Distribution Ratio of Net Photosynthate to Photosynthetic and Non-Photosynthetic Systems in Shaded Plants*

by Sumio KUROIWA**, Toshio HIROI***, Kazuo TAKADA****
and Masami MONSI***

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In the ecophysiological analysis of growth of plants, the plants should be divided into two systems, photosynthetic (F) and non-photosynthetic (C)¹⁾. Increment in dry weight of each system in a period depends, though approximately, on the total amount of photosynthate produced by the photosynthetic system in the period and also on the proportion of photosynthate distributed to the system. This distribution ratio of photosynthate decides finally the C/F -ratio²⁾, a useful term in the growth analysis, since the weight of the system at any time is an integration of the photosynthate which is distributed to the system and remains after the respiration loss.

The distribution ratio has been considered in the case of discussion of growth of plants by several workers¹⁻¹⁴⁾. Difference in the distribution ratio among plants grown in various densities was observed in *Fagopyrum esculentum*²⁾ and *Helianthus tuberosus*¹¹⁾. Recently, the effect of shading on the distribution ratio was studied in *H. annuus* by Hiroi and Monsi¹⁴⁾.

In this paper, we shall propose a theoretical method to derive the distribution ratio from the relationship between the system and the whole plant in dry weight. Applying this method to experimental data on the growth of several herbs, including sun plants, *F. esculentum* and *H. annuus*, shade plant, *Cryptotaenia canadensis* var. *japonica*, and others, the shading effect on distribution ratio will be compared with each other of these species. We shall reveal the usefulness of this theoretical method in the discussion of shade tolerability.

Theoretical assessment of distribution ratio of photosynthate

Time trend of distribution ratio of photosynthate to the photosynthetic or non-photosynthetic system was generally obtained through the following procedures^{2, 10-14)}.

(1) The distribution ratio at a given stage was calculated by dividing the increment of the said system by the increment of the whole plant in dry weight in a period. In this case, sometimes the smoothed growth curves were used to eliminate the sampling deviation. (2) The distribution ratio thus obtained was plotted against the growth stage on regular co-ordinates.

It may, however, be more interesting to demonstrate whether the distribution ratio differs or not with the size of plants which are grown under different habitat conditions. To solve this problem, we use a relationship between the photosynthetic system (F) or non-photosynthetic system (C) and the whole plant (W) in dry weight

* Contribution No. 5 from the Botanical Gardens, Faculty of Science, University of Tokyo, Koishikawa, Tokyo.

** Botanical Gardens, Faculty of Science, University of Tokyo, Koishikawa, Tokyo, Japan.

*** Department of Botany, Faculty of Science, University of Tokyo, Hongo, Tokyo, Japan.

**** Toride Upper Secondary School, Toride, Ibaraki Prefecture, Japan.

including dead parts of each system or of the plant, and we express the relationship with general formulae, $F = f(W)$ or $C = c(W) = W - f(W)$. The distribution ratio (δ) of net photosynthate to F in any growth period is defined by $\frac{dF}{dt} / \frac{dW}{dt}$, and can be represented by the differential of $f(W)$ or $dF/dW = f'(W)$.

In general, the photosynthetic system increases its weight in proportion to the growth of the plant during the early growth stage, but in the later stage the F -system or the foliage decreases its growth rate gradually to reach a maximal leaf amount, despite of further increase of the total plant weight. The relationship between F and W in such growth pattern can be expressed in the simplest form by the following formula of a rectangular hyperbola,

$$F = \mu W / (1 + \nu W), \quad (1)$$

where μ and ν are constants. Then, the distribution ratio of net photosynthate to the photosynthetic system becomes:

$$\delta = \mu / (1 + \nu W)^2. \quad (2)$$

The distribution ratio (ϵ) to the non-photosynthetic system is always expressed by $\epsilon = 1 - \delta$, as $F + C = W$. This simple relation between δ and ϵ may permit us not to have to discuss the ϵ -value and the C - W relationship in every case.

