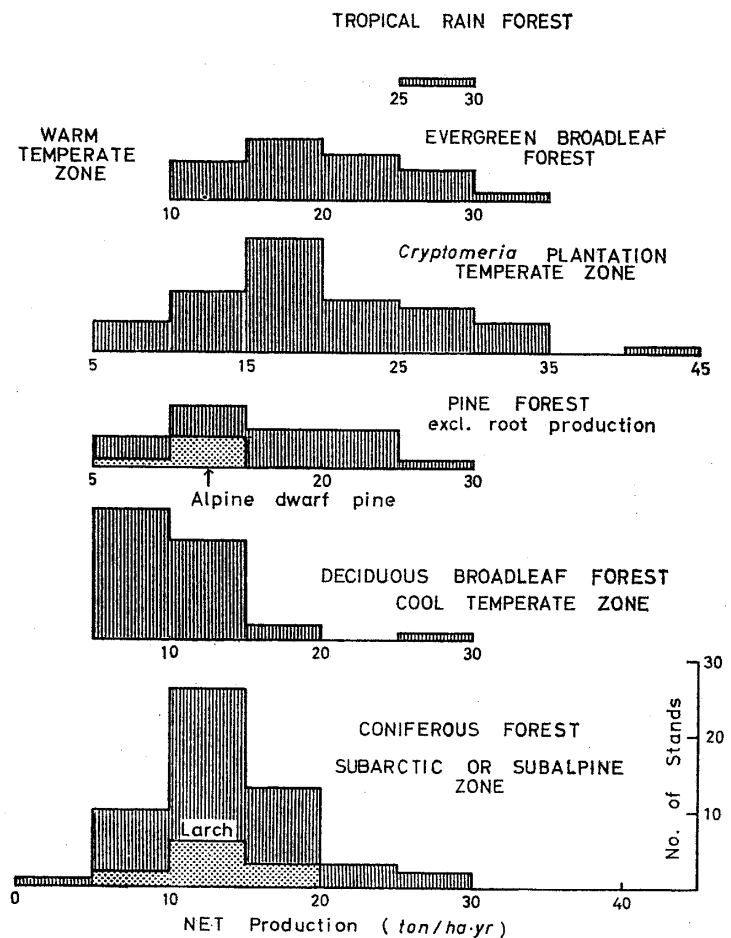


Fig. 15. Net production estimates in various forest types of the Western Pacific area

Sources of data: tropical rain forest (24), evergreen broadleaf forest (15, 18, 78, 82), *Cryptomeria japonica* plantation (53, 84, 87), deciduous broadleaf forest (7, 52, 77), pine forest (4, 9, 14, 65, 73), coniferous forest (6, 19, 51–2, 64). Certain corrections were made to the original data where necessary.

than deciduous forests.

It is rather surprising to find that any type of forest ranging from the tropics to the subarctic zone can have a net productivity as high as 30 ton/ha·yr under favorable conditions. A *Cyptomeria* plantation of Kyûsyû only 17 years old (84) can produce much more than a luxuriant rain forest of Thailand. This seems to be a challenge to the aim of the IBP itself. Can we find any basic trends in the world-wide distribution of net production?

The answer to the question may be found in further analysis of productivity data. Fig. 16 presents the trend of net production in an age-series of dense pure *Abies sachalinensis* stands in Hokkaidô. Total biomass increases with age, and with this increase of biomass the net productivity undergoes a characteristic change;

a rapid rise in the earliest stage of stand development, followed by a gradual decline. A hypothetical interpretation of this trend is presented in Fig. 17.

We have already mentioned the characteristic trend of age—leaf biomass curve (Fig. 9). As indicated by Fig. 17, the gross productivity may follow more or less the same trend with increasing stand age. The biomass of woody organs, on the other hand, increases monotonously with age, and hence the amount of organic matter consumed by the respiration of woody organs might follow the same course of increase. The respiratory consumption by leaves is

