

Mathematical models of plant communities

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INTRODUCTION

Proper management by man of the biosphere must be the final aim of the IBP. For this purpose assessment of productivities not only of cultivated lands but also of various plant communities, for instance, forests, grasslands, and phytoplankton in aquatic environment, is of prime importance.

For the assessment of productivity of a plant community during a certain period the three following methods are mainly employed.

1. Determination of the *increments in dry weight of standing crop* of a plant community in a certain time interval. The *growth analysis* which has been actively developed by the British school (e.g., Blackman, 1919; Blackman, 1968; Watson, 1952) is one of the most practical methods in this category. The first phase in the procedure is to estimate accurately the standing crop, and this implies the assessment of underground parts of plants which is quite difficult but important. Later a rough sketch will be given as to new mathematical relations in allometric approaches.

2. Calculation of total photosynthesis of a *mathematical model* of a plant community by combining photosynthetic activities of single leaves and light intensities received by the leaves. The sound mathematical model should always be based on the real *productive structure* of plant communities. In comparison with the integrated productivity in method 1, the value obtained by this method is essentially differential; in general hourly and daily values are obtained, though the production for a month or a year may sometimes be computed.

3. *Aerodynamic determination* of carbon dioxide flux. Production of CO_2 in the soil, consumption of CO_2 in the phyllosphere, and supply of CO_2 from the surrounding air give rise to a special profile of CO_2 distribution in and above a plant community. Aerodynamic analysis

of this distribution of CO_2 permits calculation of the rate of CO_2 consumption by the foliage, i.e., CO_2 assimilation photosynthesis of the plant community as a whole. For this analysis a rapid, precise measurement of CO_2 concentration in the air is necessary, and requires sophisticated techniques and equipments of high accuracy. For the measurement under natural conditions of total photosynthesis of a uniform plant community in a vast area, e.g., of a large rice field or of a forest plantation, this method should be, theoretically, one of the most adequate.

In the present paper attention is focused on method 2, calculation of matter production of the plant community based on mathematical models. Quantitative relationships between growth and photosynthetic activity of the plant will lead to some discussions on the distribution of photosynthates and repetition of matter production, i.e., on a *matter reproduction* model.

PRODUCTIVE STRUCTURE OF A PLANT COMMUNITY

Photosynthesis of a plant community is mainly carried out by the foliage which, owing to its characteristic structure, distributes the impinging light within the community. The total photosynthesis is the sum total of photosynthesis of single leaves, or more accurately of chloroplasts, which are receiving light. The light intensity depends on incident illumination as well as on inclination and position of the leaves in the foliage. The structure of a plant community has considerable influence on the intensity of light received by the photosynthetic leaves, whereas the resulting light distribution in the community can have a decisive bearing on the productive structure of the plant community through matter production and distribution of the products. The concept of productive structure of a plant community comprises distribution of leaves in the plant

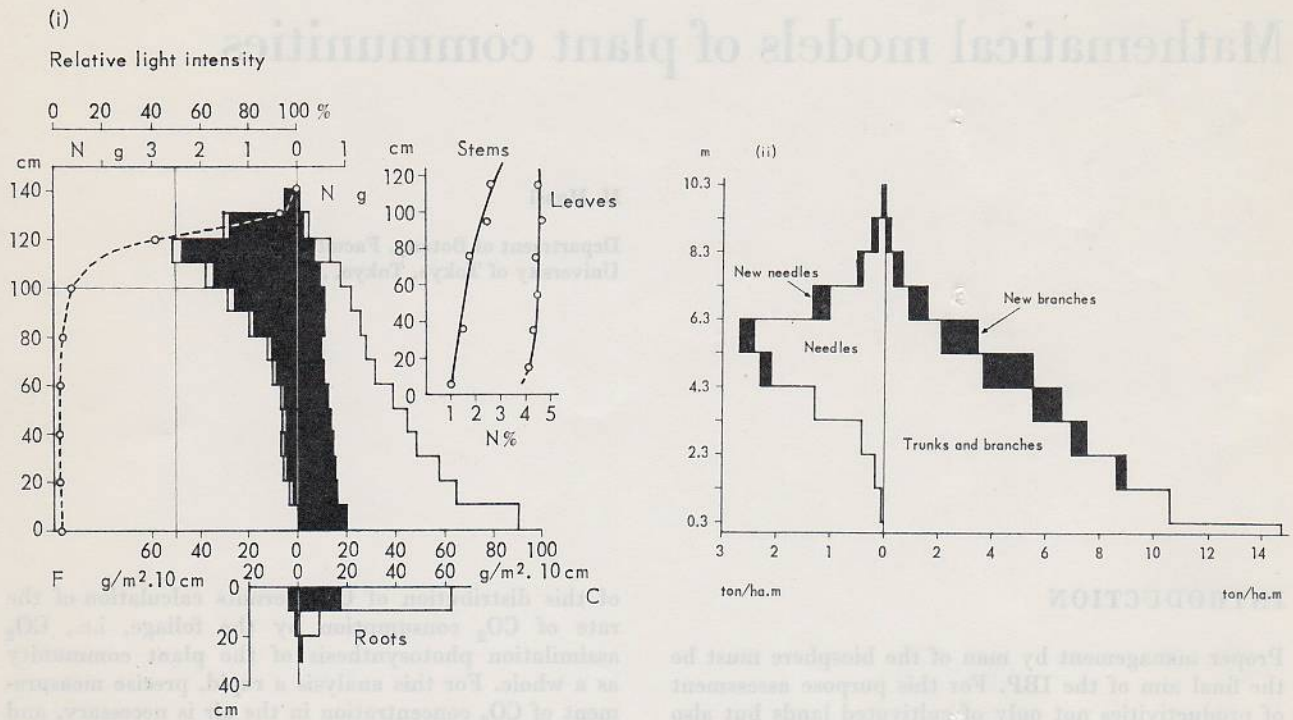


FIG. 1. Productive structures of plant communities. *F*, photosynthetic system; *C*, non-photosynthetic system.

(i) *Amaranthus patulus* community. Shaded area, the amount of nitrogen in plant tissues. Iwaki and Kuroiwa (1963).

(ii) *Picea glehni* forest stand in Hokkaido, northern Japan. *Picea glehni* 89; *Picea jezoensis* 28; and *Abies sachalinensis* 10/100 m². Forest Res. Groups (1960).

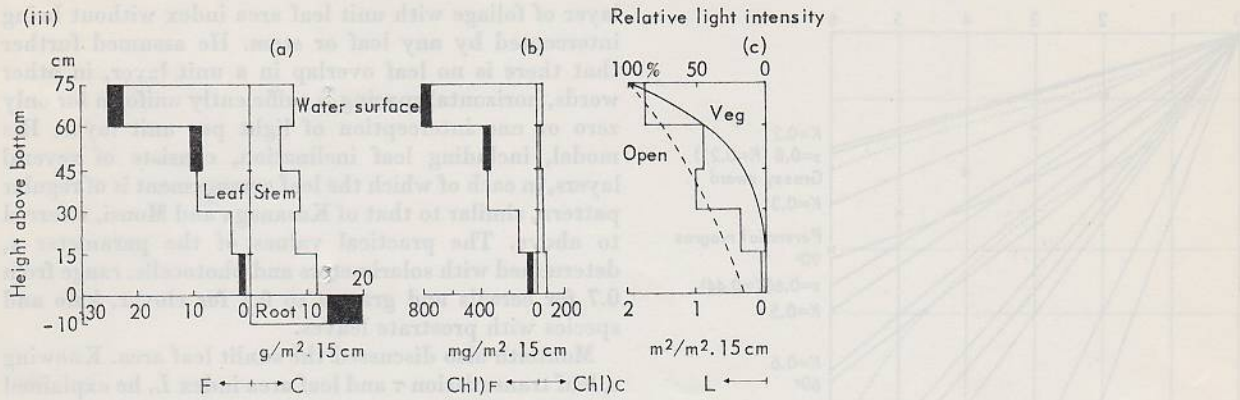
community and micro-environmental factors, such as light intensity, temperature, carbon dioxide concentration, which have decisive influences on photosynthesis. The vertical distribution of plant materials, i.e., profiles of the photosynthetic and non-photosynthetic systems, can be assessed by the stratified clip technique (Monsi and Saeki, 1953).

Although it was generally agreed that low light intensities under the forest canopy could be a limiting factor in the growth of tree seedlings, the light conditions within grassland vegetation remained a rather unattractive topic in the ecology of plant communities until 1953. The light intensity at ground level under the thick foliage of a grassland community is quite low, sometimes less than 1 per cent (Monsi and Saeki, 1953). Through repeated measurements of light intensity at various heights in the plant community under a cloudy sky—thus eliminating wide variations caused by sun flecks—information is obtained about the vertical distribution of mean relative light intensity. The relationship between the light profile and the structure of the plant community can be established only when we know the vertical distribution of plant materials, especially of leaves. After determining the light intensity profile, the plant community is clipped from top to bottom into several strata, for example, every 10 cm,

as was done by Gaird (1945) with a view to estimate the amount of plant material which could be grazed.

The main light absorbers in the plant community are of course leaf laminae. The clipped plant materials are classified into two main systems with respect to matter production: (a) the photosynthetic system—mainly laminae; and (b) the non-photosynthetic system—stems (petioles), flowers, fruits, and roots. This classification is made after determination of the species composition of the plant cover which is very important when discussing interspecific competition (Donald, 1963). In the field, length and fresh weight are generally the easiest parameters to measure. Drying of materials of a whole community is usually difficult. A small number of samples from various parts are selected therefore in order to establish relationships between fresh and dry weight, or between dry weight and leaf area.

Productive structures so far obtained of grassland communities (e.g., Midorikawa, 1959; Monsi and Saeki, 1953), weeds (Iwaki and Kuroiwa, 1963; Iwaki *et al.*, 1964; Kasanaga and Monsi, 1954; Monsi and Saeki, 1953), cultivated stands (Hogetsu *et al.*, 1960), various forests (Forest Res. Groups, 1960), and even of submerged water plants (Ikusima, 1965), have shown specific, although quite similar profiles in spite of wide difference with respect to plant species (Fig. 1).



(iii) *Potamogeton crispus* community, (a) Solid area, winter bud or turion. (b) Chlorophyll. (c) Leaf area, and light profiles in the community (solid line) and in open water (broken line). Ikusima (1965).

MATHEMATICAL MODELS OF PLANT COMMUNITIES

We have already several models which may serve as a basis for the calculation of total photosynthesis of plant communities. The total gross photosynthesis (P_g) of the plant community is the sum total of gross photosynthesis (p) of single leaves belonging to the plant community. Photosynthesis of each leaf is determined from a photosynthesis-light curve representing intensity of photosynthesis of leaves as a function of light received. The light-saturated values of net photosynthesis ($p - r$) of about 60 species measured in our laboratory at 25° C and 0.03 per cent CO_2 fell within a range of 6-26, mostly 10-16 $\text{mg CO}_2/\text{dm}^2/\text{hr}$ (Fig. 2; see also: Monsi, 1962). The vertical distribution of light intensity in the plant community is characteristic of the plant species making up the community, as mentioned above.

One of the simplest models of a photosynthetic plant community is that of Kusanaga and Monsi (1954). The foliage of the plant community consists of a number (N) of leaf-planes. In a leaf-plane there are u leaves (mean leaf area f) per unit land area A , and these are situated perfectly horizontally, without shading each other, and regularly spaced. The total area of leaves in one leaf-plane is uf , and leaf area density D is uf/A . The latter can be deduced from values obtained in horizontally extending branches of various deciduous trees, e.g., from *Zelkova serrata* where it is 0.63 and from *Fagus crenata* where it is 0.79.

In this model the practical profile of the photosynthetic system of a plant community based on results gathered by the stratified clip technique can be obtained by changing the area and number of leaves in a leaf-plane, and the number and distance of leaf-planes.

