

# *PREDICTION AND MEASUREMENT OF PHOTOSYNTHETIC PRODUCTIVITY*

*Proceedings of the IBP/PP  
Technical Meeting, Třeboň  
14 - 21 September 1969*

Separate offprint



Centre for Agricultural Publishing  
and Documentation

P.O. Box 4

Wageningen - The Netherlands - 1970

# Development of photosynthetic systems as influenced by distribution of matter

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## Abstract

The proportions in which the assimilates are distributed to various organs decide the growth and the yield of plants. The importance of the distribution ratio in plant growth is analyzed using some simple models of dry-matter production and different distribution ratios.

Relationships between the distribution ratio and environmental conditions are discussed with several examples taken particularly from Japanese IBP photosynthesis experiments on rice stands. Regional differences in the value of the distribution factor for leaf laminae in rice stands were rarely observed. The rate of crop growth, however, increased with air temperature in parallel with the rate of leaf growth.

'Light parasitism' of lianas is also discussed with reference to the vertical distribution of matter and development of photosynthetic systems.

## Introduction

Development of a photosynthetic system is determined by its photosynthetic activity and by how much of the new assimilates are returned to expanding the system. The growth of the whole plant likewise is determined by how rapidly the photosynthetic system develops. To describe the growth of a plant in detail, a sophisticated model is needed which includes all plant reactions. A simple model, however, can sometimes help to detect the essential mechanism governing the complicated system.

In earlier papers, Monsi (1960, 1968) has discussed, with simple models, the relationship between the photosynthetic apparatus and dry-matter production. Such relationships also hold for agricultural yields since these consist principally of accumulated photosynthesis product. Certain differences in the pattern of photosynthate distribution and reproduction of the photosynthetic apparatus are evident among different plant species and suggestions of classification have also been presented (Monsi, 1960; Walter, 1964). High agricultural yields can best be obtained with high photosynthetic production accompanied with conveying large proportions of the photosynthates into the organ that is harvested.

## The distribution ratio

A plant or community which has dry weight  $W_x$  at time  $t_x$  grows to dry weight  $W_{x+1}$  at time  $t_{x+1}$ . Net production  $P_n$  measured by increase of biomass is equal to

$(W_{x+1} - W_x)$ , as long as no dry matter is lost by death or shedding. Under such conditions,  $P_n$  is the sum of dry-matter increments in the structure of all organs and of stored assimilates, i.e.  $P_n = \Delta L + \Delta S + \Delta R + \Delta M$ , where  $L$  stands for leaves (photosynthetic system),  $S$  for stems (including leaf sheaths and petioles),  $R$  for roots, and  $M$  for assimilates stored in grains, tubers, rhizomes, trunks, and sometimes in evergreen needles (Kimura, 1969).

The gross production of a plant or community,  $P_g$ , can be expressed as the product  $p \cdot L$ , where  $p$  represents the mean photosynthetic rate per unit leaf amount and  $L$  the amount of leaves. The leaves themselves have first priority in the consumption of the new photosynthates so that the photosynthates exportable from leaves, or surplus production  $P_s$  are

$$P_s = P_g - m^r L \cdot L$$

where  $m^r L$  is the mean maintenance respiration per unit amount of leaves.

Part of the assimilates translocated from leaves to stems and roots must be respired for maintenance of these organs, so that the assimilates which can be used for construction of new leaves, new stems and new roots, and for storage (surplus of assimilates for new growth,  $aP_n$ ) are reduced to an amount

$$aP_n = P_s - (m^r S \cdot S + m^r R \cdot R)$$

The assimilates ( $aL$ ) allocated for new leaves ( $nL$ ) are used partly for constructive respiration ( $c^r L \cdot nL$ ), where  $c^r L$  is a mean constructive respiration per unit amount of new leaves. Similar formulae can be developed for stems and roots. The net production  $P_n$  is the sum total of newly formed tissues of each organ and matter stored, i.e.

$$P_n = nL + nS + nR + nM$$

In other words,  $P_n$  is  $P_g$  minus the sum total of respiration for maintenance and construction.

The distribution of biomass among leaves, stems, roots and stored matter can be expressed by distribution factors  $d_L$ ,  $d_S$ ,  $d_R$  and  $d_M$ ; the values of these factors are the ratios of  $nL$ ,  $nS$ ,  $nR$  and  $nM$ , respectively to  $P_n$  (Iwaki, 1958). The ratio of  $P_n$  to  $aP_n$  has been named the transformation factor or economic ratio ( $k$ ). Transformation factors  $k_L$ ,  $k_S$ ,  $k_R$  and  $k_M$  can be defined for each organ and for stored matter.

The net production of assimilates is allocated to various organs and for storage, so that

$$aP_n = aL + aS + aR + aM$$

The distribution of assimilates is governed by allotment factors  $a_L$ ,  $a_S$ ,  $a_R$  and  $a_M$  defined similarly as the various above-mentioned distribution factors.