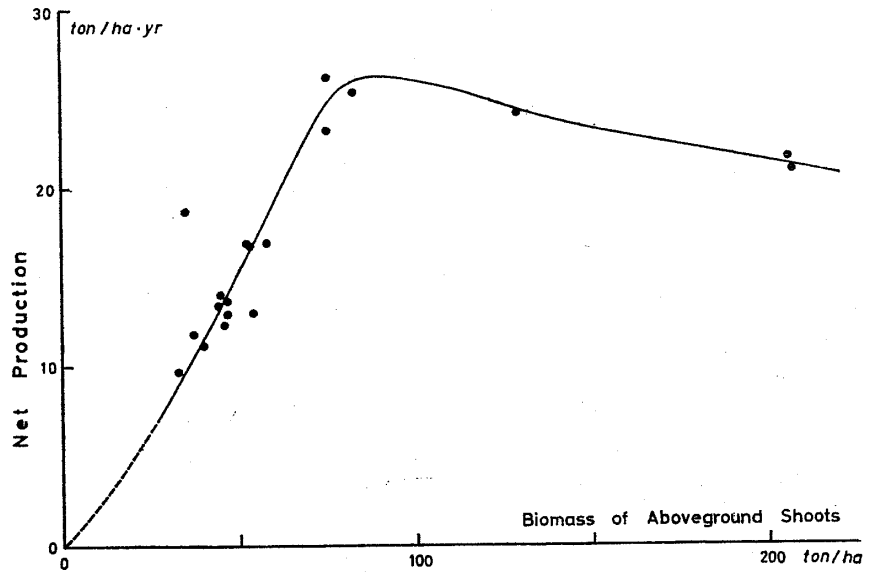


Fig. 16. Trend of net production associated with the growth of dense pure stands of *Abies sachalinensis* in northern Hokkaido (64)

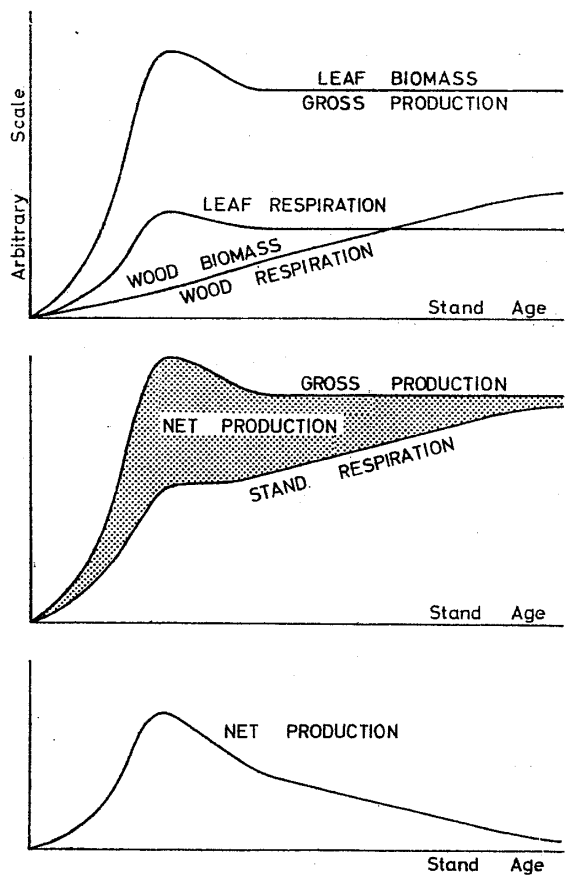


Fig. 17. Hypothetical trends of gross production, stand respiration, net production and biomass in an age-series of dense pure stands

naturally expected to be proportional to their biomass. The total stand respiration may thus undergo the change as given on the diagram. The net production is the difference between gross production and respiration indicated by the shaded area, and should change with age along the curve given at the bottom of Fig. 17. This simple speculation may be enough to demonstrate the profound influence of stand age on net productivity through the balance between gross production and respiration.

Obviously, net production alone can not always be a reasonable measure of the potential productivity of a forest community. Gross production may be fairly constant over a long period once the leaf biomass has reached an equilibrium, but the ratio of respiratory consumption to gross production varies widely with age. The significance of the realized net productivity can only be reasonably understood when it is analyzed in terms of the balance between gross production and respiration.

Gross production

Our subject now turns to the respiratory consumption of a forest community. A pending problem has long been how to estimate the total respiration of a tree too big to be enclosed in any kind of measuring apparatus. Only very recently did YODA et al. (1965) succeed in developing a new reasonable method applicable to any type of forest. Some of the important

conclusions reached will be given without going into technical details.

Fig. 18 shows how the total respiration of a tree varies with the increase of tree size or its dbh. At first the foliage respiration increases rapidly with tree size, but tends to approach a certain asymptotic value in very large trees, whereas that of woody organs continues to increase without limits. The gradient of the dbh—wood respiration curves on the logarithmic coordinates ranges between 3 and 2, telling that the respiration of woody organs tends to be proportional to $(dbh)^3$ or their weight in very small trees, while it is proportional to their surface area or to $(dbh)^2$ in very big trees.

Average respiration per unit amount of tree biomass, however, decreases progressively toward larger dbh (Fig. 19). Therefore a forest stand composed of many small trees consumes a greater amount of organic matter by respiration than another stand of the same species composed of a smaller number of bigger stems, even if the biomass is the same in both stands. Total stand respiration is thus influenced not only by the age of the component trees but also by the distribution of their size.