The C/F ratio, which was proposed by Iwaki²⁾ as an important determination factor for the net assimilation rate, has been referred for the analytical proof of growth differences among plants grown under different conditions^{2, 11, 15-21)}. The cause of difference in the C/F ratio has been attributed to the difference of the distribution ratio of photosynthate to both systems^{2, 10-14)}. In the future the distribution ratio will be determined directly by the physiological procedure e. g. with proper tracer technique, and this information may give a physiological foundation to the growth analysis which is so far carried out only on the basis of actual growth observed in dry weight. Anyhow, the C/F ratio is, if Eq. (1) is applicable, expressed with μ , ν and W as follows:

$$C/F = (\nu/\mu)W + 1/\mu - 1. \quad (3)$$

That is, there exists a linear relationship between the C/F ratio and W , because ν/μ and $1/\mu$ keep constant values in a plant species grown under a given condition. The C/F ratio- W relationship in barley was illustrated by Takada¹⁵⁾.

For the allometric relation between the plant weight and the foliage weight, a formula $F = aW^b$, where a and b are constants, has been adopted by Kira²²⁾ and others. They did not derive this equation from the growth of plants continuously grown under a certain environmental condition, but from weight variation among the same-aged plants constituting a stand or among the plants grown under different micro-environment conditions. So that, such an equation is not suited to be used for the assessment of the distribution ratio mentioned above.

Distribution ratio of net photosynthate in shaded plants

Dry-weight growth under the condition of various daylight intensities was examined in isolated plants on the tilled and manured ground. Light intensity was adjusted to be 10, 20 (or 22), 30, 50 and 75% of full daylight by screening with wooden lattice. The experiments were carried out in *Helianthus annuus*, "Large-Russian" (Expt. I in July-Aug. 1958¹⁸⁾, Expt. II in Aug.-Oct. 1960, Expt. III. in July-Sep. 1960¹⁴⁾), *Vicia faba*

(Expt. I in Aug.-Oct. 1958, Expt. II in Nov. 1959-Apr. 1960), *Fagopyrum esculentum* (Aug.-Sep. 1959), *Cryptotaenia canadensis* var. *japonica* (June-Aug. 1959), which is sometimes cultivated as vegetable on shady site in Japan, and in *Phaseolus aureus* (June-July 1959)¹⁴⁾. These plants were sampled about weekly to measure leaves, stems (including petioles), roots and reproductive organs in dry weight. These measurements were, except for *H. annuus* in Expt. III, continued till the early flowering stage, since too much amount of senescent leaves were shed in the later growth stage after flowering.

Fig. 1. Relation between the total plant dry weight (W) and the dry weight of photosynthetic system (F), and distribution ratio of net photosynthate to the F system (δ). In *Fagopyrum esculentum* grown under various light intensities which are indicated by numerals at the curves. The curves are obtained with Eqs. (1) and (2). Details, see in the text.

The graphic relations between the weight of photosynthetic system (F) and the total plant weight (W), both of which included respectively the dry weight of dead parts, are demonstrated in Figs. 1-a and 2-a. The F - W relations under various shading conditions were also given in *Impatiens parviflora* by Evans and Hughes²³⁾. To the F - W relations Eq. (1) was applied, and the constants μ and ν were calculated using the C-D rule after Shinozaki and Kira²⁴⁾. The results are summarized in Table 1.

Table 1. Constants (μ and ν) of the formula $F=\mu W/(1+\nu W)$ applied to the smoothed F - W lines (cf. Figs. 1-a and 2-a), in differently shaded plants.

