Analysis and Modeling of Dry Matter Production Rate by Soybean Community – Curvilinear Response to Radiation Intensity –

Ryoji SAMESHIMA

(Japan International Research Center for Agricultural Science)
Ohwashi 1-2, Tsukuba, Ibaraki, 305 Japan

Abstract

The linear relationship between the amount of absorbed radiation and dry matter production by crop communities has long been known, and the proportionality constant between them is known as the radiation use efficiency (*RUE*). To analyze and predict crop production using *RUE*, the assumption is often made that *RUE* is not sensitive to radiation intensity and that dry matter production rate (*DMPR*) is a linear function of radiation intensity.

However, there is evidence in opposition to this assumption, including reports of increasing *RUE* in shade tests, and hyperbolic response of photosynthetic rate to radiation intensity. The following model was developed and used to analyze the response of *DMPR* and *RUE* to daily radiation R_S :

$$DMPR = DMPR_{\max}(R_S) * g(\alpha)$$

where $DMPR_{\max}(R_S)$ is the *DMPR* of a hypothetical soybean community absorbing all radiation, and $g(\alpha)$ represents the effect of radiation absorptivity (α). A hyperbolic curve and a straight line were employed for $DMPR_{\max}(R_S)$ and $g(\alpha)$, respectively. Field experimental data including shade tests were used to determine the parameters for the model. Two sets of parameters were required to cover the entire experimental period. $DMPR_{\max}(R_S)$ had an apparent curvilinear relationship with R_S . The model successfully described dry matter production under successive low radiation conditions, which could not be estimated by a model with *RUE* insensitive to radiation.

Key words: *RUE*, *CGR*, Growth analysis, Canopy photosynthesis, *Glycine max* (L.) Merr.

1. Introduction

The linear relationship between the amount of absorbed or intercepted radiation and dry matter production by crop communities has long been known (*e.g.* Shibles and Weber, 1966; Monteith, 1977), and the proportional constant is known as the radiation use efficiency (*RUE*, $\text{g} \cdot \text{MJ}^{-1}$). *RUE* is a convenient parameter for estimating crop dry matter production (*DMP*, $\text{g} \cdot \text{m}^{-2}$), and has often been successfully used in crop growth models.

These models typically assume that *RUE* is not sensitive to radiation intensity. That is, the dry matter production rate (*DMPR*, $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) responds linearly to radiation intensity which has often been represented by the amount of daily radiation (R_S , $\text{MJ} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$). This type of model will be referred to as the R_S -linear model in this report.

There are, however, some reports that do not support the R_S -linear model. Murata (1981), Nakaseko and Gotoh (1983), and Horie and Sakuratani (1985) observed that *RUE* changed depending on R_S . Sinclair *et al.* (1992) showed theoretically that *RUE* decreased with the increase in R_S . Murata and Iyama (1961), Kumura (1965,

Presented at the Annual General Meeting on July 25, 1989.

Received on August 7, 1995.

Accepted on January 31, 1996.

Present address: Tohoku National Agricultural Experiment Station, Morioka, Iwate, 020-01 Japan.

1968), Sakamoto and Shaw (1967), and Ingram *et al.* (1981) observed that the photosynthetic rate of a soybean community responded curvilinearly to radiation intensity. These studies suggest that there is non-linear relationship between $DMPR$ and R_S , and the R_S -linear model does not necessarily describe the real relationship between $DMPR$ and R_S over the entire range of R_S . Applying the R_S -linear model to such studies as analysis or prediction of damaged crop growth caused by low solar radiation, therefore, may lead to errors in estimation.

The purposes of this study are to develop a simple model that relates $DMPR$ to R_S with a curvilinear relationship, and to examine the response of $DMPR$ and RUE to R_S . Soybean (*Glycine max* Merr. cv. Enrei) was used for the study.

2. Materials and methods

2.1 Modeling

$DMPR$ was modeled by the following equation, which is referred to as the R_S -nonlinear model in this report:

$$DMPR = DMPR_{\max}(R_S) \cdot g(\alpha) \quad (1)$$

where $DMPR_{\max}$ is the $DMPR$ of an ideal canopy with radiation absorbtivity (α) of 1.0. $g(\alpha)$ represents the effect of α on $DMPR$. Appropriate functions for $DMPR_{\max}(R_S)$ and $g(\alpha)$ were chosen based on results found in the literature. Absorbtivity was calculated by the method of sameshima (1995).