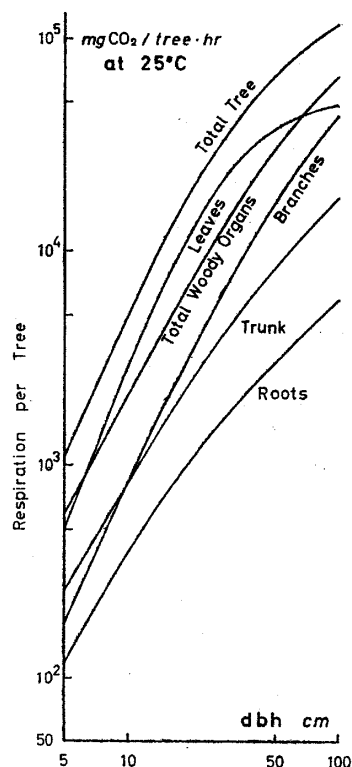


Fig. 18. Respiration of a rain forest tree as related to its dbh (100)

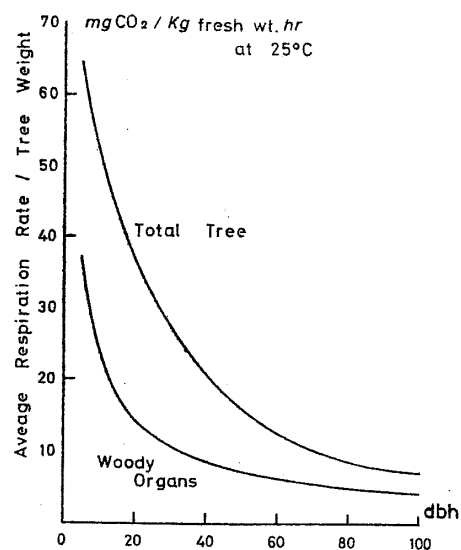


Fig. 19. Average respiration rate per unit biomass of rain forest trees as the function of dbh (100)

A natural forest is generally composed of trees of heterogeneous ages and sizes, so that the ratio of net production to gross production might be quite different in different stands.

The analyses of production relations in a tropical rain forest of southern Thailand made by KIRA et al. (1967) provide a good example of what is going on in a natural forest. The forest was a little disturbed rain forest nearly 40 m tall and with a total biomass of about 325 ton/ha and a leaf area index as great as 12 ha/ha (44, 45). In early 1962, two sample plots, each 40 m square, were set up within the forest. Seventy-four sample trees of various sizes belonging to 50 different species were felled in one of the plots. The biomass of the other plot was estimated using the allometric correlations derived from the sample tree measurements combined with the census of dbh and tree height. A part of the first plot was clear-felled to check the accuracy of biomass estimation (Table 1). Daily litterfall was recorded continuously for 6 weeks. Besides, the increments of dbh of all trees on the latter plot and their mortality were recorded during the following three-year period. Respiration rate was also measured in 1962 with some one hundred samples of various community components (100).

The results are summarized in Table 2. Assuming that the same allometric relations persisted during the three-year period, the increase of biomass of surviving trees on the

Table 2. Summary of primary production relations in Khao Chong rain forest, southern Thailand (24)

	t/ha·yr				
	Stem	Branch	Root	Leaf	Total
Biomass increase in living trees ($\Delta y'$)	4.18	1.69	0.56	0.132	6.56
Death of standing trees (D)	0.78	0.27	0.13	0.041	1.22
Biomass increase in the whole stand ($\Delta y = \Delta y' - D$)	3.40	1.42	0.43	0.091	5.33
Litterfall (L)	—	11.39*	—	11.84	23.22
Net production ($P_n = \Delta y + L$)	3.4	12.8	0.4	11.9	28.6
Loss due to respiration (R)	13.1	19.0	5.6	57.0	94.6
Gross production ($P_g = P_n + R$)	16.5	31.8	6.0	68.9	123.2

* Such minor components of litter as bark, fruit, inflorescence, etc. have been included here.

second plot was estimated based on the records of dbh increment. It amounted to 6.6 ton/ha·yr, while several trees died during the three years and resulted in an average loss of biomass of 1.2 ton/ha·yr. The rate of net biomass increase was thus only 5.3 ton/ha·yr. Adding the estimate of annual litterfall of ca. 23 ton/ha·yr, the net production was finally estimated to be at least 29 ton/ha·yr, excluding the turnover of roots and the grazing consumption which were very difficult to measure.

A very large amount, equivalent to 57 tons of dry organic matter, was consumed annually by the respiration of leaves, and additional 38 tons by the respiration of woody organs. The sum total of community respiration is about 95 ton/ha·yr. The final estimate of gross production is thus 123 ton/ha·yr, probably one of the highest values ever known in terrestrial plant communities.