Rel. light intensity	100%		75%		50%		30%		20 (or 22)%		10%	
	μ	ν	μ	ν	μ	ν	μ	ν	μ	ν	μ	ν
<i>F. esculentum</i>	0.71	0.50	0.55	0.54	0.54	0.68	0.53	1.0	0.47	3.33	0.30	10.0
<i>H. annuus</i> (Expt. I)	0.52	0.0	0.52	0.0	0.48	0.0	0.44	0.0	0.44	0.0	0.74	0.0
" (Expt. II)	0.49	0.0	0.49	0.0	0.48	0.0	0.43	0.0	0.32	0.0		
" (Expt. III)	0.62	0.012	0.44	0.012	0.44	0.012			0.36	0.0	0.27	0.0
<i>V. faba</i> (Expt. I)	0.40	0.0	0.67	0.50	0.39	0.06	0.12	0.0				
" (Expt. II)	0.63	0.048	0.61	0.061	0.58	0.091	0.56	0.12	0.54	0.18	0.50	0.30
<i>Ph. aureus</i>	0.55	0.0			0.49	0.0			0.42	0.0	0.40	0.0
" †	0.50	0.0	0.45	0.0	0.44	0.0	0.42	0.0	0.42	0.0		
<i>C. canadensis</i>	0.65	2.40	0.69	1.65	0.67	2.46	0.64	1.09	0.55	0.0	0.50	0.0

† by Nomoto *et al.*²⁵⁾

The F - W lines were clearly curved in *F. esculentum*, *H. annuus* and *V. faba* as seen in Figs. 1-a and 2-a. In *C. canadensis* var. *japonica* they curved slightly, and in *Ph. aureus* they were rectilinear. The F - W relations of young potted *Ph. aureus* plants which were obtained from the shading experimental data illustrated by Nomoto *et al.*²⁵⁾ were also represented by rectilinear lines. The F - W relation appears in a straight line, when $\nu = 0$. The constant μ in Eq. (1) indicates the increasing rate of F to the increase of W at the initial growth stage, or the tangential inclination of the F - W curve at $W=0$. The μ/ν corresponds to the maximal F , when $W \rightarrow \infty$. These constants μ and ν in Eq. (1) are also the constants in Eq. (2) which expresses the relationship between the distribution ratio (δ) and plant weight (W). This δ - W relation is deduced easily from the graphic relation of F - W . The rectilinear F - W relation indicates that

Fig. 2. F - W relation (a) and δ - W relation (b), showing the shading effect. H, *Helianthus annuus* (Expt. III); V, *Vicia faba* (Expt. II); Ph, *Phaseolus aureus*; Cry, *Cryptotaenia canadensis* var. *japonica*. Explanations, see in Fig. 1 and the text.

δ has a constant value independent of W , or $\delta = \mu$ in any growth stage. Generally, however, the distribution ratio (δ) to photosynthetic system becomes smaller with the increase of W , since $(1+\nu W)^2$ becomes larger with the increase of W .

The δ values calculated as function of W according to Eq. (2) by using μ and ν in Table 1 are plotted against W (Figs. 1-b and 2-b). In *Ph. aureus*, the distribution ratio obtained in a given relative light intensity was independent of the plant weight W , as it could be expected from the F - W relationship in Eq. (1). In the other species, such as *F. esculentum*, *H. annuus* and *V. faba*, as it was theoretically discussed above, the δ depression was accompanied with the W increment. The larger the plant weight, the less the photosynthate was distributed to the photosynthetic system.

On the other hand, the influence of shading upon the distribution ratio (δ) appeared very clearly in *F. esculentum* and *H. annuus*, and clearly *V. faba* (in the spring experiment) in the group with depressing δ with increment of W , and in *Ph. aureus* which showed a constant δ under a given light condition. In the deeper shade, the photosynthate was distributed less to the photosynthetic system and more to the non-photosynthetic system than in the strong illumination. *C. canadensis* var. *japonica*, and *V. faba* in the autumn experiment, however, did not show so clear depression of the distribution ratio δ by the shading treatment. In the former species that grows well in the shade, the highest δ appeared under the 75% light condition, and even the deep shaded plant could maintain a relatively high δ value. In *V. faba* of the autumn experiment the temperature fall in that period might suppress the shading effect on the distribution ratio, because the shading effect was clearly observed in the spring experiment as shown in Fig. 2.