The light transmitted through a leaf-plane can be given by $I_0[1 - (1 - \tau)D]$, or I_0M , where I_0 is the incident light intensity measured horizontally, τ is the transmission of single leaves, and $M = 1 - (1 - \tau)uf/A$. Concerning the light conditions of leaves, it is assumed that each leaf in a leaf-plane receives an equal intensity of light which is reduced by the leaf-planes above. The light intensity in the foliage is expressed by an equation,

$$I = I_0 M^{N-1} = I_0 \left[1 - (1 - \tau) \frac{uf}{A} \right]^{N-1}. \quad (1)$$

If the reflection of leaves is disregarded, the photosynthetic leaves receive, according to their position in the foliage, light of the same intensity I , since all the leaves are horizontally situated.

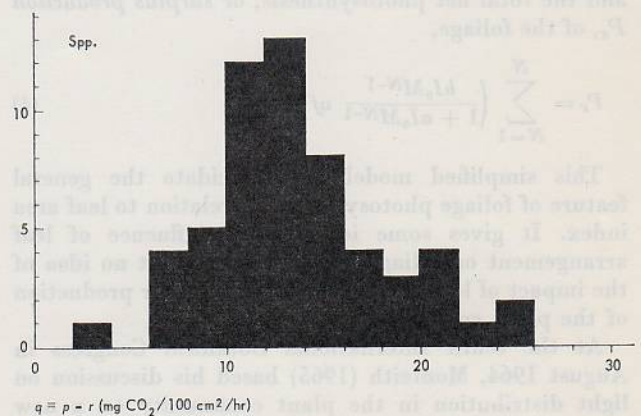


FIG. 2. Frequency distribution of light-saturated net photosynthesis ($q = p - r$) of single leaves of various broad-leaved species. Measured by Boysen Jensen's method, at 25° C and 0.03 per cent CO_2 . Monsi (1962).

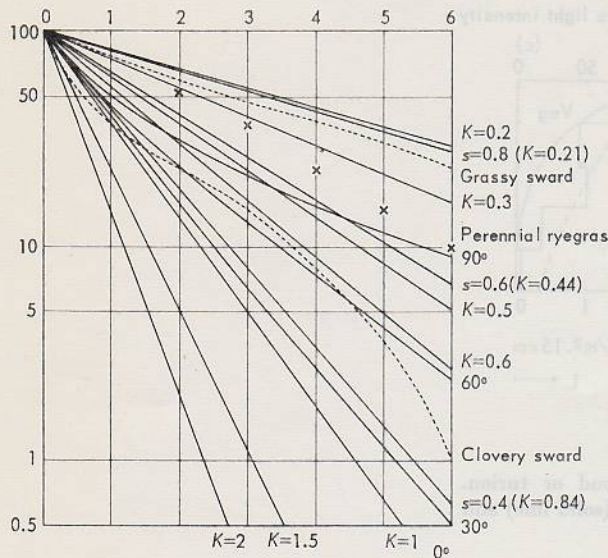


FIG. 3. Relation between leaf area index and light intensity I_h in foliage models. K = extinction coefficient. Lines for parameter s are drawn after Monteith (1965). Perennial ryegrass and cloverly sward, after Brougham (1958). Angles 90° , 60° and 30° indicate leaf inclinations.

Net photosynthesis ($q = p - r$) per unit leaf area is generally expressed by the following equation,

$$q = \frac{bI}{1 + aI} - r, \quad (2)$$

where r indicates respiration per unit leaf area. Substituting the light intensity of equation (1) for I in equation (2), net photosynthesis of the N -th leaf-plane (numbered from the top) becomes

$$qN = \frac{bI_0 M^{N-1}}{1 + aI_0 M^{N-1}} uf - ruf, \quad (3)$$

and the total net photosynthesis, or surplus production P_s , of the foliage,

$$P_s = \sum_{N=1}^N \left(\frac{bI_0 M^{N-1}}{1 + aI_0 M^{N-1}} uf - ruf \right). \quad (4)$$

This simplified model may elucidate the general feature of foliage photosynthesis in relation to leaf area index. It gives some idea of the influence of leaf arrangement on foliage photosynthesis, but no idea of the impact of leaf inclination on dry-matter production of the plant community.

At the tenth International Botanical Congress in August 1964, Monteith (1965) based his discussion on light distribution in the plant community on a new mathematical model which includes leaf inclination. In order to specify average arrangement and orientation of leaves, he adopted a parameter s which is the fraction of incident radiation that passes through a horizontal

layer of foliage with unit leaf area index without being intercepted by any leaf or stem. He assumed further that there is no leaf overlap in a unit layer, in other words, horizontal spacing is sufficiently uniform for only zero or one interception of light per unit layer. His model, including leaf inclination, consists of several layers, in each of which the leaf arrangement is of regular pattern, similar to that of Kusanaga and Monsi, referred to above. The practical values of the parameter s , determined with solarimeters and photocells, range from 0.7 for cereals and grasses to 0.4 for clover, kale and species with prostrate leaves.

Monteith also discussed the sunlit leaf area. Knowing s , leaf transmission τ and leaf area index L , he explained the light distribution, including sunlit leaf area, in a plant community with a binomial expansion of the form $[s + (1 - s)\tau]^L$. If we compare this formula with Monsi and Saeki's equation (1953) for light extinction by leaves in the plant community:

$$I_h = I_0 \exp(-KF) \quad (5)$$

($F = L$, leaf area index; I_h = light intensity horizontally measured in the community), we realize that Monteith's values of s for grasses and species with prostrate leaves roughly correspond to an extinction coefficient K of 0.3 for the grass type and 0.8 for the forb type (Fig. 3).

Monteith calculated the total photosynthesis of a plant community by combining this expansion with two other parameters which describe the shape of the light-response curve of photosynthesis of single leaves. To the photosynthesis-light curve he fitted a rectangular hyperbola, as have many authors (e.g., Davidson and Philip, 1958; Monsi and Saeki, 1953; Tamiya, 1951). Finally, the assumption that the solar radiation varies sinusoidally makes it easy to calculate daily total photosynthesis of the plant community taking into account day-length and intensity of insolation.

With the aid of calculated values of daily total photosynthesis, Monteith made clear the meaning of day-length in dry-matter production. The potential gross photosynthesis in a cloudy temperate climate with long days can be as big as that characterizing a more sunny equatorial climate with short days. He also explained the significance of the parameter s in the photosynthesis of a plant community. When the leaf area index is smaller than 3, photosynthesis increases as the parameter s decreases, namely as leaves become more prostrate. When the leaf area index is greater than 5, photosynthesis increases as the parameter s increases, or as leaves become more erect. He illustrated the variation of gross photosynthesis P with leaf area index L and parameter s at two daily insulations S of 300 and 600 cal. $\text{cm}^{-2}\text{day}^{-1}$. As a result he concluded, as for leaf posture, that differences in leaf arrangement are relatively unimportant in determining maximum (gross) photosynthesis. In his illustration of this problem, however, he was not much concerned with the importance of respiration in

dry-matter production. Assuming that total respiration of the foliage increases rectilinearly with the amount of leaves, we can obtain a new way of expressing net photosynthesis or surplus production P_s (Figure 4). The figure may give a quite different impression than the original of Monteith; it resembles rather the figure from which Saeki (1960) concluded the importance of leaf arrangement and inclination, these being mathematically combined in the extinction coefficient K in equation (5). Such relations can be seen also in the community photosynthesis of rice (Figs. 5 and 6) and sweet potato (Fig. 6). (See also: Murata, 1961; Tsuno and Fujise, 1965).

Foliage models with random leaf arrangement for calculation of plant production were presented by Monsi and Saeki (1953), Davidson and Philip (1958), de Wit (1959), and Saeki (1960). They expressed, in general, a decrease of light intensity in the plant community in accordance with Beer's law, as mentioned in equation (5).

Comparing the vertical distribution of mean relative light intensities (horizontal), measured under cloudy conditions in a plant community, with the profile of the photosynthetic system determined by the stratified clip technique, we recognize two main types of plant communities, grass and forb types, which differ from each other as to light penetration into their foliage. These types were first observed in relation with light intensity and fresh weight of leaves. Giving further consideration to mathematical relationships between distribution of leaf area and interception of light flux by leaves, we can elucidate quite clearly the role of inclination of leaves in the light distribution in the plant community (cf. Fig. 3; see also: Monsi and Saeki, 1953).

If all the leaves are horizontal, opaque, sufficiently small and scattered at random over the land area, the extinction coefficient K is theoretically 1 for a leaf area index unit. Davidson and Philip's (1958) mathematical model for subterranean clover (*Trifolium subterraneum*) is almost identical with this model, since clover could be assumed to have broad leaves of approximately horizontal habit. In another extreme case, assuming that all the leaves have a vertical habit, and provided that other conditions are the same as mentioned above, the degree of attenuation of light intensity under diffuse light condition becomes a half of that in the horizontal-leaf foliage. Although the relation between leaf area index and the logarithm of light intensity is not strictly rectilinear, it may be represented in general by a line corresponding to an extinction coefficient K of about 0.45. Leaf inclinations of 60° and 30° give K values of about 0.65 and 0.90, respectively.

Recently, the change of extinction coefficient with the sun's altitude or with the direction of the light flux was discussed. Isobe (1962) analysed this problem mathematically, adding some observations obtained in paddy fields. Kuroiwa and Monsi (1963) calculated the extinction coefficient from Brougham's data (1958) for

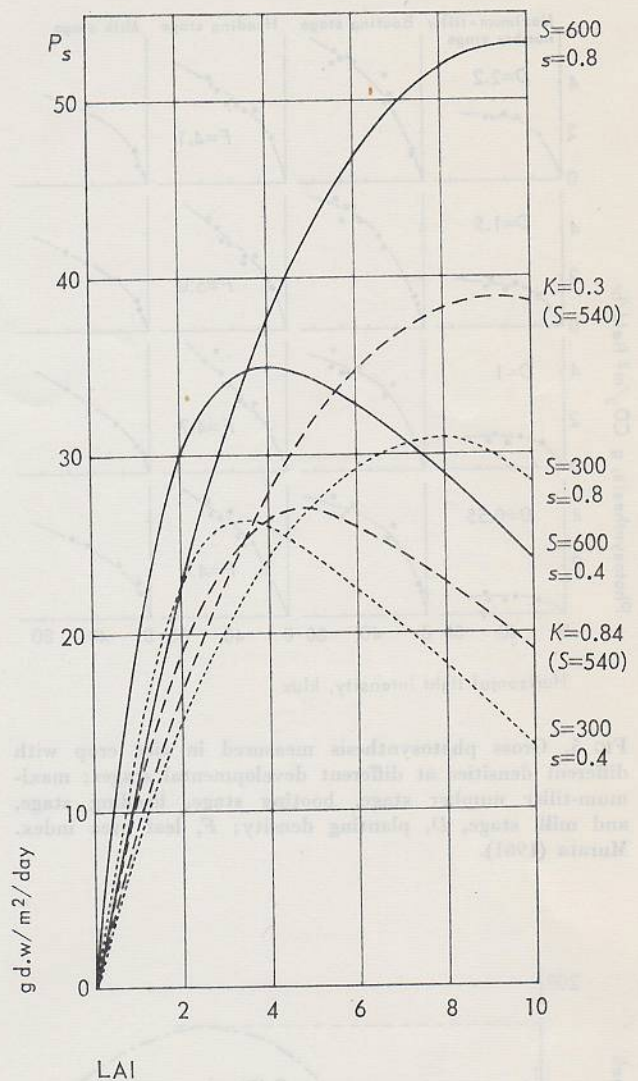


FIG. 4. Relation between leaf area index and surplus production P_s (= gross photosynthesis — respiration of foliage). Continuous lines are the curves illustrated by Monteith (1965) but with subtraction for consumption by foliage respiration ($r = 2.5 L$). Interrupted lines are obtained by calculation with Saeki's equation for *Celosia* (1960). S indicates solar insolation in $\text{cal/cm}^2/\text{day}$. Parameter s of 0.4 and 0.8 corresponds to extinction coefficient K of 0.84 and 0.44, respectively.

white clover (*Trifolium repens*) and perennial rye grass (*Lolium perenne*). At latitude $40^\circ 30' \text{S}$., the calculated K values varied with the sun's altitude within a wide range of about 0.7-1.4 in white clover and about 0.3-0.8 in perennial rye grass.