Nearly 80% of this enormous gross production is used up by community respiration, leaving only a little less than 30 ton/ha·yr as the net production. This might be caused firstly by the large amount of actively respiring leaves (30, 38, 49, 54), secondly by the great accumulation of woody organs which was nearly 40 times as much as the leaf biomass, and thirdly by the large number of small trees which filled the space under the canopy of dominant trees.

The net production of 29 ton/ha·yr is not greater than that of vigorously growing conifer forests in northernmost Hokkaidô at 45°N (Fig. 15). Furthermore, about 80% of this net production or 23 ton/ha·yr was utilized in the

turnover of leaves and twigs. The annual amount of leaf litter was some 12 tons per hectare, while the leaf biomass was only 8 tons per hectare, so that the mean longevity of leaves in this rain forest is expected to be only 8-9 months. The rate of turnover of leaves under rain forest conditions is exceedingly rapid. A part of the remaining 20% of the net production is counterbalanced by the loss of biomass due to the death of trees, leaving only 5 tons/ha·yr for the net biomass increase which is equivalent to only 5% of the gross production. If one more tree about 30 cm in its dbh had died annually on the sample plot, the net biomass increase would have been reduced to zero.

In our opinion, such a small ratio of net production to gross production and the very small biomass increment are most probably the characteristic properties of a stabilized climax community, by which means it maintains its biomass at a more or less constant level from year to year. KIMURA (1960) also obtained a net production/gross production ratio as small as 0.3 in a climax broadleaf evergreen forest of southern Kyûsyû, although the procedure of estimation differed somewhat from ours. If a young secondary forest or an artificial plantation of moderate age had existed under the same climatic conditions of the rain forest,

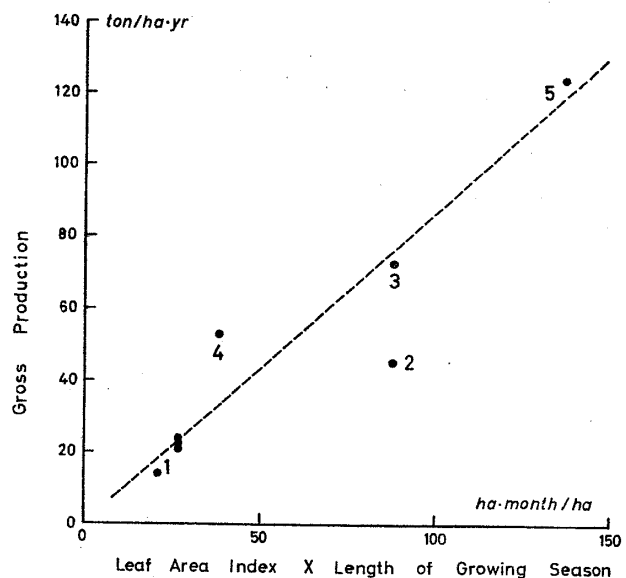


Fig. 20. Correlation between gross production, leaf area index and length of growing season

1: European beech forest of Denmark (35). 2: *Castanopsis cuspidata* forest of central Kyûsyû, Japan (82). 3: Broadleaf evergreen forest of southern Kyûsyû, Japan (18). 4: tropical humid forest of Ivory Coast (37). 5: tropical rain forest of southern Thailand (24).

we might well have expected a much greater net productivity.

Anyhow, there is little doubt that gross production in the humid tropics is greater than in temperate regions. The decline of productivity at higher latitudes may be caused either by the shortened growth period or by the decrease of solar radiation and associated decrease of leaf area index. We have as yet very few examples of similar gross production analyses, but a tentative trial is made here to correlate gross productivity with these two factors (Fig. 20). So far as these rather poor evidences are concerned, the gross productivity of broadleaf forests tends to be proportional to the length of growing season in months multiplied by the leaf area index.

Litterfall

In spite of its importance as one of the major pathways of matter and energy flow through a forest ecosystem, the litterfall has not yet been properly studied in most parts of the world. More researches need to be made on the amounts of litterfall in different forest types, seasonal distribution and year-to-year fluctuation, changes of chemical composition associated with defoliation, etc.