The parameters of the model were determined by the following procedure. The square sum of differences (e^2) between the actual and calculated DMP obtained by the model was calculated as follows:

$$e^2 = \sum_{i=1}^{10} \sum_{j=1}^{N_i} (\text{Actual } DMP_{i,j} - \text{Calculated } DMP_{i,j})^2$$

where i indicates plot number (Table 1) and N_i is the number of samples for of the i th plot. A parameter set yielding minimum e^2 was determined by the Simplex method with the computer program developed by Kobayashi (1981). In this procedure, α was calculated using actual LAI . Solar radiation data (R_S) from the observatory of the National Institute of Agro-Environmental Sciences (NIAES, about 300m apart from the experimental field) were used.

In this study RUE was estimated on a daily time scale using total above-ground dry matter and absorbed radiation (see Arkebauer *et al.*, 1994).

2.2 Field experiment

Soybean (*Glycine max* Merr. cv. Enrei) was grown in 1987 and 1988 at the experimental field of the National Agriculture Research Center (lat. 36°01'N, long. 140°07'E, 25m above sea level, black volcanic ash soil). In each year, soybean was seeded on the days shown in Table 1. Plant spacing, row spacing and planting density were 0.2m, 0.6m and 8.3 plant·m⁻², respectively. 30kg·ha⁻¹ of nitrogen, 100kg·ha⁻¹ of phosphoric acid and 100kg·ha⁻¹ of potassium were applied before seeding in all the plots. The soybeans were chemically protected against pests and diseases throughout the growth period.

In three plots, shading treatments were conducted by spreading nets of cheese cloth over the plots at the height of 1.2m. At every side of these plots, the net was hung down 0.5m from the top. The shading treatments were carried out starting on August 7, 1987 and Jun 30, 1988. Soybeans of 1988b_{sh} grew spindly and could not stand

Table 1 Names, dates of seeding, flowering, and maturity, shading ratio, and size of each experimental plot.

No.	plot name	seeding	flowering	maturity	shade ratio	plot size (m)
1	1987a	Jun 30	Aug. 7	Oct. 5	—	10×20
2	1987a _s	Jun 30	Aug. 6	Oct. 5	0.48	5×20
3	1988a	May 10	Jul. 12	Oct. 5	—	10×20
4	1988b	Jun 10	Jul. 31	Oct. 6	—	10×20
5	1988b _{sl}	Jun 10	Jul. 30	Oct. 6	0.48	5×20
6	1988b _{sh}	Jun 10	Jul. 30	Oct. 1	0.78	5×20
7	1988c	Jul. 11	Aug. 21	Oct. 17	—	10×20
8	1988d	Aug. 4	Sep. 6	Oct. 31	—	10×20
9	1988e	Aug. 24	Sep. 26	—	—	10×20
10	1988f	Sep. 8	Oct. 28	—	—	10×20

straight, and glass fiber poles with a diameter of 0.005m were used to support them.

In each plot, five plants that showed average growth were sampled two or three times a week, then the median of the five was chosen for leaf area measurement (m^2) with a leaf area meter (Hayashi Inc., AAC-400). The sampled plant was placed in a dryer at 80°C for 72 hours and the total dry weight of the part above the primary leaf node was measured. Leaf area index (*LAI*) and *DMP* were determined by multiplying the leaf area and the dry weight of a plant by the planting density. These samplings and measurements were conducted from emergence until the leaves became yellow and began to fall in each plot.

To compare the inside and outside conditions of the shaded plot, solar radiation was measured in 1987a, 1987a_s, 1988b, 1988b_{sl}, 1988b_{sh} at 1.0m above the ground with solarimeters (Eiko Inc. MS42) using a data logger (Eiko Inc. SOLAC-III) connected to with a PC (NEC Inc. PC98-LT). Shading ratio was expressed as $\{1 - (\text{daily radiation inside the shaded plot}) / (\text{daily radiation outside the shaded plot})\}$.