The amount of new leaves can be expressed by the following equation,

$$nL = P_n \cdot d_L = [(p \cdot L - m^r L \cdot L) - (m^r S \cdot S + m^r R \cdot R)] \cdot a_L \cdot k_L$$

Similar equations can be derived for stems and roots and stored matter. The values of  $k_L$ ,  $k_S$  and  $k_R$  are almost equal and range from 0.5 to 0.8 according to growth stage and species (Yokoi, 1967). Translocation of assimilates and their conversion into stored substances require very little energy compared with that used in construction of new tissues, so that for simplicity  $k_M$  is assumed to be 1.0 in the following discussion.

The photosynthetic system becomes  $L_x + nL$  at time  $t_{x+1}$  as long as no leaves are

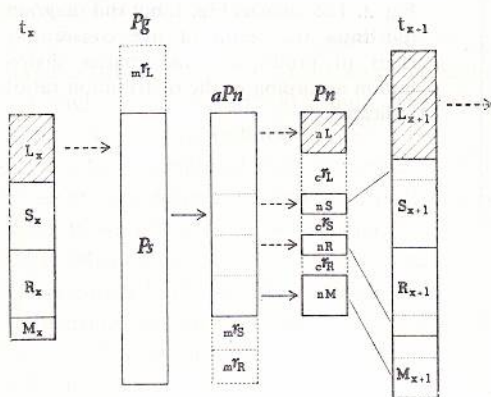


Fig. 1. A diagrammatical representation of the processes considered and calculations involved in one step of production and matter distribution. Symbols  $L$ ,  $S$ ,  $R$  and  $M$  indicate leaves, stems, roots and stored matter, respectively.  $m^r$  and  $c^r$  stand for maintenance and constructive respiration of unit dry weight of the various organs denoted by the subscripts.  $P_g$ ,  $P_n$ ,  $P_s$  and  $aP_n$  denote gross, net, surplus production and net production of assimilates respectively. The distribution factors for leaves ( $d_L$ ), stems ( $d_S$ ), roots ( $d_R$ ) and stored matter ( $d_M$ ) are defined as  $nL/P_n$ ,  $nS/P_n$ ,  $nR/P_n$  and  $nM/P_n$ , respectively.  $P_n = nL + nS + nR + nM$  and so the values of the distribution factors are, as can be seen, 2:1:1:2/6.

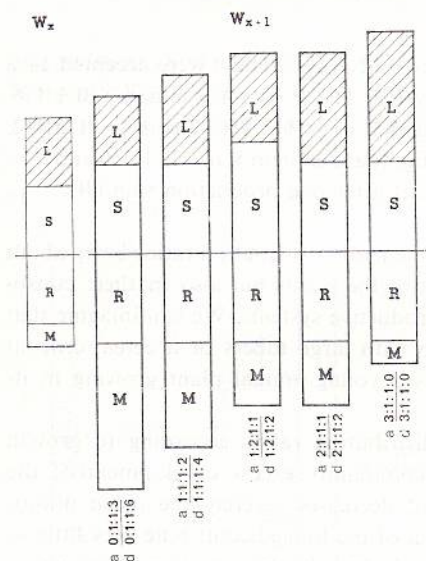


Fig. 2. A diagrammatical representation of the changes in the composition of the plant bodies after one step of production and matter distribution when different distribution ratios are assumed for the various cases shown. The first column ( $W_x$ ) gives the initial composition of the plant body, the other columns ( $W_{x-1}$ ) show the composition after one production step with the distribution ratios for assimilates (a) and new biomass (d) given in the fractions at the bottom of the columns (distribution factors are written in the usual order, i.e. leaves: stems: roots: stored matter).

shed, and the new system produces more material than  $L_x$  at time  $t_x$ . One of the simplest models is illustrated in fig. 1, where the plant body ( $W_x$ ) is composed of  $L$ ,  $S$ ,  $R$  and  $M$  in a ratio of 3:3:3:1;  $P_g = p \cdot L = 5 \cdot 3$ ;  $m^rL = 1$ ,  $m^rS = m^rR = 0.5$ ;  $aL:aS:aR:aM = 2:1:1:1$ ;  $k_L = k_S = k_R = 0.5$ ,  $k_M = 1$ ; and  $d_L:d_S:d_R:d_M = 2:1:1:2$ .

We can calculate the growth of plant biomass for a series of similar productive systems having different parameters characterizing photosynthetic production and different distribution factors. The main purpose of the present paper is to evaluate the effect of different values of the distribution factors. Therefore widely different

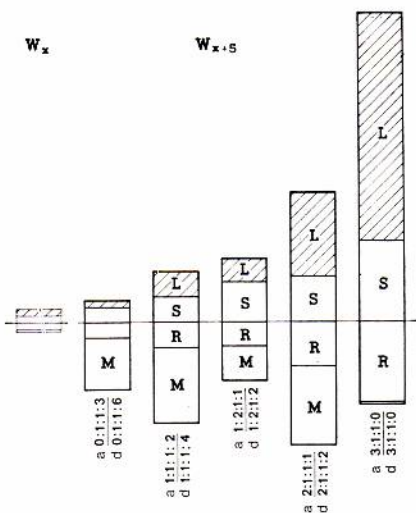


Fig. 3. The same as Fig. 2, but this diagram illustrates the result of five consecutive steps of production and matter distribution according to the distribution ratios indicated.

allotment and distribution ratios ( $a_L:a_S:a_R:a_M$  and  $d_L:d_S:d_R:d_M$ ) were accepted as a basis for the following model calculation: System 1:  $a = 0:1:1:3$  and  $d = 0:1:1:6$ . System 2:  $a = 1:1:1:2$  and  $d = 1:1:1:4$ . System 3:  $a = 1:2:1:1$  and  $d = 1:2:1:2$ . System 4:  $a = 2:1:1:1$  and  $d = 2:1:1:2$  (as in fig. 1) and System 5:  $a = 3:1:1:0$  and  $d = 3:1:1:0$ . Fig. 2 shows these production systems after one production step ( $W_{x+1}$ ), and fig. 3 after five production steps ( $W_{x+5}$ ).