OHMASA & MORI (1937) were the first to publish annual amounts and seasonal trends of litterfall in various forest types of Japan, but their records were restricted to leaf litter. Complete records of total litterfall including such non-leaf components as branch and twig, bark, inflorescence, seed and fruit, etc. are still restricted in number (Table 3). Although some of the data presented in the table might

Table 3. Annual rates of litterfall in some forest types of the Western Pacific

Forest type & locality	Leaf	Non-leaf components	Total	Author & period
Tropical rain forest, Khao Chong, Thailand	11.9 (51)*	11.5 (49)	23.3 (100)	KIRA et al. (24), 2 mos.
Young stand of <i>Castanopsis cuspidata</i> , Kumamoto, Japan	3.7 (68)	1.8 (32)	5.4 (100)	TADAKI (85), 2 yrs.
Mixed evergreen broadleaf forest, Nara, Japan	3.6 (59)	2.5 (41)	6.0 (100)	KIRITA (25), 1 yr.
<i>Pinus densiflora</i> forest, Osaka, Japan	5.2 (66)	2.6 (34)	7.8 (100)	KIRITA (MS), 1 yr.
Subalpine conifer forest (<i>Tsuga-Abies-Picea</i>), Yatugatake, Japan	2.3 (66)	1.2 (34)	3.5 (100)	KIMURA (19), 4 yrs.
Subalpine conifer forest (<i>Abies</i> spp.), Yatugatake, Japan	2.7 (55)	2.2 (45)	4.9 (100)	KIMURA (19), 4 yrs.

* Relative values in italics in parentheses.

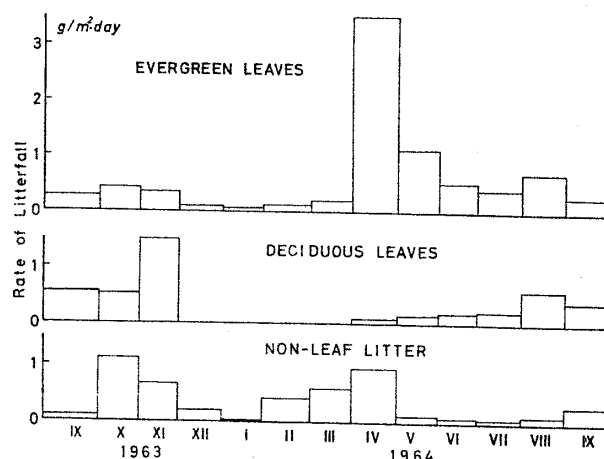


Fig. 21. Seasonal distribution of litterfall in a warm temperate evergreen hardwood forest at Nara, central Japan (25)

Most of the evergreen leaves belong to *Castanopsis cuspidata* and *Cyclobalanopsis gilva*, while *Carpinus laxiflora* is practically the sole deciduous component of the forest.

be less reliable than others owing to the use of shallow trays as the litter trap (which is likely to result in a slight underestimation), it can be noticed that the ratio of non-leaf components to leaves is not so small as is usually believed (e. g. BRAY & GORHAM 1964). It is greater than 1/2 in all cases and sometimes approaches 1/1 in certain climax forests, so that more attention should be paid to the reasonable estimation of non-leaf litter production.

Seasonal trends of litterfall in a climax broadleaf evergreen forest of central Japan are illustrated separately for evergreen leaf, deciduous leaf and non-leaf components in Fig. 21. The leaf fall of evergreens was concentrated in April and May, but nearly 40% of annual evergreen leaf litter was rather evenly distributed over the other 10 months. One of the characteristics of broadleaf evergreens is that the average duration of life of leaves differs widely among the species; for instance, it is about 1 year in *Cyclobalanopsis gilva*, between 1 and 2 years in *Castanopsis cuspidata*, 4-5 years in *Pieris japonica* (dominant in the shrub layer), and so forth. The amount of annual litterfall is therefore quite different from the leaf biomass at a certain season of the year. Even in deciduous species (mostly *Carpinus laxiflora*), only 50% of total leaf litter fell in two autumn months and the amount of leaf fall during summer months was by no means negligibly small. These facts point to the

necessity of continuous observation throughout the year for the exact estimation of litterfall.

Accumulation and breakdown of soil organic matter

A simple mathematical model of the dynamics of soil organic matter (especially of A₀ layer) accumulation and decay was proposed by JENNY, GESSEL & BINGHAM in 1949, and was later elaborated by OGAWA et al. (1961) and OLSON (1963). Though this is only a crude approximation of this complicated process, it seems sufficient to show that the accumulation of decaying organic materials on and in the forest soil depends upon the rates of both litterfall and organic matter breakdown in the soil.

SHIDEI & TSUTSUMI (1962) examined the accumulation of organic matter in A₀ layer and mineral soil down to a 60 cm depth in 27 different forests all over Japan, and found that the amounts decreased with the increase of monthly temperature summation during the growing season. Similar dependency of soil organic matter accumulation on temperature (32) was also observed along an altitudinal transect up to the summit of Khao (Mt.) Luang, the highest peak in peninsular Thailand (Fig. 22).

The contrast between different thermal regions becomes all the more apparent if the patterns of distribution of organic matter in different parts of the ecosystem are compared.