As for light distribution in the plant community, intensive measurements were carried out by Kumura (1965) and Ito (1965) in soybean and sugar-beet crops, respectively. Their purpose was to clarify the cause of light saturation of community photosynthesis under high light intensity of 40-90 kilolux in cases where

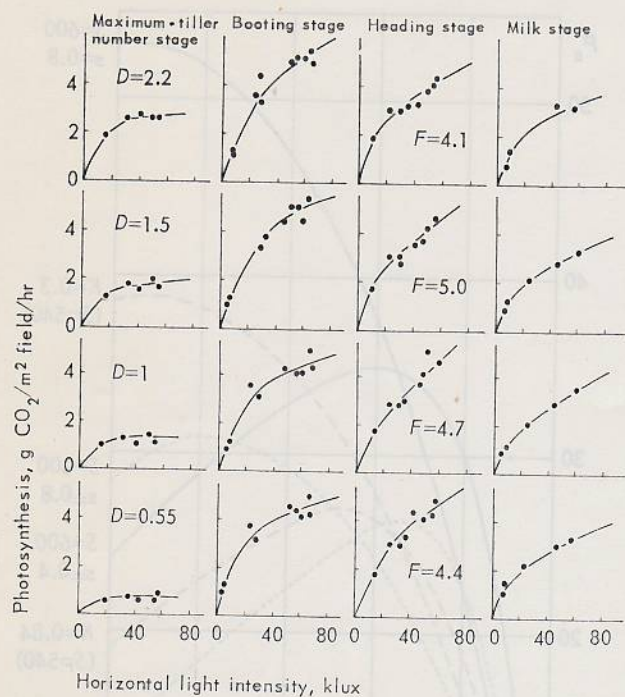


FIG. 5. Gross photosynthesis measured in rice crop with different densities at different developmental stages; maximum-tiller number stage, booting stage, heading stage, and milk stage, D , planting density; F , leaf area index. Murata (1961).

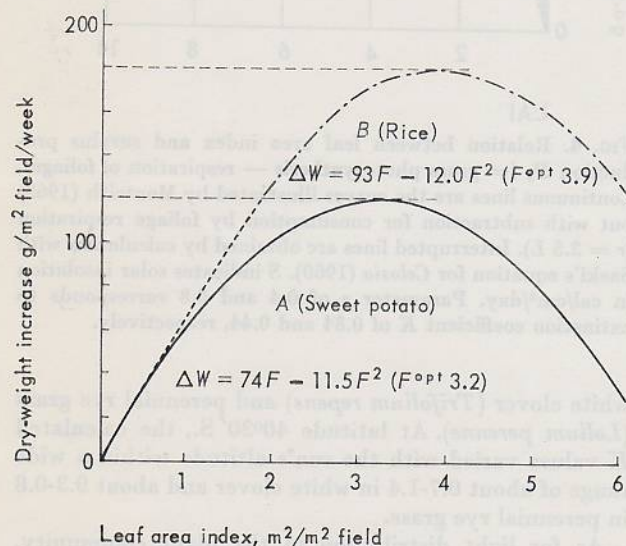


FIG. 6. Relation between dry-weight increase and leaf area index in sweet potato (prostrate leaves) and rice (erect leaves) crops. Both plants are nearly the same in photosynthetic activities of single leaves. Tsuno and Fujise (1965).

theoretically a continued increase of community photosynthesis is to be expected (Fig. 7). They measured illumination on the leaves by means of a photocell exposed to the same light as that received by the leaves. In young crops with low LAI (less than 1), all the leaves received illumination stronger than the saturation light intensity for photosynthesis of single leaves. However, in mature communities with leaf area indices exceeding 3, an increase of solar radiation could result only in an increase of illumination of the already light-saturated leaves situated in the upper part of the foliage, while unsaturated leaves situated in the shade remained practically unaffected (Fig. 8). Such light conditions in the presence of luxuriant plant communities might bring about no further increment in community photosynthesis despite the increase of solar radiation.

Ito (1965) calculated the total net photosynthesis of a sugar-beet stand as the sum total of net photosynthesis of each leaf by using leaf photosynthesis-light curves determined with single leaves in the laboratory and light intensities measured at the leaf surfaces in the field. The community photosynthesis-light curves plotted from calculated values indicated somewhat higher ratios than those obtained from directly measured values in the sugar-beet stand, but there was high similarity in the general trends between the calculated and the observed and it may be expected that the observed values would become somewhat higher with increase of velocity of air flow. Here also Kuroiwa's calculation of foliage photosynthesis under direct sunlight (Kuroiwa, 1968) should be cited.

For the calculation of the *potential photosynthesis* of the plant community under a clear sky, de Wit (1959) used a random-distribution model in which the inclina-

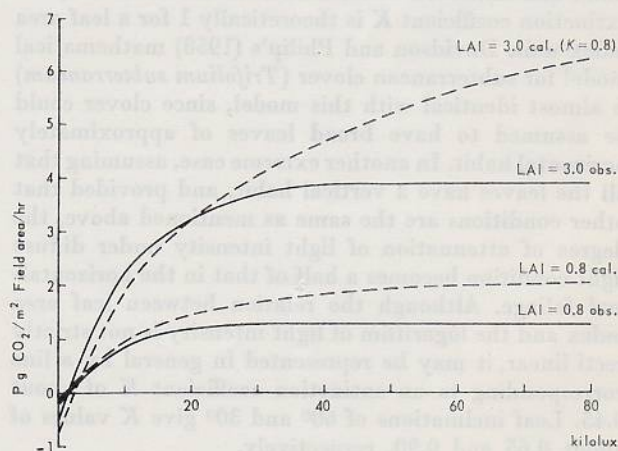


FIG. 7. Net photosynthesis of soybean crop. Thick lines are field observations by Kumura (1965). Broken lines are values calculated by Saeiki's equation (1960) with Kumura's photosynthesis-light curve for single leaves of soybean ($a = 0.125$, $b = 4.05$, $K = 0.8$, $\tau = 0.1$, $\bar{r} = 0.24$).

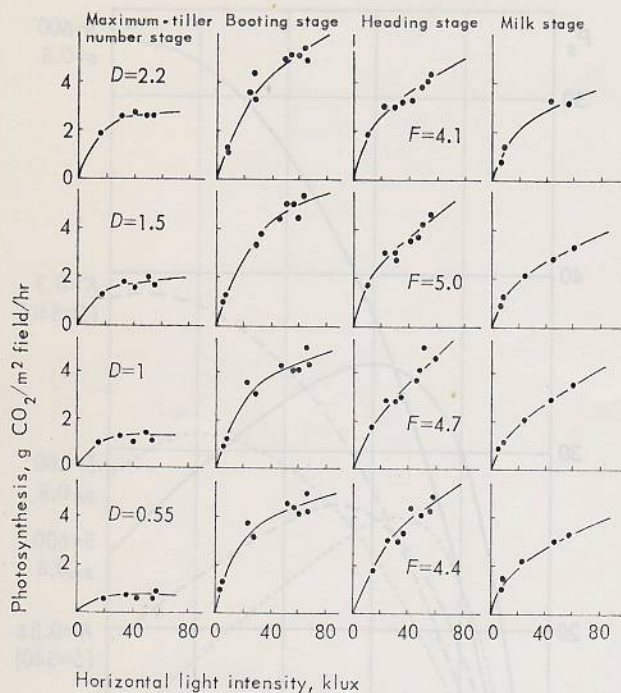


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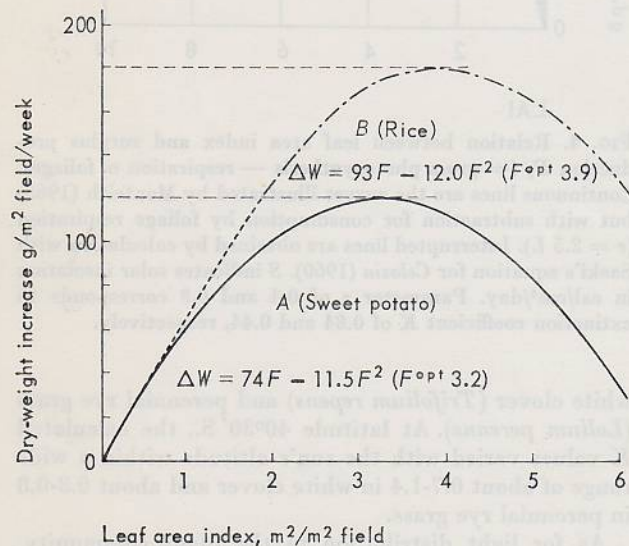


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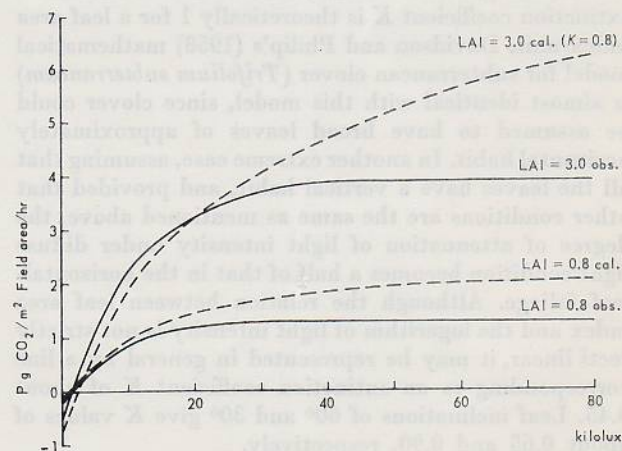


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tion and orientation of leaves are non-preferential. The amount of leaves is assumed to be sufficient to absorb the solar illumination perfectly. As to light conditions he divided the leaf area into a sunlit area and another which receives only diffuse light. Furthermore, the leaf photosynthesis curve (hourly, after Gaastra, 1958) was divided into two straight lines, corresponding to a weak-light part and a light-saturated part. These

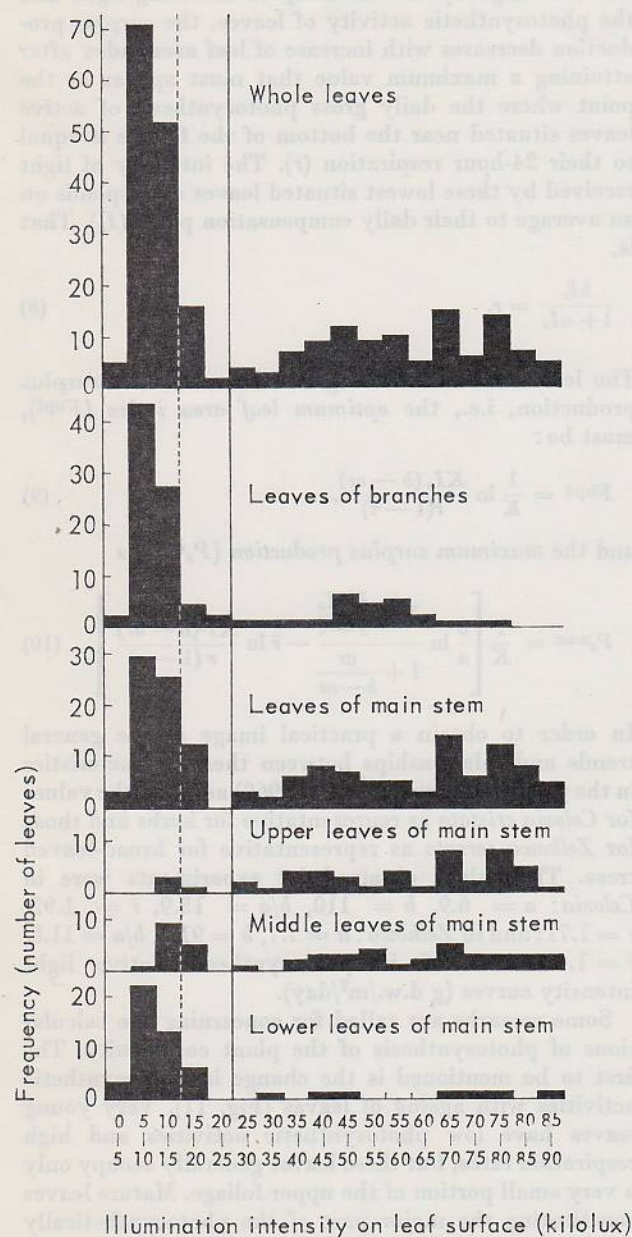


FIG. 8. Frequency distribution of light intensities measured on the leaves in a soybean crop. Incident illumination was 86 kilolux (perpendicular to the sun) and 83 kilolux (horizontal). LAI = 4.3. Kumura (1965).

assumptions might make it easier to calculate the potential photosynthesis at any latitude and in any season.