As seen in fig. 3, the differences in the allotment and distribution ratios bring about large differences not only in total dry weight of the plants but also in their constitution i.e. in the structure of the plants as productive systems. We can imagine that System 1 represents a spring perennial herb with large tubers or a cereal crop at heading stage, and that System 5 represents a young annual plant growing in its exponential phase of growth.

The plant is characterized by different distribution ratios according to growth stage and environment. In a closed plant community excess development of the foliage causes mutual shading of leaves and decreases severely the mean photosynthetic rate. Many leaves in the lower strata of the foliage contribute very little to total photosynthesis, become senescent and are shed. In this situation a low distribution factor for leaves means rather high productivity of the community.

### Distribution ratio as influenced by environmental factors

**Light** There are many papers dealing with the influence of light on the distribution ratios. So, for example, Kuroiwa et al. (1964) found that the distribution factor for leaves ( $d_L$ ) with *Fagopyrum esculentum*, *Vicia faba* and *Helianthus annuus* decreases with the growth of plants from about 0.6 to 0.4 or even 0.2, but that with *Vigna radiata f. aurea* (= *Phaseolus aureus*) the factor remains constant throughout the growth

period. The ageing curves of  $d_L$  for sun-plants ran lower as light intensity at which the plants were grown was decreased. In the shade-plant *Cryptotaenia canadensis* var. *japonica* the highest curve of  $d_L$  was obtained at 75% light and the curve at 50% light ran higher than that at 100% light. The influence of daylength was investigated by Mokronosov with potatoes (1967).

Another example of light influence has been given by H.S. Choe (pers. comm.). After etiolation for 5, 12, and 25 days from germination, *Phaseolus vulgaris* seedlings were grown in cycles of 16 hours light (about 10 klx) and 25°C, and 8 hours dark and 20°C. Mean areas of the first leaf of seedlings grown in light all the time and seedlings etiolated for 5, 12 and 25 days were 76, 59, 17 and 13 cm<sup>2</sup>, respectively. The changes in distribution factors for leaves, stems and roots after exposure to light are illustrated in fig. 4. Photosynthetic rates at 10 klx, 25°C and 0.03% CO<sub>2</sub> of the mature first leaves were 13.6, 12.2, 10.6 and 7.6 mg(CO<sub>2</sub>) dm<sup>-2</sup> h<sup>-1</sup> in the controls and seedlings etiolated for 5, 12 and 25 days, respectively. The small leaf areas and low rates of photosynthesis caused low rates of growth in the plants etiolated for 12 and 25 days but they reached the highest values of  $d_L$  among all variants; this occurred on the 7th to 8th day after the etiolated seedlings were placed into light again.

**Soil moisture** Soil moisture has great influence on the distribution ratio. Furuhashi & Monsi (1969), for instance, demonstrated striking changes in the distribution ratios of young soybean seedlings grown in a growth cabinet (at 20°C in cycles with 14 hours of

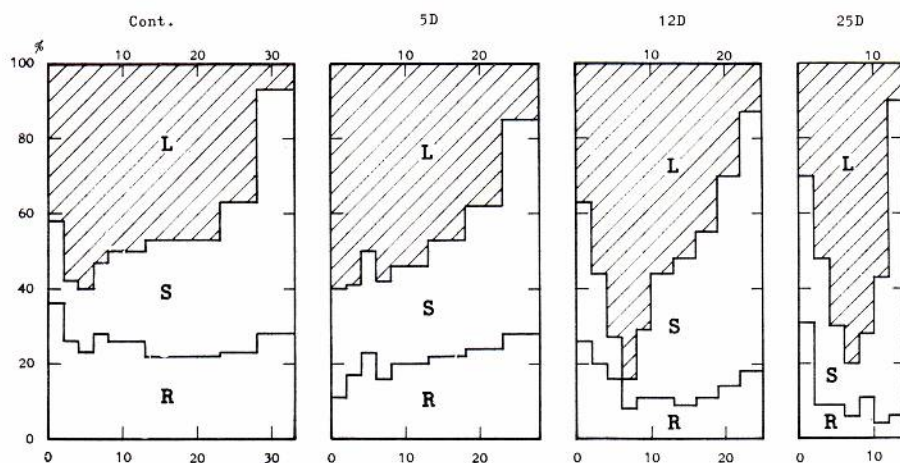


Fig. 4. Changes in the values of distribution factors for leaves (L), stems (S) and roots (R) in seedlings of *Phaseolus vulgaris*, grown in light from the start of the experiment (Cont.) or kept initially in dark for five (5D), twelve (12D) and twenty five (25D) days and then grown in light. After etiolation the seedlings were grown in controlled environment with 16 hours of light (10klx) at 25°C and 8 hours of darkness at 20°C. On the ordinate: values of the distribution factors in per cent. On the abscissa: number of days of culture in the controlled environments, following etiolation.