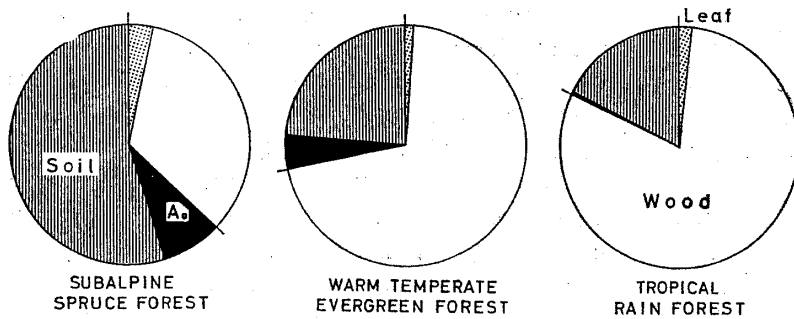


Fig. 23. Distribution of organic carbon accumulated in different parts of an ecosystem

Total accumulation of organic carbon: subalpine spruce forest on Mt. Ōdaigahara, central Honsyū, 225 ton/ha; broadleaf evergreen forest of Nara, central Honsyū, 272 ton/ha; tropical rain forest of southern Thailand, 270 ton/ha.

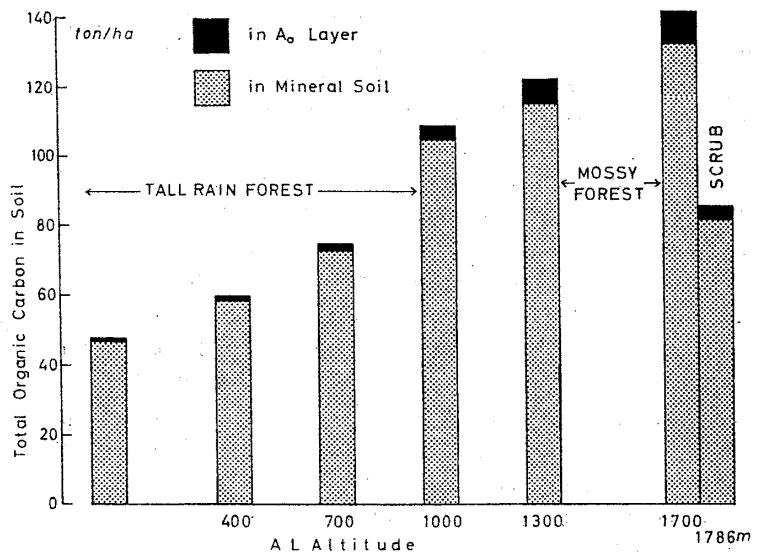


Fig. 22. Changes of total soil organic matter accumulation (including A₀ layer and mineral soil layer down to a 50 cm depth) on the way up the slope of Khao Luang in southern Thailand

The lowest point represents Khao Chong rain forest, some 130 km south of Khao Luang.

Fig. 23 illustrates the percentage distribution of organic carbon in three climax forest ecosystems in the tropical, warm temperate and subalpine zones. The total accumulation of organic carbon in the whole ecosystem does not differ greatly among the three forests, but the distribution within each system is quite different. In the tropical rain forest of Thailand, more than 80% of organic carbon was contained in living plant components, while in the subalpine spruce forest at 1,650 m above sea level in central Honsyū as much as 63% existed as A₀ layer and soil organic matter.

The accumulation of soil organic matter is expected to increase with increasing litter supply and with a decreasing rate of decay (Eq. 6). Since the rate of litterfall tends to be smaller in cooler regions (Table 3), the most important factor responsible for the contrast shown in Fig. 23 may be the temperature-dependent difference in the rate of decay of organic materials in the soil.

An earlier work by OHMASA & MORI (1937) on the process and rate of leaf litter breakdown

was followed by several others. Aside from chemical (17, 90, 91) and microbiological (56-61) aspects, emphasis will be laid here on the rate of litter decomposition under natural conditions. According to the results obtained by the litter bag technique, the percentage of decrease of the dry weight of leaf samples, left to decay on the forest floor during the first year, was 25% (conifer needles) in a subalpine conifer forest at 2,200 m altitude (19), 35% (beech leaves) in a montane beech forest at 900 m (92), and 43% (*Castanopsis* leaves) in a warm-temperate evergreen forest at 200 m (25), all in the central part of Japan. The influence of temperature is obvious.