3. Results and Discussion

3.1 Modeling

The simplest function for $DMP_{\text{max}}(R_S)$ and $g(\alpha)$ in equation (1) is:

$$DMP_{\text{max}}(R_S) = RUE \cdot R_S \quad (2a)$$

$$g(\alpha) = \alpha \quad (2b)$$

Substituting equations (2a) and (2b) into (1) with a constant value of *RUE* gives the R_S -linear model. Therefore, the R_S -linear model is regarded as a specific case of the R_S -nonlinear model.

As reported in the introduction, it has been observed that the photosynthetic rate of soybean communities has a hyperbolic response to radiation intensity. Although these results in the literature were obtained from CO_2 exchange rates on a time-scale of an hour or shorter, they suggest that *DMP* has a hyperbolic relationship with R_S . Saeki (1960) calculated that daily photosynthesis of a cockscomb (*Celosia cristata*) community responded hyperbolically to R_S . The use of the following function, therefore, should be reasonable:

$$DMP_{\text{max}}(R_S) = \{a \cdot (R_S - c)\} / \{b + (R_S - c)\} \quad (3)$$

where *a*, *b* and *c* are parameters. *c* represents the light compensation point and was ignored in this

study because it is quite small (Kumura, 1965).

Pearce *et al.* (1967) and Wells (1991) observed that the canopy photosynthesis increased in proportion to the fraction of intercepted radiation by the canopy (τ). Sameshima (1995) showed that τ is linearly related to α . These results indicate that $g(\alpha)$ is linear. It is also apparent from the definition of the R_S -nonlinear model that $g(\alpha)_{\alpha=1} = 1$ and $g(\alpha)_{\alpha=0} = 0$. Equation (2b), therefore, is applicable also to the R_S -nonlinear model.

3.2 Overview of the experimental data by the conventional method

First, the field experimental data were studied by the conventional plotting method, which will be referred to as a R_{absorbed} -*DMP* chart in this report.

Fig. 1 shows air temperature and rain fall at the NIAES observatory in 1988 and the period from seeding to the end of sampling in each plot.

The relationship between accumulated absorbed radiation (R_{absorbed} , $\text{MJ} \cdot \text{m}^{-2}$) and *DMP* for the experiments of 1988 is shown in Fig. 2. The slope of the regression line is the *RUE*. As shown in Fig. 2, the *RUE* in the five plots was nearly the same, and the averaged value was $1.36 (\text{g} \cdot \text{MJ}^{-1})$.

Air temperature in the experiments was between 14°C and 26°C (Fig. 1). Fukui *et al.* (1965) and Murata and Iyama (1961) observed that soybean

Fig. 1. Air temperature and precipitation in 1988. ◆, ●, ▲ indicate seeding, flowering, and end of the sampling of each plot, respectively. Change in five-day average temperatures is illustrated.

Fig. 2. R_{absorbed} -DMP charts.

Line in each plot indicates $RUE=1.36(\text{g}\cdot\text{MJ}^{-1})$.

photosynthesis had little response to temperature in the temperature range from 15°C to 30°C, and from 25°C to 35°C, respectively. Muchow *et al.* (1993) reported that RUE was not sensitive to temperature. Although discussing temperature effect is beyond the scope of this study, it can be assumed that air temperature had little effect on $DMPR$ and RUE in this experiment.

The R_{absorbed} -DMP charts shown in Fig. 3 use the same data as those in Fig. 2, but focus on the early growth period. RUE in this period was apparently smaller than the averaged value over the whole period ($=1.36 \text{ g}\cdot\text{MJ}^{-1}$). Nakaseko and Gotoh (1981), and Shiraiwa and Hashikawa (1993) also reported that RUE changed depending on the growth stage (they used other terminology instead of RUE).

In Fig. 4, data of the five plots in 1988 were combined. In the range where DMP was less than $20 \text{ g}\cdot\text{m}^{-2}$ ($2.4 \text{ g}\cdot\text{plant}^{-1}$), marked by the broken lines in the figure, RUE was low. In this range, RUE was $0.88 (\text{g}\cdot\text{MJ}^{-1})$. In Fig. 4, calculated DMP with RUE of $0.88 (\text{g}\cdot\text{MJ}^{-1})$, when $DMP <$

Fig. 3. R_{absorbed} -DMP charts.