Table 1. Climatic conditions for some representative stations for the JIBP/PP-Photosynthesis Level I Experiments. Data from the Meteorological Agency. Average for 1931-60.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual mean or total
<i>Monthly mean air temperature, °C</i>													
Sapporo (1)	-5.5	-4.7	-1.0	5.7	11.3	15.5	20.0	21.7	16.8	10.4	3.6	-2.6	7.6
Morioka (4)	-3.0	-2.3	1.2	7.5	13.3	17.5	21.7	23.2	18.1	11.5	5.5	-0.1	9.5
Takada (6)	1.7	1.6	4.2	10.1	15.5	20.1	24.3	25.7	21.3	15.1	9.6	4.6	12.8
Kumagaya*	2.5	3.2	6.4	11.9	16.6	20.6	24.7	25.6	21.6	15.6	10.1	5.0	13.7
Okayama**	3.7	4.5	7.4	12.7	17.0	21.3	25.6	26.7	22.5	16.2	10.8	6.2	14.5
Kumamoto (15)	4.6	5.7	9.2	14.1	18.6	22.4	26.5	27.0	23.4	17.4	12.3	7.1	15.7
<i>Monthly mean rainfall, mm/month</i>													
Sapporo (1)	111	83	67	66	59	67	100	107	145	113	112	104	1136
Morioka (4)	59	57	80	101	92	113	169	154	180	110	85	75	1275
Takada (6)	501	327	218	119	100	121	193	151	224	216	332	536	3037
Kumagaya*	28	42	60	87	103	170	182	158	201	173	61	30	1294
Okayama**	36	52	77	100	109	159	166	99	150	94	60	38	1139
Kumamoto (15)	52	80	109	170	186	345	331	167	199	95	64	72	1869
<i>Monthly mean sunshine hours, h/month</i>													
Sapporo (1)	99	112	158	199	213	205	190	201	173	166	112	91	1916
Morioka (4)	130	140	177	194	213	186	163	183	148	162	136	115	1945
Takada (6)	73	87	144	199	217	183	186	234	154	142	122	81	1821
Kumagaya*	221	199	209	202	207	148	166	190	134	153	172	205	2205
Okayama**	159	155	191	208	225	194	222	250	182	183	172	160	2303
Kumamoto (15)	134	142	180	189	200	173	202	237	184	193	173	143	2148
<i>Monthly mean air humidity, %</i>													
Sapporo (1)	76	75	73	69	72	78	82	82	80	77	74	75	76
Morioka (4)	74	72	70	67	70	78	83	83	82	79	76	75	76
Takada (6)	79	78	75	71	74	79	83	80	81	80	80	80	78
Kumagaya*	61	60	63	68	75	80	83	84	84	80	74	66	73
Okayama**	72	71	71	71	74	80	80	78	79	77	77	74	75
Kumamoto (15)	74	72	71	73	75	79	81	78	79	76	76	76	76

\* Near Konosu (9). \*\* Near Fukuyama (12).

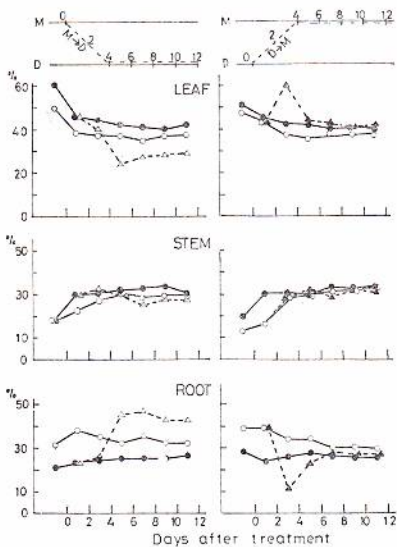


Fig. 5. Influence of soil moisture and its change on the values of the distribution factors in young soybean plants grown under controlled conditions. The curves connecting solid circles refer to plants grown throughout the experiment in moist sand (22.8 w./w. per cent of water) and curves with open circles to plants grown in dry sand (5.2 w./w. per cent of water). Open triangles denote plants shifted from the moist to the dry condition and solid triangles plants shifted from dry to moist condition. The time schedule of the shifts is marked at the top of the figure. On the ordinates: values of distribution factors in per cent.

light, approx. 10 klx, and 10 hours of dark), when the water content of soil was changed from 22.8 per cent to 5.2 per cent and vice versa (fig. 5). There is a clear complementary relationship between the distribution factors for leaves and those for roots as the plants adapt to the changed soil moisture. The changes in distribution factors caused changes in the development of the photosynthetic system and in the extension of the leaf area; these changes resulted in retardation or enhancement of plant growth.

#### Matter distribution and productivity of the photosynthetic systems in different geographic conditions

By using the data obtained in the Level I — Maximal Growth Experiments carried out in 1967 by the Local Productivity Group of Japanese IBP/PP, analyses have been made on the local differences in productivity of five crops: rice, maize, soybean, sugar-beet and sunflower. Some of the results concerning distribution of dry matter and leaf growth in rice and maize are presented here.