According to the model proposed by OGAWA et al. (1961) and OLSON (1963), the amount of organic matter accumulated in soil (m) at a time t is given by

$$(dm/dt) = L - \mu m \quad (3)$$

$$\text{or } m = (L/\mu) (1 - e^{-\mu t}), \quad (4)$$

where L is the rate of organic matter supplied to the soil and μ is a factor that characterizes the rate of decomposition. After a sufficiently long time, an equilibrium between supply and decomposition is reached, when the soil organic matter accumulation is expected to become constant, as follows:

$$m)_{t \rightarrow \infty} = M = L/\mu, \quad (5)$$

provided L and μ remains unchanged independently of t . Since L and M can be estimated in the field, μ is evaluated as

$$\mu = L/M. \quad (6)$$

These formulations are most properly applied to the dynamics of A_0 layer (49), but they may also be used to describe the budget of total soil organic matter including surface litter, leafmold and humus in mineral soil. It is known that the rate of decomposition is greater in freshly fallen litter than in humus, so that μ in the latter case represents no more than an overall average for various kinds of soil organic materials at different stages of decay.

The strong effect of temperature on the values of μ calculated by Eq. (6) for both A_0 layer and total soil organic matter was also demonstrated by SHIDEI & TSUTSUMI (1962). The greater part of the forest stands they examined were, however, artificial plantations or young secondary growths. Evidently Eqs. (5)-(6) can best simulate the dynamic balance in a stable climax forest, which has developed

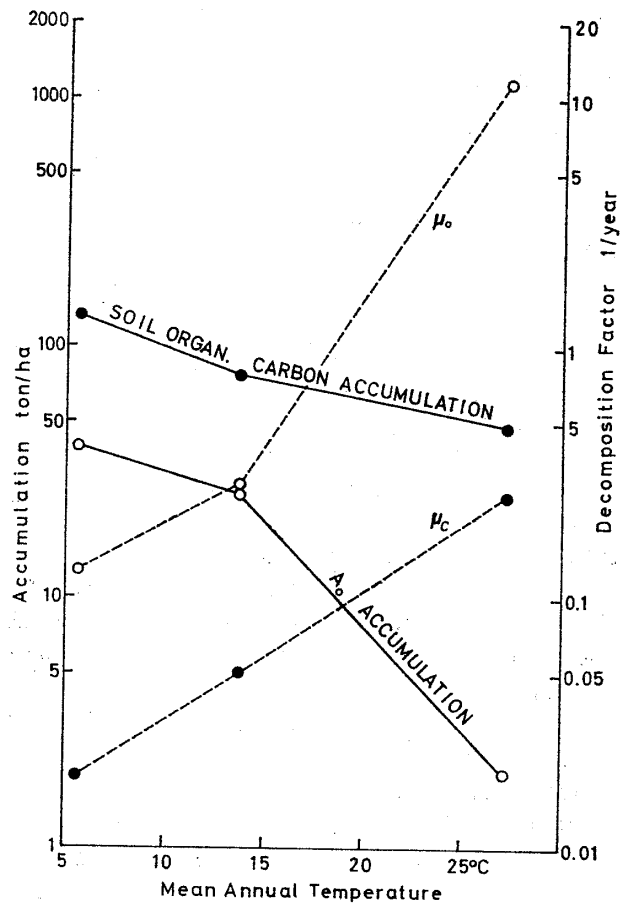


Fig. 24. Accumulation and average decomposition rate of total organic carbon in the soil (including A_0 layer) and A_0 layer (in oven-dry weight) in three climax forest communities (see Fig. 23) of the Western Pacific in relation to mean annual temperature

μ_o and μ_c respectively refer to the decomposition factor for total soil organic carbon and A_0 layer.

on a flat topography where the losses of organic materials due to soil erosion and runoff are negligible. The three forests given in Fig. 24 satisfy these conditions approximately, so that the values of μ calculated for these forests were correlated with corresponding mean annual temperatures in Fig. 24.

With the rise of the mean annual temperature, the amount of soil organic matter accumulation rapidly decreases, while the rate of decomposition becomes greater. The influence of temperature seems more pronounced on surface litter (A_0 layer) than on total soil carbon. It is noticed that the decomposition factor for total soil carbon (μ_c) increases almost exponentially with rising temperatures with the temperature coefficient Q_{10} slightly larger

than 3.0. The factor for A_0 breakdown (μ_0) differs even more widely between the tropical rain forest and the subalpine spruce forest. The length of time necessary for the breakdown of 95% of freshly fallen litter ($3/\mu_0$) is estimated to be only 0.26 years in the former, whereas it is 23.3 years in the latter forest. The corresponding time for soil organic matter mineralization ($3/\mu_c$) is about 12, 60 and 155 years respectively.

There were not included in these calculations the supplies of organic materials to the soil through the sporadic death of standing trees and through the turnover of fine roots, as well as the amount of organic matter contained in subsoil under 50 cm depth. The figures obtained of μ are therefore not exact enough. Nevertheless, they may well allow a reasonable understanding of the rate of organic matter turnover in forest ecosystems in different climatic zones. There is little doubt that not only a favorable supply of light and heat but also the rapid circulation of bio-elements through the ecosystem contribute to the high primary productivity in the humid tropics.