Line in each plot indicates $RUE=1.36(\text{g}\cdot\text{MJ}^{-1})$.

Fig. 4. R_{absorbed} -DMP chart.

—: calculated DMP.

$20 \text{ g}\cdot\text{m}^{-2}$) and $1.36 (\text{g}\cdot\text{MJ}^{-1})$, when $DMP \geq 20 \text{ g}\cdot\text{m}^{-2}$) is illustrated.

Changes in dry matter and LAI of the three plots (1988b, 1988b_{sl}, 1988b_{sh}, each of which was seeded in the same day) are shown in Fig. 5. Decreases in dry matter and LAI caused by the shading treatments were particularly large in 1988b_{sh}. Fig. 6 is the R_{absorbed} -DMP chart for

Fig. 5. Changes in dry matter, LAI and SLA of 1988b, 1988b_{sl}, 1988b_{sh}.

Fig. 6. R_{absorbed} -DMP chart for 1988b, 1988b_{sl}, 1988b_{sh}.

1988b, 1988b_{sl} and 1988b_{sh}. RUE apparently increased in the shading treatments.

3.3 R_S -nonlinear model

Parameters for the R_S -nonlinear model, expressed by equation (2b) and (3), were derived from all the data for all plots, and the parameter set p1 given in Table 2 was obtained. Actual and calculated dry matter by R_S -nonlinear model with P1 is shown in Fig. 7 (a) for 1988b. It appears that the model estimated dry matter production successfully. Calculated dry matter in the early growth period, however, is overestimated as shown in Fig. 7 (b). This error was anticipated from the fact that RUE in the early growth period was lower than the rest of the growth period as noted above.

Table 2 Parameters for the R_S -nonlinear model.

Name	a	b	used data
P1	63.2	29.6	whole experimental period
P2	30.3	30.0	dry matter ≤ 2.4 (g·plant ⁻¹)
	40.6	12.9	dry matter > 2.4 (g·plant ⁻¹)

Fig. 7. Actual and calculated dry matter.

○ : actual

----- : calculated with the parameter set P1

————— : calculated with the parameter set P2

(b) is the enlarged figure of the early growth period of (a).

To overcome this error, the whole growth period was divided into two parts and a parameter set for each period was obtained. The obtained parameter set (P2) is given in Table 2. Dry matter production calculated with P2 agreed better than that with P1 as shown in Fig. 7 (b).

Although equation (3) can express a straight line with the proper parameters, $DMPR_{\text{max}}$ curvilinearly responded to R_S as illustrated in Fig. 8 (a). Fig. 8 (b) illustrates the dependence of RUE on R_S that is obtained by combining equation (2a) and (3). RUE decreases with an increase of R_S . Nakaseko and Gotoh (1983) and Sinclair *et al.* (1992) reported similar results. In addition to the direct effect of radiation intensity, the proportion of diffuse radiation possibly had some effect on $DMPR_{\text{max}}$ and RUE . Kumura (1968) reported that photosynthetic rate was larger when there

was a higher proportion of diffuse radiation even if the radiation intensity was the same.

$DMPR_{\max}$ has a non-linear relationship to R_S as shown in Fig. 8 (a), but DMP under normal weather conditions was successfully estimated with the R_S -linear model, except for the initial growth period. Calculated DMP by the R_S -linear model with $RUE=1.36$ was the same as the solid line in Fig. 7 (a). This indicates that DMP can be estimated well by the mean RUE corresponding to the mean R_S over the entire growth period under normal weather conditions. The R_S -linear model, however, can not be applied to conditions

Fig. 8. Dependence of $DMPR_{\max}$ and RUE on R_S calculated with the parameter set P2.

-----: when dry matter is less than 2.4 (g·plant⁻¹)
 ———: when dry matter is larger than 2.4 (g·plant⁻¹)

Fig. 9. Actual and calculated dry matter production of the shaded plots.