The plants were grown in a fertile field at each of the seven stations lying from the north (Station No. 1, 43° 3' N. Lat.) to the south of Japan (Station No. 15, 32° 53' N. Lat.) (fig. 6). Best cultural practices and varieties well suited to each locality were used. Temperatures and other climatic conditions at the representative stations are shown in table 1.

*Regional differences in the pattern of dry-matter distribution to different organs* The courses of foliage development in rice and maize stands as characterized by the leaf area index (LAI, leaf area per unit ground area) are shown in fig. 7 in which the time of heading or silking is taken as reference time for normalizing the curves. The





Fig. 6. A map showing the positions of the experimental stations which participated in the level-I-Experiments of the Japanese IBP/PP Photosynthesis subsection activities.

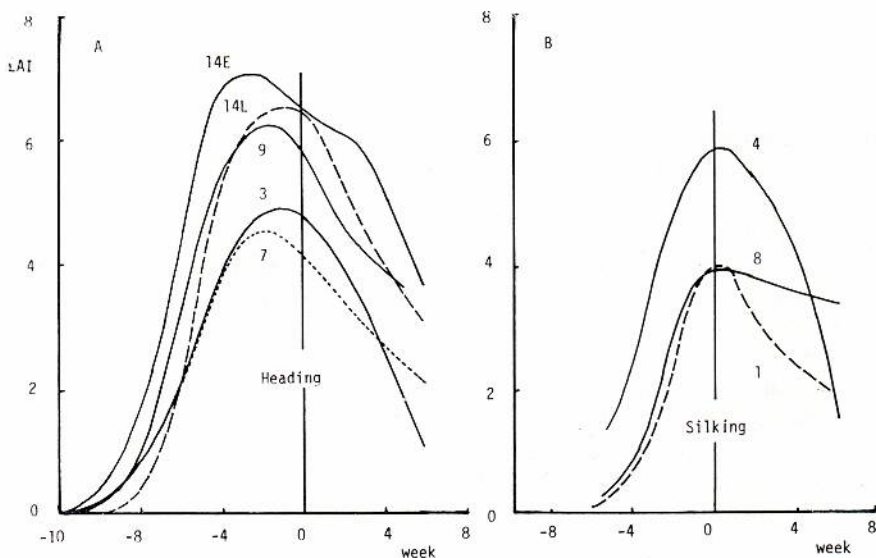


Fig. 7. Development of the photosynthetic system in rice (A) and maize (B) as illustrated by the course of leaf area index values. The numbers labelling the curves refer to the stations as numbered in Fig. 6. (E and L denote early and late crop). The time of heading in rice and of silking in maize were taken as reference for normalizing the curves.

highest LAI observed in rice fields was 7.08 in an early crop at Hainuzuka, Kyushu, on August 3, 1967. In maize fields the highest LAI value was 5.85 observed at Morioka on the same date.

The variation of distribution factors for leaves and roots during the development of rice plants in crops at various stations is illustrated in fig. 8. Again heading is adopted as reference stage for normalizing the curves. In young plants, 3 to 4 weeks after transplanting (i.e. 7 to 6 weeks before heading) the distribution factors for leaves and roots had greatest values,  $d_L \cong 0.4$  and  $d_R \cong 0.1-0.2$ . Hardly any regional differences in  $d_L$  were observed.

From these high values in early developmental stages the distribution factors declined steadily to reach zero at about the heading stage. This means that the amounts of import and export of dry matter to and from these organs were then balanced. The factors  $d_L$  and  $d_R$  generally continued to decrease until seed maturity, though  $d_R$  often increased slightly during the grain-filling stage. The negative values of distribution factors imply an active export of assimilates.

Fig. 9 shows the seasonal changes of distribution factors for stems including leaf sheaths ( $d_S$ ) and for ears ( $d_E$ ). The value of  $d_S$  in young plants was about 0.4, being nearly equal to  $d_L$ . It gradually increased to a maximum value of 0.6 to 0.7 attained 2 to 3 weeks before heading. Thereafter the  $d_S$  value decreased very rapidly passing zero at the heading stage and reaching a minimum ( $-0.4$  to  $-0.8$ ) two weeks after heading; finally towards maturity, an abrupt increase of  $d_S$  values was observed.