The distribution ratio (δ) to the photosynthetic system is an elemental factor in determination of the F amount and the C/F ratio, and consequently of dry-matter productivity. The higher δ must bring about an advantage for the shade tolerance with larger photosynthetic system, if plants are grown singly. The constant δ independent of plant weight also gives some advantageous effect on the shade tolerance by saving the increasing of respiration loss of the non-photosynthetic system.

Considering the trend of δ changing with enlarging of W under various light intensities, we can obtain a clearer image for the shade tolerance than before. Shade intolerance is characteristic of *F. esculentum* and *H. annuus* which showed evident lowering of δ with increasing W and shading. Shade tolerance with the highest δ in the light shade of 75% and the slight depression of δ in the deep shade and at higher W has been observed in a vegetable cultivated in shady places, *C. canadensis* var. *japonica*. A typical shade plant in Europe, *I. parviflora*, showed also the highest F/W ratio in the 68% light²³). This fact may suggest that the high distribution ratio of net photosynthate to the photosynthetic system in the shade is characteristic of the plants high-tolerable in the deep shade.

Summary

A method how to assess the distribution ratio of net photosynthate was mathematically derived and adopted in an analysis of shading effect on photosynthate distribution in *Fagopyrum esculentum*, *Helianthus annuus*, *Vicia faba*, *Phaseolus aureus* and *Cryptotaenia canadensis* var. *japonica*.

1. In general, photosynthetic system (F) increases its dry weight proportionally to individual plant weight (W) in the initial growth stage, but it decreases its growth

rate with progressing W growth. This was formulated as $F = \mu W / (1 + \nu W)$, where μ and ν are constants. Then, the distribution ratio ($\delta = dF/dW$) of photosynthate to F was derived as $\delta = \mu / (1 + \nu W)^2$.

2. As to the plant growth in the shading experiments, μ and ν were obtained by using the C-D rule²⁴⁾, and the δ - W relation was derived from the above formula.

In *Ph. aureus* δ was independent of W , and in the other species it decreased with increasing W . The depression of δ with shading was evident in *F. esculentum*, *H. annuus* and *V. faba*. A shade plant, *C. canadensis* var. *japonica* has the highest δ values in the 75% light and its δ values were hardly depressed with shading. The trend of change of the distribution ratio with increasing W and shading can indicate nicely the shade tolerability of plants.

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摘 要

黒岩澄雄*・広井敏男**・高田和男***・門司正三**:

遮光された植物における光合成産物の分配率

光合成系および非光合成系への光合成産物の分配率は各系の乾物増加の個体重増加にたいする割合として求められる。従来は、乾量測定値を直接利用して算術計算で求めた。われわれは光合成系の乾量 (F) と個体重 (W) との関係から算定する方法を見いだした。すなわち F への分配率 δ を $F=f(W)$ なる関係式を微分して求めた ($\delta=dF/dW=f'(W)$)。したがって、非光合成系への分配率 ε は $\varepsilon=1-f'(W)$ となる。一般に、 W と F との増加率のちがいにともなう $f(W)$ は近似的には (1) 式で示される。したがって、 δ は (2) 式で示される。以上のことから C/F は (3) 式で表わすことができ、 $C/F \sim W$ 関係は直線になることが数式的に明らかになった。

上記の方法を 100, 75, 50, 30, 20 (または 22) および 10% の自然光下で育てたヒマワリ、ソバ、ソラマメ、ヤエナリおよびミツバに適用した。C-D 尺²⁴⁾ を用いて (1) 式の常数 μ, ν を求めて $F \sim W$ 関係式をたて、これから $\delta \sim W$ 関係を得た。ヤエナリでは W の増加に伴って δ が変化せず、他は多少の差こそあれ、 W の増加に伴って δ は減少した。また δ の遮光による低下はソバ、ヒマワリ、ソラマメで明らかにみられた。一般に δ の遮光による低下のすくないものほど耐陰性が大きいことが推論される。(*東京大学理学部附属植物園, **東京大学理学部植物学教室, ***茨城県立取手第一高等学校)。