Although many points remain to be investigated in order to gain precise information about the distribution of light intensity in the plant community under direct solar illumination, results obtained by Kumura (1965) and Ito (1965) give a clear image of the light conditions of each photosynthesizing leaf. The intensity of light effective for photosynthesis in leaves must be considered as equal to that falling on the leaves. The light intensity measured horizontally in the plant community does not indicate the light conditions for photosynthesis until the inclination and arrangement of leaves are taken into account. Mean light intensity received by leaves (I) can be derived with a general equation (Saeki, 1960, 1963) in connexion with the extinction coefficient K and transmission coefficient τ :

$$I = \frac{K}{1-\tau} I_0 \exp(-KF). \quad (6)$$

Daily net photosynthesis or surplus production (P_s) of a leaf community was calculated by Saeki (1960) with the following mathematical model (cf. Fig. 9a, b, c):

$$P_s = \frac{1}{K} \frac{b}{a} \ln \frac{(1-\tau) + KaI_0}{(1-\tau) + KaI_0 \exp(-KF)} - \bar{r}F, \quad (7)$$

where a , b , τ , I_0 , F and K have already been denoted. \bar{r} indicates the mean value of 24-hour respiration of variously aged leaves constituting the foliage (Fig. 10). P_s is equal to the total gross photosynthesis (P_g) of the community minus total respiration of foliage ($R_f = \bar{r}F$). This equation was derived from Monsi and Saeki's (1953) where hourly net photosynthesis in mg CO_2 of the foliage was calculated as a function of light intensity in lux.

The procedure for calculating daily photosynthesis of the community from hourly photosynthesis of single leaves is as follows. Diurnal photosynthesis curves for unit leaf area are drawn by using the photosynthesis-light curve (Fig. 9a) and diurnal illumination (lux) curves which correspond to relative light intensity (Fig. 9b). The area of the diurnal photosynthesis curves gives the daily amount of photosynthesis under given light conditions, from which the daily photosynthesis-relative light intensity curve is constructed (Fig. 9c). The amount of CO_2 is converted into dry matter ($\text{C}_6\text{H}_{10}\text{O}_5$) $_n$ according to results of elementary analysis of *Zea mays* ($\text{C}_6\text{H}_{10.2}\text{O}_{4.6}\text{N}_{0.17}\text{P}_{0.011} \dots$) (Litchaw and Miller, 1924) and of *Medicago sativa* ($\text{C}_6\text{H}_{8.7}\text{O}_{4.1}\text{N}_{0.37}\text{P}_{0.014} \dots$) (Rankana and Sahama, 1950).

Davidson and Philip's (1958) equation for calculation of the daily photosynthesis of subterranean clover is principally the same as Saeki's (1960). However, their formulation does not include an allowance for the intensity of light which is actually received by photosynthetic leaves—in the plant they studied the difference in intensity between incoming light and light

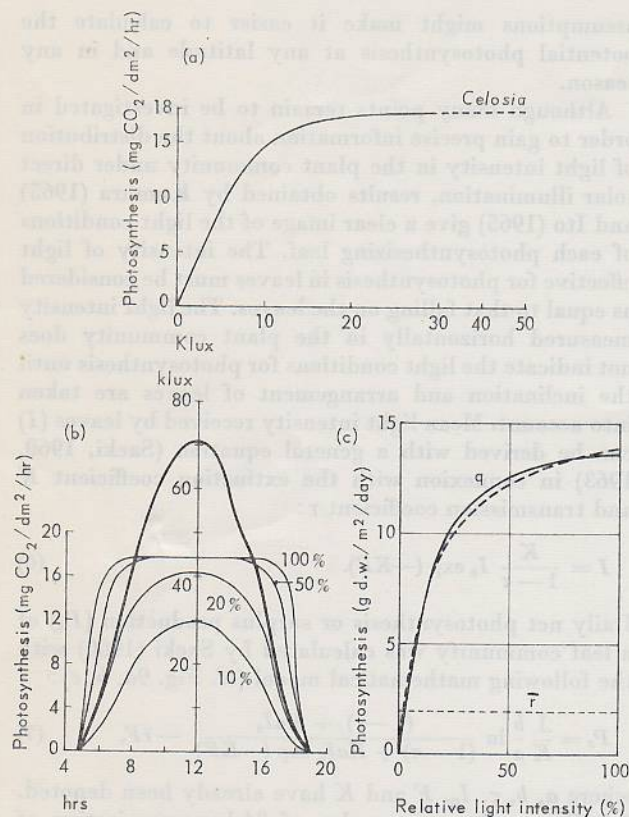


FIG. 9. Procedure of calculation of foliage photosynthesis. After Saeki (1960).

(a) Hourly gross photosynthesis-light curve of single matured leaves of a representative herbaceous plant, *Celosia cristata* (mg CO₂/dm²/hr-lux).

(b) Mean light intensity (horizontal) in the summer season in Tokyo, and diurnal gross photosynthesis curves at light intensities of 100, 50, 20 and 10 per cent.

(c) Daily gross photosynthesis-light curve of the single leaves (g C₆H₁₀O₅/m²/day-rel. light intensity). \bar{r} , mean daily respiration of leaves.

received by leaves must be slight because of the horizontal habit of the *Trifolium* leaves. Neglect of this difference may limit the application of their equation to a plant community with horizontal leaves.

The amount of photosynthates which can be used for the growth of new leaves, new stems, new roots and for grain production, etc., as well as for respiration necessary to maintain the non-photosynthetic systems (R_c), is equal to that of the photosynthates built up by the leaves minus the consumption due to respiration for maintenance of activities of leaves themselves (R_f). This amount of photosynthates, i.e., net photosynthesis of foliage or gross photosynthesis (P_g) minus R_f , is a very important quantity in the growth of the plant. This quantity should be distinguished from the so-called "net production" that is in general use as the term for photosynthetic products which correspond to the

increase of dry matter in the plant. Net production P_n in this paper is defined as $P_n = P_g - R_f - R_c = \Delta W$ (cf. details in dry-matter reproduction), and Monsi (1960) suggested the adoption of a new term, "surplus production P_s ", for photosynthates $P_g - R_f$. Briefly, $P_g = P_s + R_f = P_n + R_c + R_f$.

Since the total respiration of foliage increases in direct proportion to the increase of the leaf area index, and the total gross photosynthesis is limited within a definite range by the intensity of incoming light and the photosynthetic activity of leaves, the surplus production decreases with increase of leaf area index after attaining a maximum value that must appear at the point where the daily gross photosynthesis of active leaves situated near the bottom of the foliage is equal to their 24-hour respiration (r). The intensity of light received by these lowest situated leaves corresponds on an average to their daily compensation point (I_c). That is,

$$\frac{bI_c}{1 + aI_c} = r. \quad (8)$$

The leaf area index that gives the maximum surplus production, i.e., the optimum leaf area index (F^{opt}), must be:

$$F^{\text{opt}} = \frac{1}{K} \ln \frac{KI_0(b - ar)}{r(1 - \tau)}, \quad (9)$$

and the maximum surplus production (P_s^{max}) is

$$P_s^{\text{max}} = \frac{1}{K} \left[\frac{b}{a} \ln \frac{1 + \frac{KaI_0}{1 - \tau}}{1 + \frac{ar}{b - ar}} - \bar{r} \ln \frac{KI_0(b - ar)}{r(1 - \tau)} \right]. \quad (10)$$

In order to obtain a practical image of the general trends and relationships between these characteristics in the plant community, Saeki (1960) adopted the values for *Celosia cristata* as representative for herbs and those for *Zelkova serrata* as representative for broad-leaved trees. The values obtained by experiments were in *Celosia*: $a = 6.9$, $b = 110$, $b/a = 15.9$, $\bar{r} = 1.92$, $r = 1.71$; and in *Zelkova*: $a = 7.7$, $b = 91.2$, $b/a = 11.8$, $\bar{r} = 1.47$, $r = 0.88$ in photosynthesis-relative light intensity curves (g d.w./m²/day).

Some remarks are called for concerning the calculations of photosynthesis of the plant community. The first to be mentioned is the change in photosynthetic activities with ageing of leaves (Fig. 11). Very young leaves have low photosynthetic activities and high respiration rates, but these leaves generally occupy only a very small portion of the upper foliage. Mature leaves constituting the major part of the photosynthetically active foliage have equally high photosynthetic activities. Old leaves show a photosynthetic behaviour which is changed into a shade-leaf type behaviour with a depressed light-saturated photosynthesis. Sometimes such changes should be considered in the calculation of

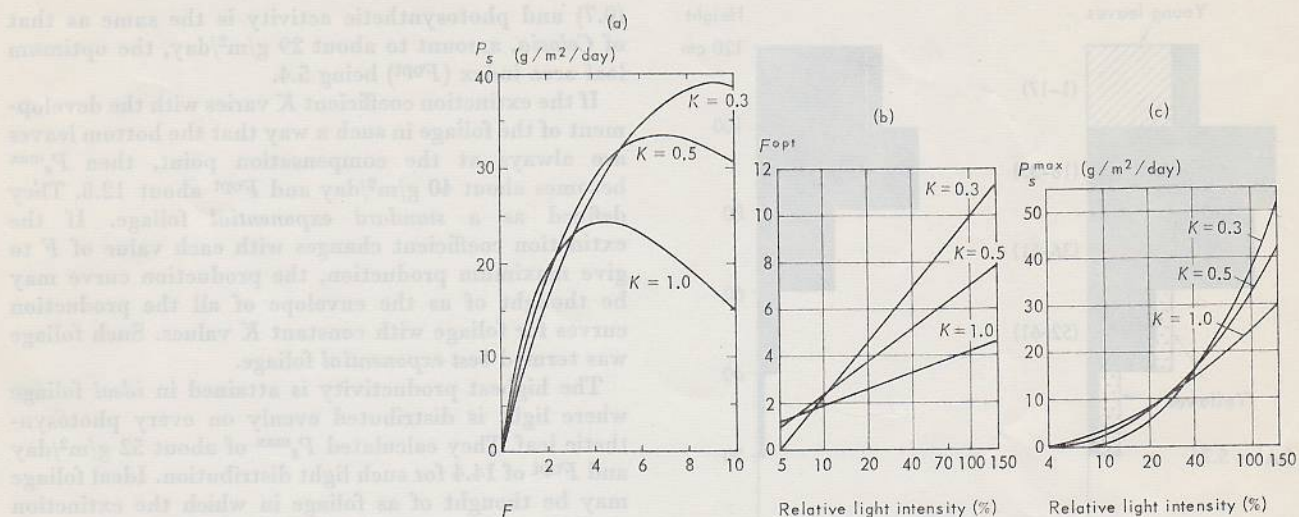


FIG. 10. Relationships between relative light intensity, leaf area index F , extinction coefficient K , and surplus production P_s . After Saeki (1960).