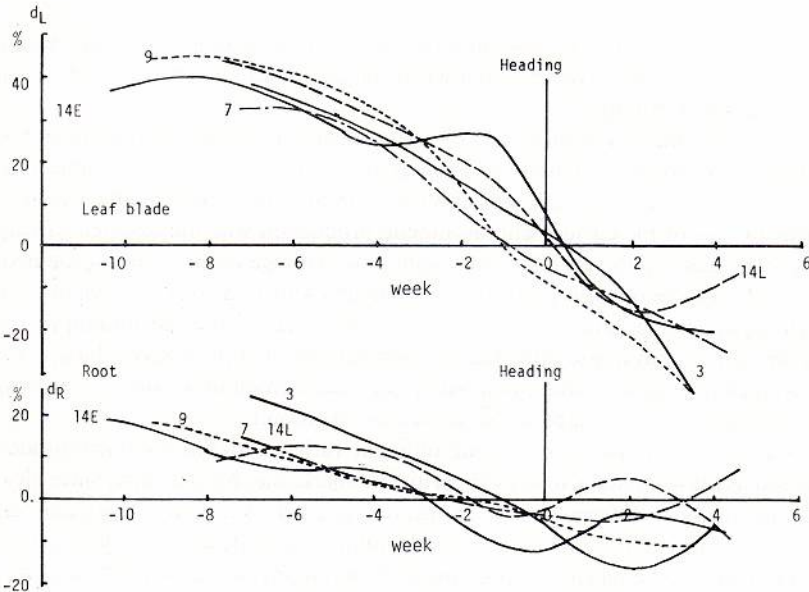


Fig. 8. Variation in the values of distribution factors for leaves and roots during the growth of rice plants at various localities. The values of the distribution factors given in per cent. Other notation see Fig. 7.

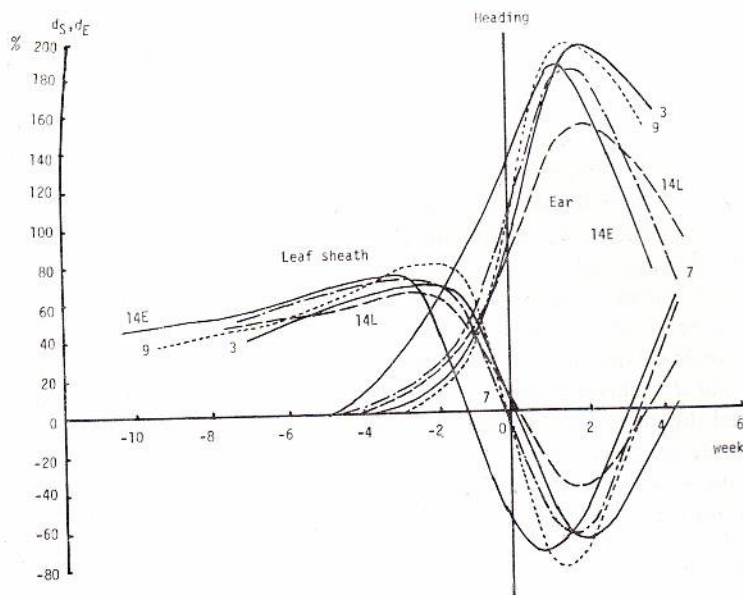


Fig. 9. Variation in the values of distribution factors for leaf sheaths ( $d_s$ ) and ears ( $d_E$ ) during the growth of rice plants. Notation of curves and coordinates the same as in Fig. 8.

The flux of dry matter into the ears started 4 weeks before heading, increased rapidly to a maximum two weeks after heading when the  $d_E$  values amounted to 1.5 to 2.0 and then decreased rapidly.

The contrasts in the course of  $d_s$  and  $d_E$  values clearly demonstrates the role of the leaf sheath as an organ for temporary storage of assimilates. It is remarkable that  $d_E$  reached as high values as 2.0, indicating that an amount of dry matter which is equivalent to that of the current photosynthetic production was translocated mainly from the leaf sheath to the ear. A similar temporary storage occurred in the stem of maize, though its role in grain production was small (Allison & Watson, 1966).

Fig. 10 illustrates the developmental course of the values of the distribution factor for leaf laminae ( $d_L$ ) in maize grown at various stations; as can be seen, the general picture is much the same as that observed in rice plants. With maize also hardly any regional differences in the shape of the curves can be found.

The absence of variation in  $d_L$  among different varieties and at various latitudes, if compared at the same stage of growth, is most remarkable. All the more, since clear varietal and regional differences can be demonstrated in the values of  $d_s$  and  $d_R$ . This becomes particularly clear if the transplanting date instead of heading date is taken as reference. The mean values of the distribution factors for leaves, stems and roots in rice plants during the six weeks following transplanting are given in table 2. As can be seen  $d_s$  decreases and  $d_R$  increases with increasing latitude and slight differences among early and late varieties are also observed.

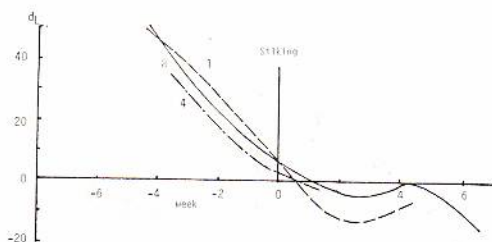


Fig. 10. Variation in the values of the distribution factors for leaf blades during the growth of maize at various localities. Notation similar to Fig. 8.

Table 2. Distribution factors (as percentages) for leaf laminae ( $d_L$ ), leaf sheaths ( $d_S$ ) and roots ( $d_R$ ) in rice plants grown at various localities in Japan. Mean values for 6 weeks after transplanting.  $T$ , mean air temperature ( $^{\circ}\text{C}$ ) for the six weeks. The numbers of the stations are those used in fig. 6.