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meeting of the Ecological Society of Japan, Sapporo, 1964. Unpublished (1964) 98) *YODA, K.: A preliminary survey of the forest vegetation of eastern Nepal. I. Methods of survey and original data. NUMATA, M. (ed.): *Ecological study and mountaineering of Mt. Numbur in Eastern Nepal, 1963*, Chiba, pp. 45-73 (1965) 99) YODA, K., K. SHINOZAKI, H. OGAWA, K. HOZUMI & T. KIRA: Estimation of the total amount of respiration in woody organs of trees and forest communities. *J. Biol. Osaka City Univ.* 16, 15-26 (1965) 100) YODA, K.: Comparative ecological studies on three main types of forest vegetation in Thailand. III. Community respiration. *Nature & Life in SE Asia* 5, 84-148 (1967)

記 事

I. 日本生態学会第14回大会総会での承認及び議決事項

松山市愛媛大学でおこなわれた日本生態学会第14回大会総会(4月8日)で承認及び議決された事項は次のとおりです。

なお、各種委員会で協議された事項も、このなかに含まれております。

[A] 全国委員会提出事項

(I) 承認事項

a. 庶務・会計報告

1. 1966年度会誌発行状況:

i) 発行ページ数(1966, Vol. 16, Nos. 1-6) 272, 発行予定ページ260/年を12ページ超過した。

ii) 会誌内容(1966, Vol. 16, Nos. 1-6)

	原 著		総 説		短 報		雑 録		計
	和	欧	和	欧	和	欧	和	欧	
動物	29	4	0	0	2	0	1	0	36
植物	5	1	0	0	0	1	1	0	8
共通	1	0	1	0	0	0	2	0	4
計	35	5	1	0	2	1	4	0	48

iii) 発行部数の内訳(1966, Vol. 16, No. 6の場合)

個人会員(外国会員を含む) 1,223

団体会員 144

贈 呈 13

外国交換 60

編 集 用 7

計 1,449

(印刷部数 1,600)

2. 会員数(1967.3.10 現在): 1,343名, ただし1年間会費滞納のため Vol. 17より会誌発送停止になる人数(271名)を含む。

3. バックナンバーの複製: 欠号分についてバックナンバーの注文があった場合は事務局で複製する。

4. 会誌交換: 1967年 Vol. 17 から, 次の出版物との交換をおこなう。

◦Allan Hancock Monograph in Marine Biology.

Published by Univ. of Southern California

◦Micronesia Journal of the College of Guam.

Published by the College of Guam, Guam

◦Kansas Entomological Society. Journal

(Quarterly)

◦Tropical Ecology (Annual). Published by International Society for Tropical Ecology (Prof. Misra, Head of Dept. of Botany, Banaras Hindu Univ., India)

なお、これまでの交換リストの再検討をおこなう。

5. IBPに関する News の生態学会誌の掲載について: Up-to-date な IBP に関する News を学会員に流すことについて, IBP の幹事会にはかって技術的なことを協議してもらい, その結果に従って事務局と連絡の上で主旨に沿うようにする。(この件に関して, 4月18日, IBP 事務局と学会事務局で連絡の結果, 次のように決った。すなわち, IBP に関する News は IBP 事務局と連絡のうえ, 学会記事として掲載するが, 掲載のページは年間予定ページ数(260)外としてとり扱う。)

6. DR. WORTHINGTON 招へいの件: 記事Ⅱ参照

7. 学術会議各種研連・委員会への委員推せん: 学術会議各種研連・委員会へ, 次のように委員を推せんした。

◦動物学研連—加藤陸奥雄

◦自然保護研連—宝月欣二

◦生物科学研究交流センター及び生物研究

所設立準備委員会—北沢右三

◦生物科学将来計画小委員会

—沼田 真・加藤陸奥雄

8. 尾瀬ヶ原保護問題についての声明書作成配布: 1966年度(第13回)大会での決定に基づいて「尾瀬ヶ原ダム築造計画に対する要望書」(吉岡・吉良・鈴木・北沢4氏起草)を, 1966年5月4日関係部局へ発送した。(会誌 Vol. 16, No. 2, p. 87参照)

9. 天然記念物の所在等調査資料: 文部省文化財保護委員会から依頼のあった(1965年5月29日)「天然記念物の所在等調査資料」については, 各地区及び自然保護専門委員からの意見及び資料をまとめて1965年11月25日, 同委員会へ回答したが(会誌 Vol. 15, No. 3, p. 127及び Vol. 16, No. 2, p. 85参照), これらをまとめて「天然記念物の所在等調査資料」として昨年, 文化財保護委員会記念物課により印刷され, 学会へ