(a) P_s , calculated with three K 's 0.3, 0.5 and 1.0, and F . 100 per cent light = ca. 540 cal/cm²/day.

(b) Optimum leaf area index F^{opt} and relative light intensity (logarithmic).

(c) Maximum surplus production P_s^{max} and relative light intensity (logarithmic).

total photosynthesis of the plant community, but in general these differences can be neglected because young leaves have small undeveloped laminae and old leaves situated in the lower layer of foliage are exposed to low illumination (Fig. 12). Total photosynthesis calculated by taking into account the mean photosynthetic activity of mature leaves only, is accurate enough, compared with that obtained after correcting for leaf ageing (Iwaki *et al.*, 1965).

From equation (9) it is clear that the optimum leaf area index is in a rectilinear relationship with the logarithm of the light intensity. Hiroi and Monsi (1966) performed an experiment to follow the development of the leaf area index of *Helianthus annuus* communities planted in three densities, 25, 100 and 400 plants/m², and at three relative light intensities, 100, 60 and 23 per cent (Fig. 13). Natural and semi-natural plant communities which were matured under various light intensities were also studied with respect to their leaf area indices (Fig. 14). From the results obtained, it may be concluded, though very roughly, that the leaf area index of the mature plant community increases in general rectilinearly with the logarithm of the relative light intensity prevailing above the community. Furthermore, Figure 15 indicates striking similarities between the growth curve calculated with equation (10) and those observed in the *Helianthus* communities, this fact proving a general applicability of the equation to the calculation of foliage photosynthesis.

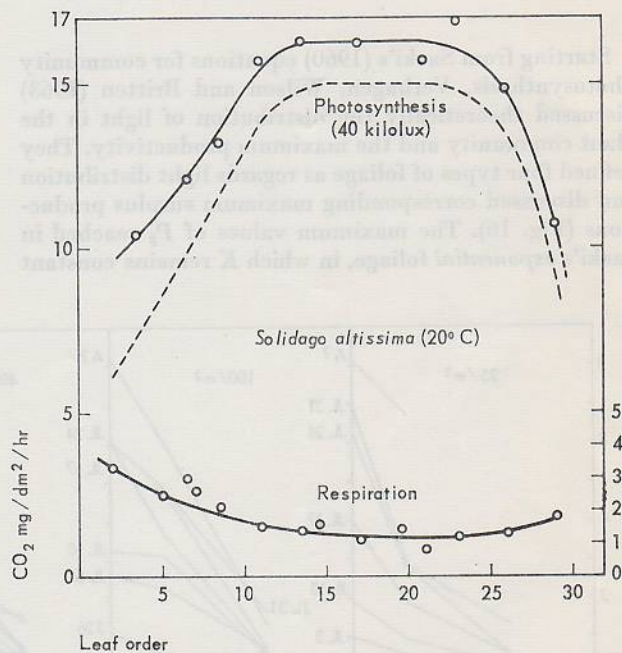


FIG. 11. Changes of photosynthetic and respiratory activities with ageing of leaves in *Solidago altissima*. Leaf order from top to bottom. Photosynthesis: the solid line shows gross photosynthesis, and the broken line net photosynthesis. Measured with URAS gas analyser in late May 1964. Iwaki, Nakajima and Monsi (1964).

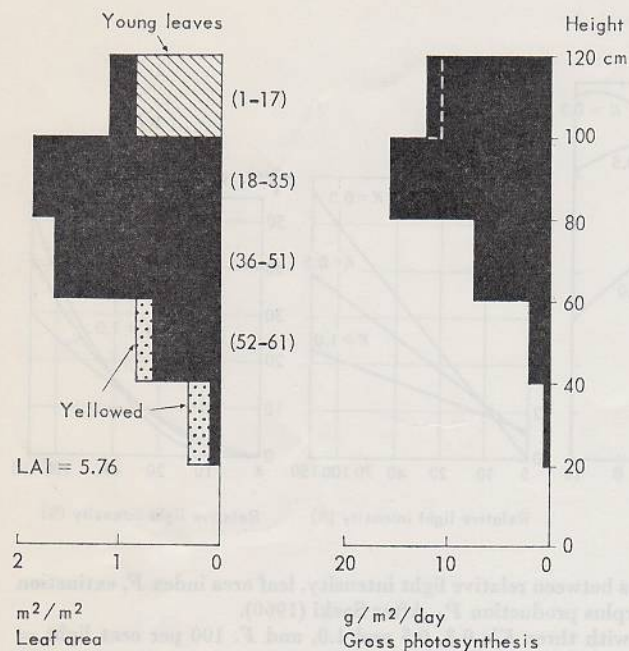


FIG. 12. Vertical distribution of leaf area and of gross productivity in a *Solidago altissima* community. Productivity corrected as to low photosynthetic activities of young leaves is shown by a broken line at a height of 100-120 cm. July 1964. (1-17), etc., leaf order. Iwaki, Nakajima and Monsi (1964).

Starting from Saeki's (1960) equations for community photosynthesis, Verhagen, Wilson and Britten (1963) discussed theoretically the distribution of light in the plant community and the maximum productivity. They defined four types of foliage as regards light distribution and discussed corresponding maximum surplus productions (Fig. 16). The maximum values of P_s reached in Saeki's *exponential* foliage, in which K remains constant

(0.7) and photosynthetic activity is the same as that of *Celosia*, amount to about 29 g/m²/day, the optimum leaf area index (F^{opt}) being 5.4.

If the extinction coefficient K varies with the development of the foliage in such a way that the bottom leaves are always at the compensation point, then P_s^{max} becomes about 40 g/m²/day and F^{opt} about 12.8. They defined as a *standard exponential* foliage. If the extinction coefficient changes with each value of F to give maximum production, the production curve may be thought of as the envelope of all the production curves for foliage with constant K values. Such foliage was termed *best exponential* foliage.

The highest productivity is attained in *ideal* foliage where light is distributed evenly on every photosynthetic leaf. They calculated P_s^{max} of about 52 g/m²/day and F^{opt} of 14.4 for such light distribution. Ideal foliage may be thought of as foliage in which the extinction coefficient K changes with depth in the foliage (K would be small near the surface of the foliage and would increase as the amount of light available falls off with increasing depth). The light intensity, and not its logarithm, in the foliage decreases rectilinearly with increase of leaf area index.

Does such an ideal foliage exist in practice? Most of the models so far used for calculation of foliage photosynthesis have leaves distributed in general uniformly or randomly. In reality, however, leaves together with a stem make up a shoot. The extinction coefficient K in the presence of vertical leaves should theoretically be about 0.45 under diffuse light conditions, as discussed already, but K values of 0.3 or less have been observed for instance in many grass communities (Fig. 3 and cf. Monsi and Saeki, 1953). This discrepancy may suggest the existence of some clusters of leaves in the foliage.

On the basis of such properties of plants, Saeki, Iwaki and Monsi (1965) proposed a cluster model. The cluster is represented by a square pillar of aggregated leaves,

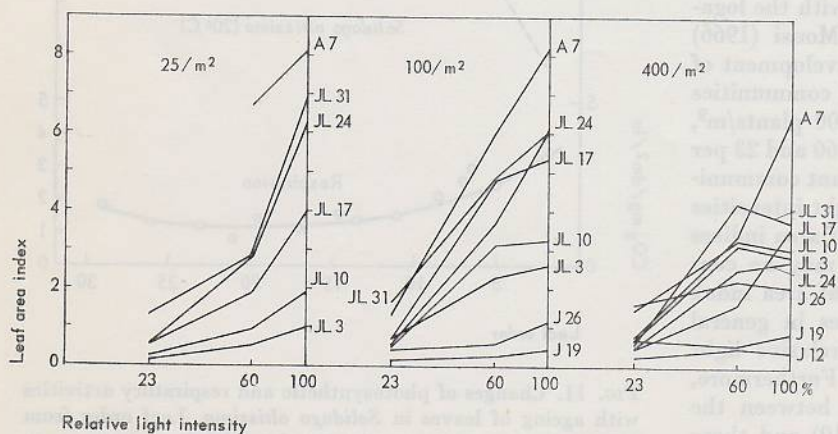


FIG. 13. Development of leaf area index in *Helianthus annuus* communities grown at three densities, 25, 100 and 400 plants/m², and under three light conditions, 23, 60 and 100 per cent light, controlled with reed screens. Hiroi and Monsi (1966).

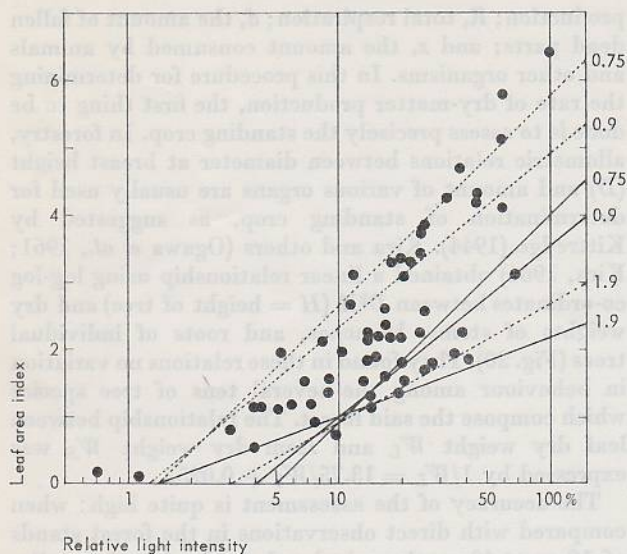


FIG. 14. Leaf area indices of natural and semi-natural plant communities grown under various light conditions. Thick lines correspond to the leaf area index calculated by Saeki's equation (1960) by using photosynthetic curve of a sun plant, the dotted lines using that of a shade plant. The numbers on lines are values of extinction coefficient. In autumn in Tokyo. Hiroi and Monsi (1966).

and such clusters are distributed regularly on a horizontal plane (Fig. 17). Light intensity is attenuated much faster inside a cluster of leaves than in foliage in which leaves are uniformly distributed, but the clusters allow more light to pass than leaves in uniform or random models with the same leaf area index. In the case of illumination attenuated by a group of clusters, leaves at the lower layer of the plant community model are distributed at random or homogeneously with a leaf inclination of 45° ; below this layer the leaves have a horizontal habit. The attenuation of light intensity in this foliage model is illustrated in Figure 18. A typical example of such cluster models can be seen in some of the mulberry fields of Japan.