Station No.	Variety	$d_L$	$d_S$	$d_R$	$T$
3	Early	36	45	19	18.2
	Late	34	46	20	18.2
6	Early	38	48	14	19.9
	Late	37	52	11	19.9
7	Early	35	53	12	20.5
	Late	32	57	11	20.5
9	Early	34	61	5	22.2
	Late	38	54	8	22.2
12	Early	34	57	9	23.9
	Late	31	56	13	23.9
14	Early culture	32	60	8	24.5
	Late culture	30	58	12	27.4

*Regional differences in leaf and crop growth rate* If the Leaf Weight Increase Rate (LWIR, g of leaf dry weight per  $\text{m}^2$  of ground and day) of rice plants is compared during early growth (e.g. for six weeks after transplanting), it is clear that this rate decreases with increasing latitude of the station. As the relation between LWIR and the mean air temperature shown in fig. 11A was highly significant ( $r = 0.9540^{***}$ ) the influence of temperature was compared with other climatic factors by path-coefficient analysis as developed by Dewey & Lu (1959).

Three climatic factors, mean air temperature ( $X_1$ ), solar radiation ( $X_2$ ) and rainfall ( $X_3$ ), were chosen and the regression of LWIR ( $Y$ ) to them was calculated. The following standardized multiple regression equation was thus obtained:

$$y = 1.152 X'_1 - 0.203 X'_2 - 0.367 X'_3$$

The three climatic factors explain about 93 per cent ( $R = 0.9647^{***}$ ) of the deviations in LWIR and the contribution of air temperature is considerably larger (58 per cent) than that of the two other factors, solar radiation (10 per cent) and rainfall (18 per cent), both working in the negative direction. Strong solar radiation is generally

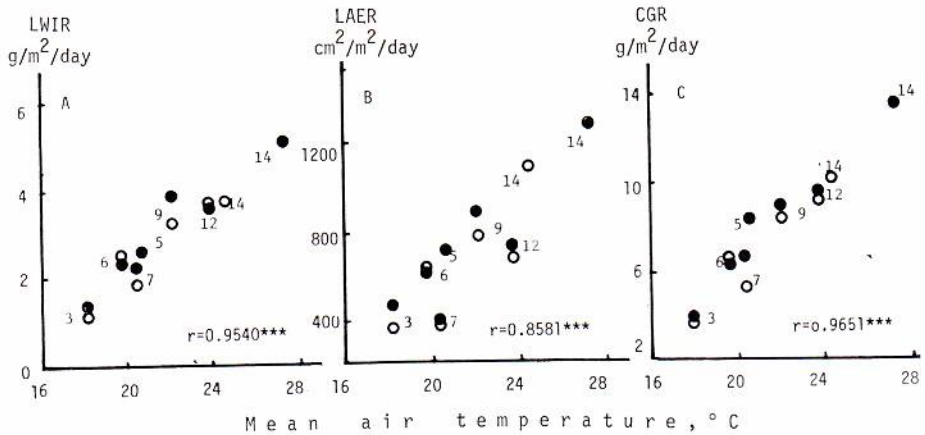


Fig. 11. Correlations between the mean air temperature and the leaf weight increase rate (LWIR, 11A) the leaf area expansion rate (LAER, 11B) and the crop growth rate (CGR, 11C) in young rice plants at various localities. Numbers labelling the circles refer to the various experimental stations as numbered in Fig. 6. Solid and open circles denote late and early varieties respectively.

associated with dry air and sometimes with scanty rainfall, and a large amount of rainfall is often accompanied with long periods of insufficient illumination.

A highly significant correlation ( $r = 0.8581^{***}$ ) was also found between the Leaf Area Expansion Rate (LAER, cm<sup>2</sup> leaf surface per m<sup>2</sup> ground area and day) and the mean air temperature (see fig. 11B). The latter was found to be the most important factor in geographic differences of LAER, just as it was also for LWIR. Thus mean air temperature is one of the most important factors in the large geographic variation of the growth parameters.

From these results we have drawn more general conclusion: although regional differences are hardly found in the dry-matter distribution factors for leaves, the growth of leaves is heavily dependent on temperature. This was proved earlier by Bull (1968) with *Vicia faba* grown in the field at one locality but in different seasons.

Finally also the Crop Growth Rate (CGR, g of dry weight per m<sup>2</sup> of ground and day) of young, exponentially growing stands of rice was almost entirely dependent on mean air temperature as shown in fig. 11C. Similar results were obtained by Weihing (1963) with field-grown ryegrass.

### Ecological significance of matter distribution to various components in the photosynthetic system

The development of the photosynthetic apparatus determines the growth of the whole plant, and is determined on its turn by the rate of photosynthesis and the distribution of assimilates.

The distribution of photosynthates, particularly insofar as it governs the vertical

development of the photosynthetic systems, has great bearing on plant competition. In an analytical study with mixed stands of *Vigna radiata f. aurea* (= *Phaseolus aureus*) and *Fagopyrum esculentum*, Iwaki (1958) discussed the importance of height growth. The taller photosynthetic system of *Fagopyrum* than of *Vigna* in mixed stands ensures the dominance of the former. Such plant competition has been further discussed by C. M. Donald (1963). Recently Oikawa & Monsi (1969) discussed the height growth of *Helianthus annuus* stand by clarifying two kinds of response in stem elongation to strong light: the photomorphogenic retardation and the photosynthetic enhancement.

A typical example of the importance which the vertical structure of the photosynthetic apparatus has for light competition is presented by the lianas and climbers in general. In Japan we have about 80 species of herbaceous and woody climbers. Most of them grow very vigorously, causing heavy damage by 'light parasitism' to supporting herbs, shrubs or trees. Climbers develop their leaves mainly in the upper portion of the foliage of the mingled canopy as is illustrated in fig. 12. On the basis of the difference between climbers and support plants in these developmental patterns of leaves we can design a simplified model of a plant community being destroyed by climbers. Let us assume that in climbers three quarters of net photosynthates are used

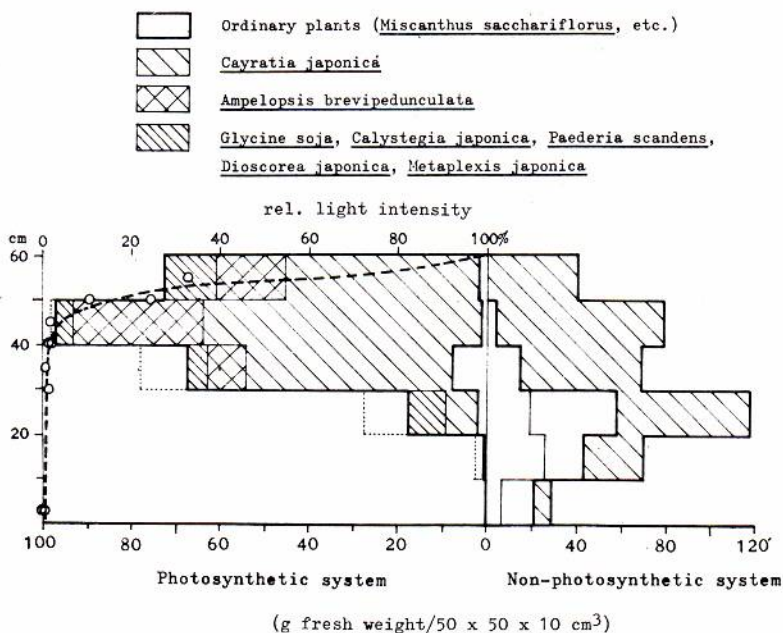


Fig. 12. Profile diagram of a mixed community consisting of a tall grass and several climbers. Profile taken at Tazima-ga-hara, near Tokyo on August 22. Hatched areas indicate the fresh weight of the climber plants, areas delimited by dotted lines denote the weight of yellowing leaves.

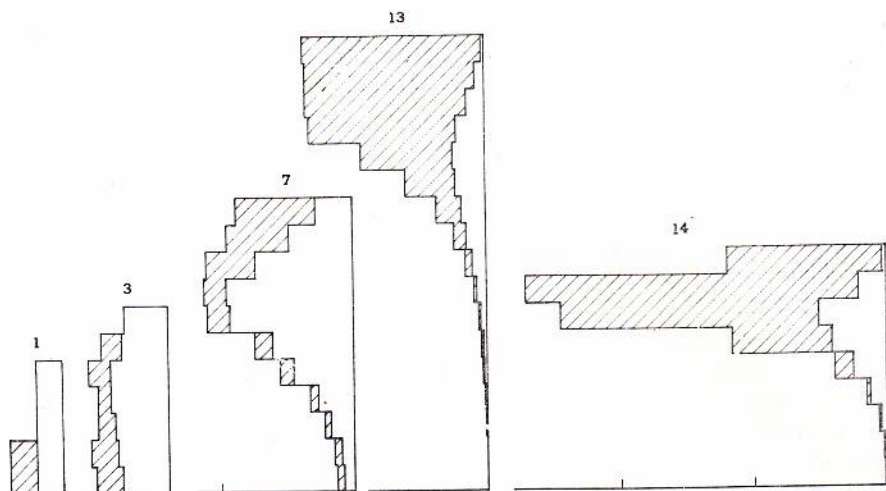


Fig. 13. A model of the development of the photosynthetic system in a mixed community of climbers and support plants. Hatched areas: the photosynthetic apparatus on the climbers. Blank areas: the photosynthetic apparatus of the support plants. The numbers on the top of the profiles denote the number of production and matter distribution steps taken in the model calculation the assumptions for which are specified in the text on p. 176. Following production step 13 the height of the community decreases due to the weight of the climber leaves.

for growth of the top leaves and only the remaining quarter is used for other organs. In support plants half of net photosynthates contributes to vertical development of the canopy and only one quarter is used for the growth of the top leaves and the other quarter for growth of other organs. The light intensity decreases from top to bottom in the mixed canopy in proportion to the leaf density. Fig. 13 demonstrates the profile development of the photosynthetic systems of lianas and support plants and the final image (14) resembles the profile of the *Cayratia japonica* - *Miscanthus sacchariflorus* community illustrated in fig. 12.

The simple models and experimental data discussed in this paper demonstrate clearly that the distribution of assimilates, particularly the portion allotted to the photosynthetic system, can determine the growth and ultimately the yield of plants and plant communities. The factors which regulate the distributions remain as subjects for future research.

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Size 15 × 23 cm

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632 pages

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ISBN 90 220 0323 X

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