In a plant community with combined cluster and homogeneous foliage (Fig. 18), light penetrates nearly as in the ideal foliage of Verhagen *et al.* (1963). Iwaki made observations of light intensity profiles in *Solidago altissima* communities (*S. altissima* is a tall weed now widely distributed in Japan) (Saeki *et al.*, 1965). There it was found that the light intensity measured with horizontal photocells decreased rectilinearly with increase of the leaf area index (Fig. 19). In strong illumination, the leaves in the clusters, even those in the innermost part of the vegetation, can keep their photosynthesis at a high level, at the same time as they permit considerable amounts of light to pass through to the leaves in the lower layer. These cluster models, as already suggested by many authors, may explain the high productivity of forests, especially of tropical rain

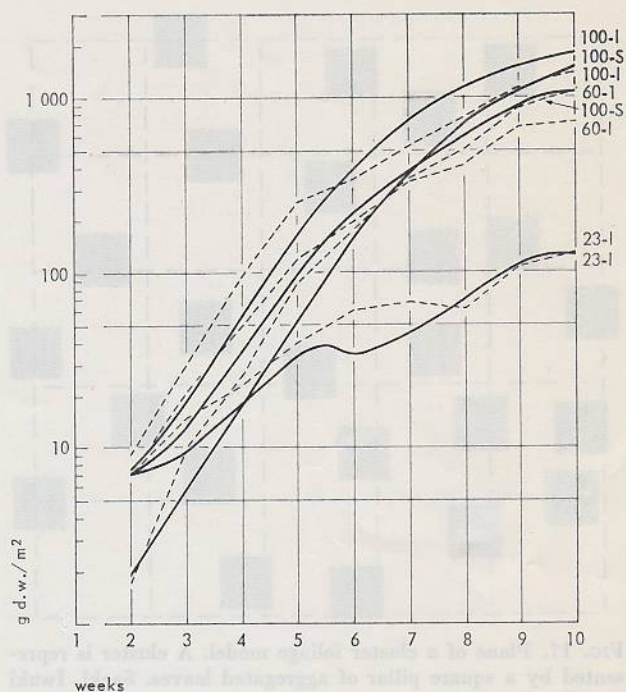


FIG. 15. Growth of *Helianthus annuus* communities. Solid lines, the observed values. Broken lines, those calculated by Saeki's equation for photosynthesis of foliage (1960) using light intensities, photosynthetic activities and transmission measured in the single leaves of the *Helianthus* plants, and extinction coefficient of the communities. 100-I = 100 per cent light and 100 plants/m². 60-I = 60 per cent light and 100 plants/m². 23-I = 23 per cent light and 100 plants/m². 100-S = 100 per cent light and 25 plants/m². Hiroi and Monsi (1966).

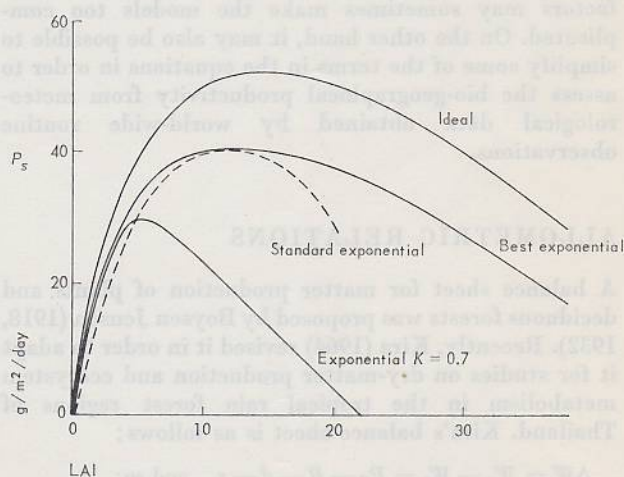


FIG. 16. Surplus production P_s from various types (exponential, standard exponential, best exponential, and ideal) of foliage as a function of leaf area index. Constants for photosynthesis are the same as for *Celosia* in Saeki (1960). After Verhagen, Wilson and Britten (1963).

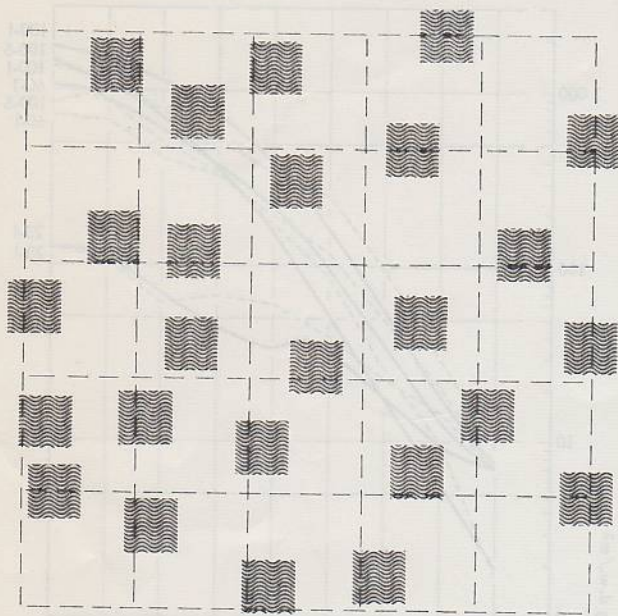


FIG. 17. Plane of a cluster foliage model. A cluster is represented by a square pillar of aggregated leaves. Saeki, Iwaki and Monsi (1965).

forests, where tall tree crowns emerge from the forest canopy.

In the near future, besides the light factors, distribution of CO₂ (cf. aerodynamic works), vertical difference as well as diurnal and seasonal changes of temperature (e.g., Nomoto, 1964), water potential, (e.g., Totsuka, 1963), etc., must be included in mathematical models if these are used as a basis for an exact calculation of plant productivity, although the inclusion of these factors may sometimes make the models too complicated. On the other hand, it may also be possible to simplify some of the terms in the equations in order to assess the bio-geographical productivity from meteorological data obtained by world-wide routine observations.

ALLOMETRIC RELATIONS

A balance sheet for matter production of plants and deciduous forests was proposed by Boysen Jensen (1918, 1932). Recently, Kira (1964) revised it in order to adapt it for studies on dry-matter production and ecosystem metabolism in the tropical rain forest regions of Thailand. Kira's balance sheet is as follows:

$$\Delta W = W_2 - W_1 = P_g - R - d - z, \text{ and so:}$$

$$P_g = \Delta W + R + d + z,$$

where ΔW indicates an increase of the standing crop, or dry-matter production, in a period from t_1 to t_2 ; W_1 and W_2 , the standing crops at t_1 and t_2 ; P_g , gross

production; R , total respiration; d , the amount of fallen dead parts; and z , the amount consumed by animals and other organisms. In this procedure for determining the rate of dry-matter production, the first thing to be done is to assess precisely the standing crop. In forestry, allometric relations between diameter at breast height (D) and amount of various organs are usually used for determination of standing crop, as suggested by Kittredge (1944). Kira and others (Ogawa *et al.*, 1961; Kira, 1964) obtained a linear relationship using log-log co-ordinates between D^2H (H = height of tree) and dry weights of stems, branches, and roots of individual trees (Fig. 20). They found in these relations no variation in behaviour among the several tens of tree species which compose the said forest. The relationship between leaf dry weight W_L and stem dry weight W_S was expressed by $1/W_L = 13.75/W_S + 0.025$.

The accuracy of the assessment is quite high: when compared with direct observations in the forest stands of 10 m x 40 m, the calculated results based on allometric relations were smaller, with respect to dry weight of leaves, by 4.9 per cent, of stems 4.7 per cent, of

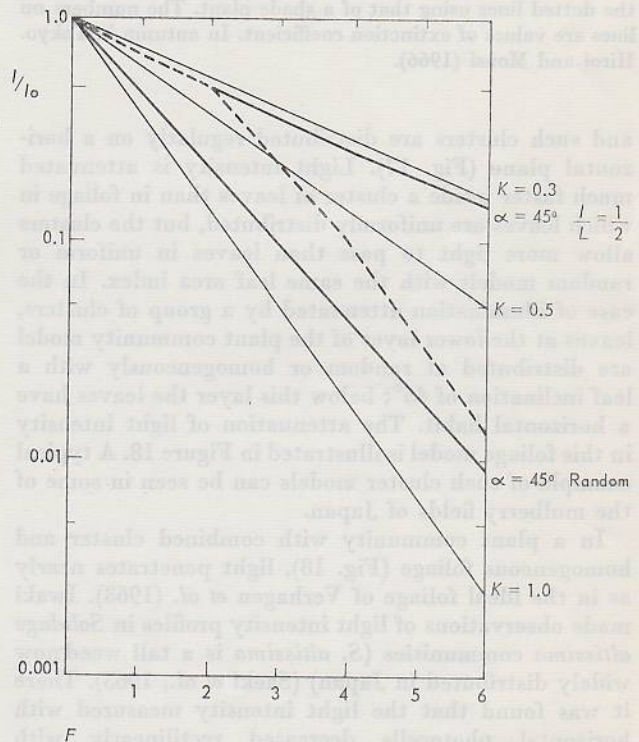


FIG. 18. Light intensity attenuation (thick broken line) with increase of leaf area index F in a cluster-homogeneous foliage model with three leaf arrangements. Saeki, Iwaki and Monsi (1965).

Leaf area index	Leaf angle	Distribution of leaves
0-2	45°	Cluster
2-4	45°	Random
4-6	0°	Random

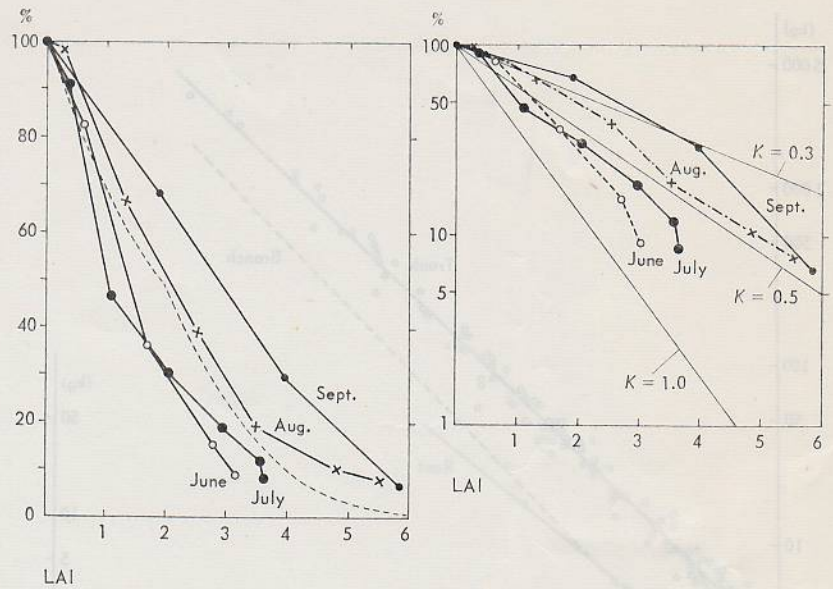


FIG. 19. Light intensity attenuation with increase of leaf area index in *Solidago altissima* communities. Thin broken line in the left figure indicates the light intensity in the cluster-homogeneous foliage model in Figure 18. Saeki, Iwaki and Monsi (1965).

branches 10.3 per cent, and of total above-ground parts, including lianas, only 0.25 per cent. Mean leaf area index of these forest stands was 12.3, and total gross production, 7,740 ton/km²/year; total respiration, 4,890 ton/km²/year; net production, 2,850 ton/km²/year, including dead leaves of 1,100 ton/km²/year, and dead branches of 1,150 ton/km²/year. The growth (ΔW) in standing crop of this climax rain forest was determined to be only 310 ton/km²/year.

DRY-MATTER REPRODUCTION

Growth of plants is regulated not only by the rate of photosynthesis but also by the rate of development of each organ, as well as by the ratio of distribution of assimilates into the non-photosynthetic and the photosynthetic systems (see C/F ratio, Iwaki, 1958). Such repetition of dry-matter production and development of organs constitutes the general process of dry-matter reproduction (Monsi, 1960). We can recognize several types in dry-matter production of various life forms as discussed in detail by Monsi (1960) and Walter (1964). In the present paper the growth of plants will be analysed as a dry-matter reproduction process with one of the most simplified schemata (Fig. 21).

In Figure 21 $(p)(F) = P_g$ means gross production, which is a function of productivity of single leaves and amount of leaves as discussed already. P_s , surplus production, is $P_g - R_f = (p - r_f)(F) = (q)(F)$. P_n , foliage net production, is $P_g - R_f - R_c = (q)(F) - rC$.

The symbol k is a transformation factor (Monsi, 1960) or economy ratio (Midorikawa, 1959), and it is in a range of 0.5-0.8 (Hiroi and Monsi, 1964; Hogetsu *et al.*, 1960; Midorikawa, 1959).

The increment (ΔW) of plant weight in a production term (t) is:

$$\begin{aligned} W_2 - W_1 &= (F_2 - F_1) + (C_2 - C_1) \\ &= \Delta F_a + \Delta C_a = (\Delta F - F_d) + (\Delta C - C_d), \end{aligned}$$

where ΔF_a and ΔC_a indicate apparent (or net) increment of each system (Hiroi and Monsi, 1964). Furthermore,

$$\Delta W = [(p)(F) - r_f F - rC]k - (F_d + C_d), \quad \text{and}$$

$$\begin{aligned} P_g = (p)(F) &= \left[\Delta F + \frac{\Delta F}{k} (1 - k) + r_f F \right] + \\ &+ \left[\Delta C + \frac{\Delta C}{k} (1 - k) + rC \right]. \end{aligned}$$

These equations indicate that gross production P_g is distributed for construction of new photosynthetic and non-photosynthetic systems (ΔF and ΔC) including constructive respiration

$$\left[{}_c R_f = \frac{\Delta F}{k} (1 - k), \quad \text{and} \quad {}_c R_c = \frac{\Delta C}{k} (1 - k) \right],$$

and maintenance respiration (${}_m R_f = r_f F$, and ${}_m R_c = rC$) of each system (Fig. 22). Practically, however, in growth analysis the amount of tissues newly built up can be determined from the sum total in dry weight of apparent increment and dead parts ($\Delta F = \Delta F_a + F_d$ and $\Delta C = \Delta C_a + C_d$).

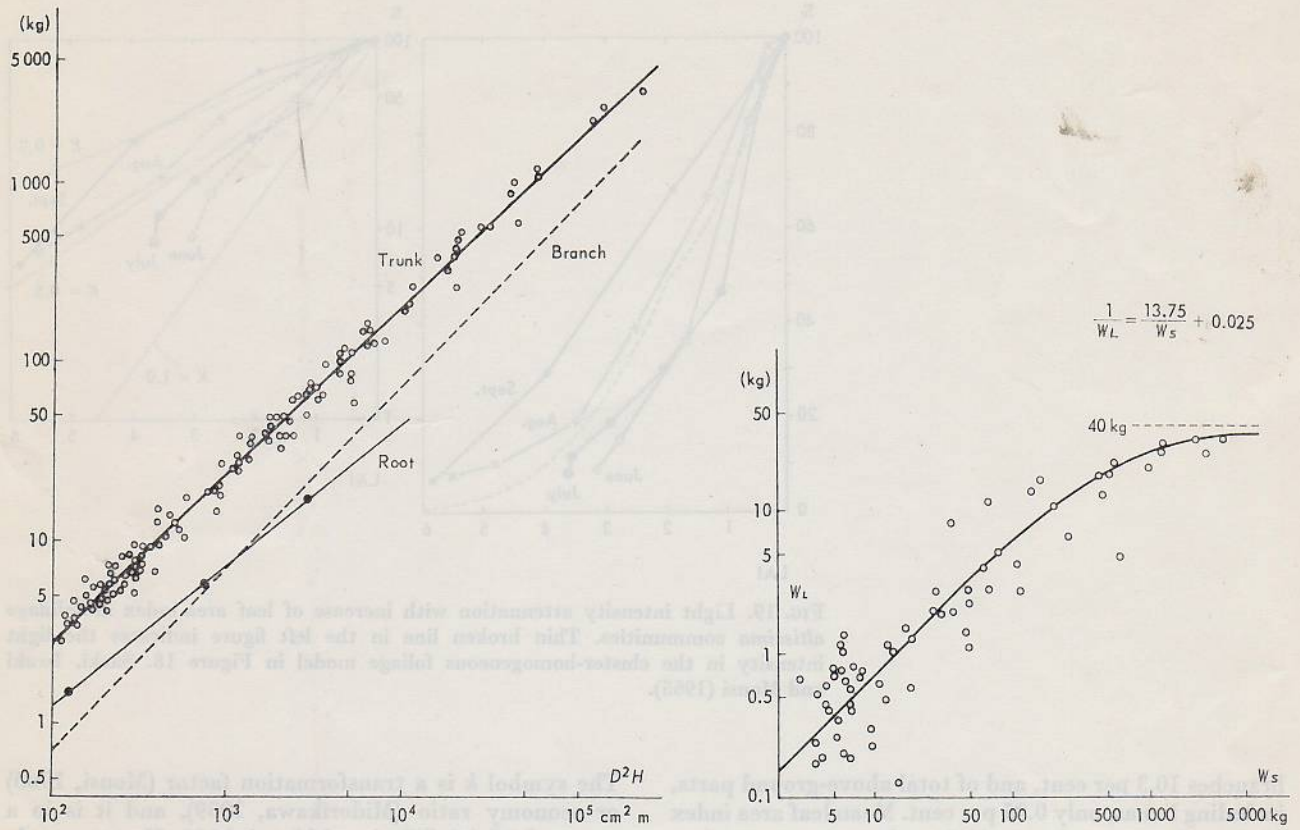


FIG. 20. Allometric relationships between D^2H ($dbh^2 \times$ tree height) and dry weight of stems, branches, and roots of individual trees in a tropical rain forest in Thailand. W_L , dry weight of leaves; W_S , dry weight of stem. Kira (1964).

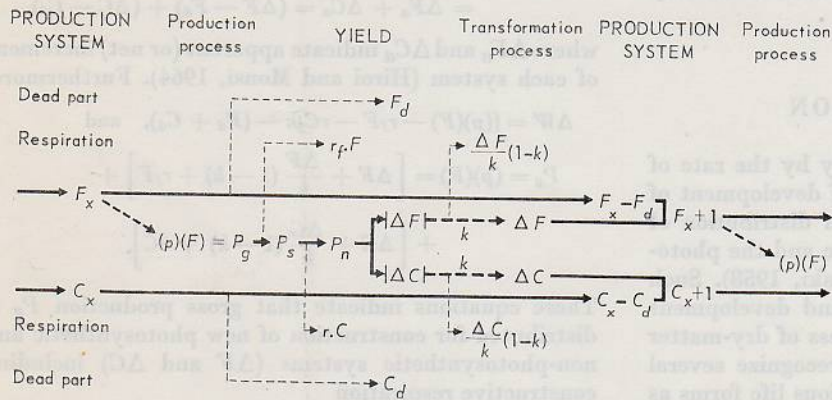


FIG. 21. A simplified schema of dry-matter reproduction. F , photosynthetic system; C , non-photosynthetic system. ΔF and ΔC , newly constructed systems; ΔF_d and ΔC_d , apparent increments ($= \Delta F - F_d$ and $\Delta C - C_d$, where F_d and C_d are the dead parts). P_g , gross production; P_s , surplus production; P_n , net production. r_f and r_c , respiration rate of unit amount of F and C . k , transformation factor.

Plant growth based on the photosynthetic activity of the foliage has been discussed extensively by Davidson and Philip (1958). In the present paper, growth will be discussed in a rather simple way in order to elucidate growth analytically in other words, the internal mechanism of growth as a function of different characteristics of the plant. If the transformation factor (k), distribution ratio ($n/m = \Delta C/\Delta F$, and $n + m = 1$), and photosynthetic and respiration capacities of the photosynthetic and non-photosynthetic systems remain constant, the following equations can be fitted to the plant growth, though actually these values, especially photosynthetic capacities in a plant community, change in general with development of the plant and plant community.

$$\begin{aligned}
 F_1 &= F_0 + kmP_n = F_0 + km(qF_0 - rC_0) = \\
 &= F_0 + km \left(qF_0 - \frac{n}{m} rF_0 \right) = F_0 [1 + k(mq - nr)] = \\
 &= F_0(1 + g), \text{ where } g = k(mq - nr), \\
 F_2 &= F_1(1 + g) = F_0(1 + g)^2, \\
 &\dots\dots\dots \\
 F_x &= F_0(1 + g)^x. \\
 C_x &= C_0(1 + g)^x = \frac{n}{m} F_0(1 + g)^x. \\
 W_x &= F_x + C_x = W_0(1 + g)^x = \frac{1}{m} F_0(1 + g)^x.
 \end{aligned}$$

If the turnover number increases infinitely and growth continues without interruption, we can introduce an

equation which corresponds to Blackman's compound interest law (Blackman, 1919).

$$W_x = W_0 e^{gx} = W_0 e^{k(mq-nr)x}.$$

Substituting proper values for the factors in these equations, we obtain growth curves for plants (Figs. 23 and 24). The importance of high photosynthetic activity in leaves for plant growth is very clearly shown in Figure 23. For instance, if $p = 20$ and 50 (g dry matter/g.d.w. of F /year), and $C/F = \Delta C/\Delta F = n/m = 0.7/0.3$, the plant dry weight after three production periods (years) reaches 7.5 and 400 (g), respectively. The ecophysiological meaning of the C/F ratio for rate of growth can also be demonstrated by changing m and n , and keeping the other factors constant (Fig. 24). For instance, if $p = 20$, and $C/F = 0.7/0.3$ and $0.3/0.7$, the plant dry weight after three production periods is 7.5 and 115 respectively. An example illustrating the importance of the turnover number or the value of the production term (here $t = 1/2$) is also given in Figure 23.

The compound-interest law equations cannot be accurately applied to the growth of deciduous plants, even provided no depression of photosynthesis occurs in leaves of the plants (see Figs. 23 and 24). Replacement of the photosynthetic system after every production term retards the growth of deciduous plants. In other words, the interest diminishes with growth of the plants (depression of efficiency index, Blackman, 1919). The replacement of the photosynthetic system has such a strong effect, especially when photosynthetic activity

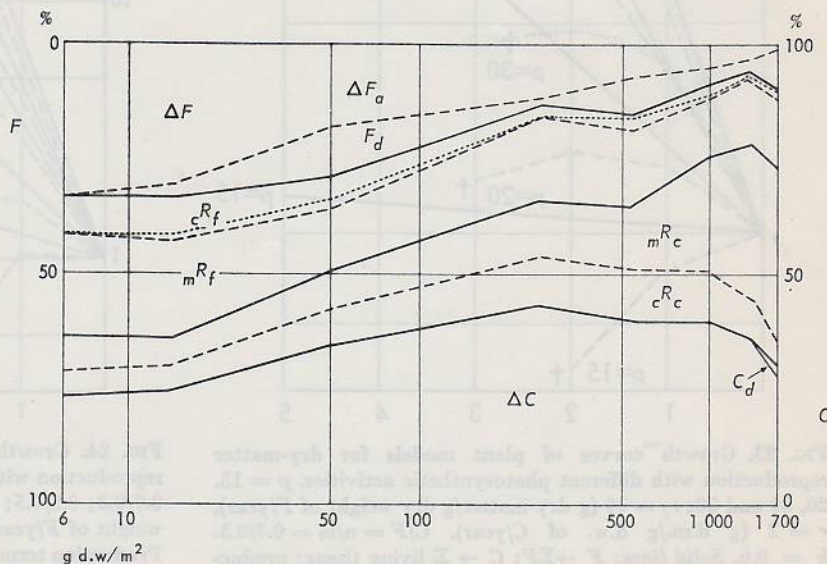


FIG. 22. Distribution ratio of gross production in a *Helianthus annuus* community (100 per cent light and 100 plants/m²). Abscissa, g dry weight of the community. cR_f and cR_c , constructive respiration of photosynthetic and non-photosynthetic systems. mR_f and mR_c , maintenance respiration of both systems. Others in Figure 21. Hiroi and Monsi (1966).

is reduced—for example, under deep shade (Monsi, 1960), or when the C/F ratio is high—that sometimes these plants may die owing to deficiency of carbohydrates.

In order to obtain a better understanding of the relationships between photosynthetic activity and plant

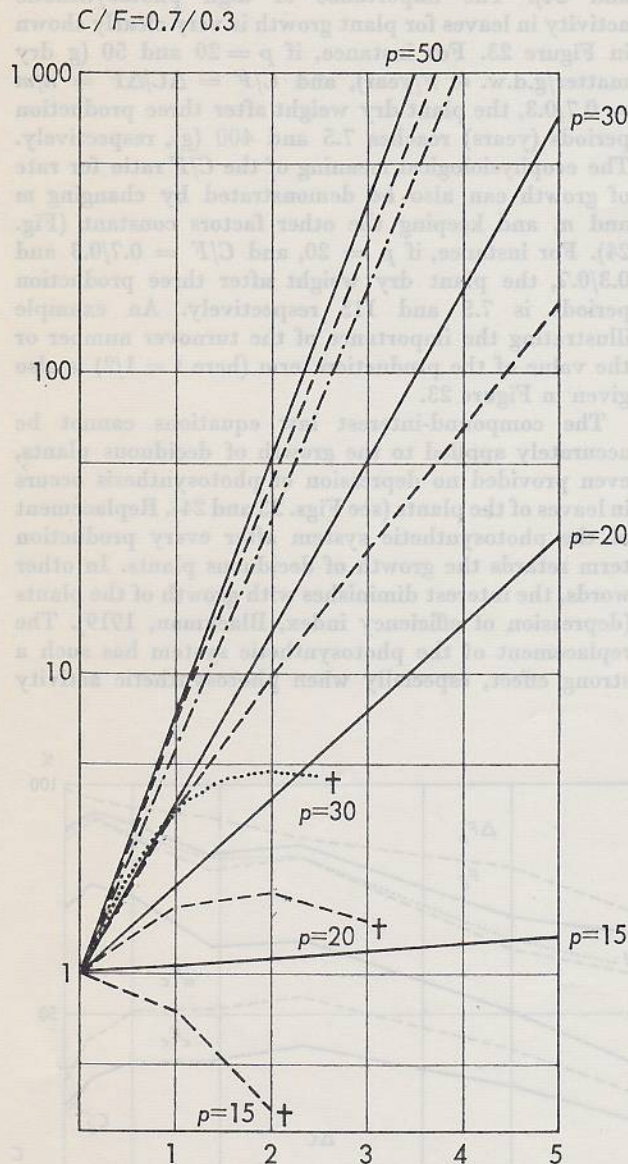


FIG. 23. Growth curves of plant models for dry-matter reproduction with different photosynthetic activities. $p = 15, 20, 30$ and 50 ; $r_f = 10$ (g dry matter/g dry weight of F /year), $r = 2$ (g d.m./g d.w. of C /year). $C/F = n/m = 0.7/0.3$. $k = 0.6$. Solid lines: $F \rightarrow \Sigma F$; $C \rightarrow \Sigma$ living tissue; production term $t =$ production period = 1 (year). Broken lines (deciduous): $F \rightarrow F_d$; $C = (C/2 \rightarrow \Sigma$ living tissue) + $(C/2 \rightarrow \Sigma$ dead tissue); $t = 1$. Chain line: $p = 30$; $F \rightarrow \Sigma F$; $C \rightarrow \Sigma$ living tissue; $t = 1/2$ production period = $1/2$ (year). Dotted line (deciduous): $F \rightarrow F_d$; $C = (C/2 \rightarrow \Sigma$ living tissue) + $(C/2 \rightarrow \Sigma$ dead tissue); $t = 1/2$.

growth or final yield, we should investigate the internal physiology of plants as regards distribution ratio, rate of translocation of assimilates, and rate of development of leaves, stems, and roots, in parallel with ecological studies of community production and its environmental factors. Furthermore, special attention must be paid to the fact that growth of the plant community cannot be deduced directly from the growth of single plants grown without mutual influence. Growth of a closed plant community is controlled primarily by incoming light, because of the thickness of the foliage. The maximum matter production is limited therefore ulti-

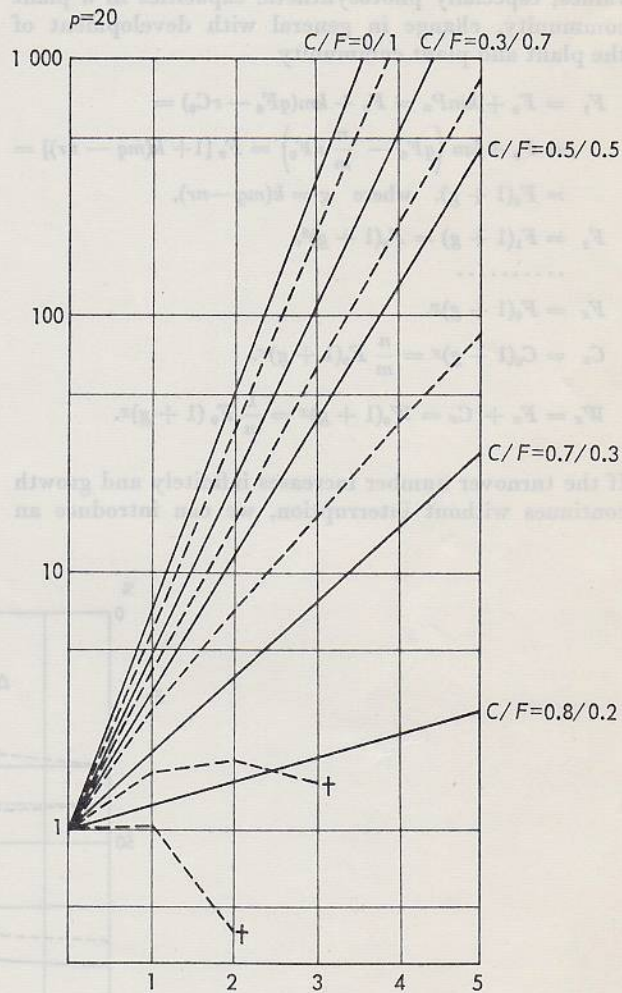


FIG. 24. Growth curves of plant models for dry-matter reproduction with different C/F ratios. $C/F = n/m = 0.8/0.2$; $0.7/0.3$; $0.5/0.5$; $0.3/0.7$ and $0/1$. $p = 20$ (g dry matter/g dry weight of F /year). k, r_f and r are the same as in Figure 23. Production term $t =$ production period = 1 (year). Solid lines: $F \rightarrow \Sigma F$; $C \rightarrow \Sigma$ living tissue. Broken lines (deciduous): $F \rightarrow F_d$; $C = (C/2 \rightarrow \Sigma$ living tissue) + $(C/2 \rightarrow \Sigma$ dead tissue).

mately by incident solar illumination, although the amount of matter production of the community varies to some extent with photosynthetic and respiratory activities and with light penetration which is much influenced by the specific leaf arrangement of its constituent species.

In attempting to find the biological basis for productivity on earth, many problems remain to be studied in photosynthesis, growth and development of plant

communities. Photosynthesis, however, must be the starting point when studying growth of green plants as well as the development of ecosystems. The theoretical considerations discussed should have given an idea of what potential productivity is. The values calculated by mathematical models with specific data for plant species under local climatic conditions may indicate the highest target figure for plant production of the area.

Résumé

Modèles mathématiques des groupements végétaux (M. Monsi)

L'évaluation de la productivité des groupements végétaux constitue un problème important dans le Programme biologique international. Il y a trois façons de l'aborder : a) déterminer la biomasse en présence dans un groupement végétal à deux moments consécutifs; b) calculer la photosynthèse d'un groupement végétal en se basant sur les activités photosynthétiques des feuilles et sur des modèles mathématiques, ou bien sur la structure productive des populations; c) estimer par des méthodes aérodynamiques les échanges de gaz carbonique.

L'étude des structures productives dans les groupements végétaux herbacés ou ligneux peut se faire selon la méthode de récolte par strates. La photosynthèse nette d'un groupement végétal est essentiellement déterminée par : a) la capacité photosynthétique des feuilles et la respiration des feuilles et des autres organes; b) l'éclairement énergétique incident, variable

dans le temps et dans l'espace; c) la pénétration et la répartition de la lumière dans la population végétale, qui se traduit par l'existence d'un coefficient d'extinction lié à la nature et à l'inclinaison des feuilles. L'intensité photosynthétique des feuilles adultes est de l'ordre de 10 à 20 mg de gaz carbonique par heure pour 100 cm² (en lumière totale, à 25 °C, avec 0,03 % de gaz carbonique), ceci pour nombre d'espèces. L'âge des feuilles, les variations de température, la distribution du gaz carbonique dans la population végétale doivent également entrer en ligne de compte.

En évaluant la productivité des arbres forestiers, on ne doit pas négliger les relations allométriques existant entre le diamètre à hauteur d'homme, le poids sec total et la hauteur des arbres, la quantité de feuilles, le type d'exploitation. Il faudrait en outre évaluer les modalités de reproduction de matière dans les différents types biologiques pour connaître exactement la croissance et les limites de productivité d'une plante ou d'un groupement végétal.

Discussion

H. LIETH. What was the optimal leaf area index you found in your experiments? In Europe we found a LAI of 3-5 to be the optimum. No increase of productivity was obtained with higher leaf area indexes.

M. MONSI. The optimum leaf area index is theoretically calculated using equation (9). It depends on incident light intensity (and day-length), light extinction coefficient of foliage, photosynthetic and respiratory characteristics and transmissibility of single leaves. In Japan it may be 3-10. Practically it can be obtained by a crop-growth-rate-LAI diagram (e.g., in sweet potato 3.2 and in rice 4.0, as in Tsuno and Fujise, 1965). The optimum LAI thus obtained, however, must be some-

what lower than that calculated with equation (9) because of respiration of the non-photosynthetic system.

E. INOUE. With reference to Dr. Lieth's question to Dr. Monsi, the optimal LAI should be dependent upon the latitude. Hence, it might be difficult to compare the results obtained in Germany with those at Tokyo obtained by Monsi.

M. MONSI. Optimum LAI is not directly correlated with the latitude, but it is dependent upon the incident light intensity and day-length which must differ with the latitude.

W. R. STERN. The calculation of the extinction coefficient has been an effective vehicle in developing models for photosynthesis of plant communities. However, there are published light curves and further evidence is accumulating that light attenuation in vegetation does not necessarily occur according to Beer's law. In view of these developments, does Dr. Monsi consider it worth persisting with this concept or could it now be safely discarded? Would it not be more effective to concentrate our efforts to defining more precisely the relationship between foliage distribution and light attenuation, especially since leaves are seldom distributed randomly. Furthermore, the questioner doubts the usefulness of the Britten, Wilson and Verhagen model and wonders why Dr. Monsi has used the concept of standard exponential foliage to little effect.

M. MONSI. Variation of light attenuation in plant communities with Beer's law was already discussed by Monsi and Saeki (1953) with special reference to the leaf inclination. Light intensity in plant communities is influenced not only by leaves but also by stems, and

the light intensity cannot be correlated strictly with the LAI. However, without any concept of extinction coefficient, including parameter s of Monteith (1965), no development of mathematical models for foliage photosynthesis would be possible.

Precise measurements of light intensities, especially under direct sunlight, is of great practical importance in promoting the study of photosynthesis of plant communities, as shown in the figure after Kumura (1965). We are now planning some field experiments to get precise records of light intensities received by leaves.

Verhagen, Wilson and Britten's model is principally based on Saeki's (1960). Their paper could demonstrate to us that it is possible to increase the leaf photosynthesis by suitably changing the extinction coefficient, so as to match the standard exponential and best exponential foliage. Their ideal foliage did not give any realistic image in their paper. The deviation of light attenuation from Beer's law may lead to some practical solution in this ideal foliage, as shown in *Solidago* by Dr. Iwaki (1965) and Saeki (1965) which I have introduced here.

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