———: by the R_S -nonlinear model with P2
 -----: by the R_S -linear model with $RUE=1.36$

such as an extended period of low radiation as shown in Fig. 9. The calculation made using the R_S -linear model underestimates the dry matter production under low radiation intensity. On the other hand, the R_S -nonlinear model can estimate dry matter production even in such an extremely low radiation intensity as the 78% shaded plot (1988b_{sh}).

In this study, the response of $DMPR_{\max}$ to R_S was set to change suddenly when the dry matter of a plant reached 2.4 g. This was determined empirically based on the data given in Fig. 4. Shiraiwa and Hashikawa (1993) also reported that RUE was low in early growth period using cv. Enrei, however, the time of the change was later than that in this report. During the rest of the growth period, the response of RUE to R_S did not change in this study. However, Shiraiwa and Hashikawa (1993) and Muchow *et al.* (1993) reported that RUE decreased during the seed filling period. These changes of RUE are attributable to the decrease in the leaf nitrogen content (Ojima, 1965; Lugg and Sinclair, 1981; Sinclair and Horie, 1989) due to the translocation of nitrogen from vegetative to reproductive organs (Sinclair and de Wit, 1975). For more detailed description of RUE , therefore, RUE should be modeled in connection with leaf nitrogen content as in the model developed by Sinclair (1986).

Acknowledgment

The author wishes to express his gratitude to Dr. Satoshi Iwakiri and Masao Nakajima for their encouragement and suggestions.

References

- Arkebauer, T. J., Weiss, A., Sinclair, T. R. and Blum, A., 1994: In defense of radiation use efficiency: a response to Demetriades-Shah *et al.* (1992). *Agric. For. Meteorol.*, **68**, 221–227.
- Fukui, J., Ojima, M. and Watanabe, I., 1965: Studies on the seed production of soybean. *Jpn. J. Crop Sci.*, **33**, 432–436.
- Horie, T. and Sakuratani, T., 1985: Studies on crop-weather relationship model in rice (1) Relation between absorbed solar radiation by the crop and the dry matter production. *J. Agric. Meteorol.*, **40**, 331–342.
- Ingram, K. T., Herzog, D. C., Boote, K. J., Jones, J. W. and Barfield, C. S., 1981: Effects of defoliating pests on soybean canopy CO_2

- exchange and reproductive growth. *Crop Sci.*, **21**, 961–968.
- Kobayashi, K., 1981: A subroutine for function minimization by the simplex method. *Bull. Compu. Cen. Res. Agr. For. Fish., Ser. A.*, **17**, 51–71.
- Kumura, A., 1965: Studies on dry matter production in soybean plant. 2. Influence of light intensity on the photosynthesis of the population. *Jpn. J. Crop Sci.*, **33**, 473–481.
- Kumura, A., 1968: Studies on dry matter production in soybean plant. 3. Photosynthetic rate of soybean plant population as affected by proportion of diffuse light. *Jpn. J. Crop Sci.*, **33**, 473–481.
- Lugg, D. G. and Sinclair, T. R., 1981: Seasonal changes in photosynthesis of field-grown soybean leaflets. II Relation to nitrogen content. *Photosynthetica*, **15**, 138–144.
- Monteith, J. L., 1977: Climate and the efficiency of crop production in Britain. *Phil. Trans. R. Soc. Lond. B.*, **281**, 277–294.
- Muchow, R. C., Robertson, M. J. and Pengelly, B. C., 1993: Radiation use efficiency of soybean, mungbean and cowpea under different environmental conditions. *Field Crops Res.*, **32**, 1–16.
- Murata, Y. and Iyama, J., 1961: Studies on photosynthesis in upland field crops. I. Diurnal changes in the photosynthesis of eight summer crops growing in the field. *Jpn. J. Crop Sci.*, **29**, 151–154.
- Murata, Y., 1981: Dependence of potential productivity and efficiency for solar energy utilization on leaf photosynthetic capacity in crop species. *Jpn. J. Crop Sci.*, **50**, 223–232.
- Nakaseko, K. and Gotoh, K., 1981: Comparative studies on dry matter production, plant type and productivity in soybean, azuki bean and kidney bean III. Dry matter production of soybean plant at various population densities. *Jpn. J. Crop Sci.*, **50**, 38–46.
- Nakaseko, K. and Gotoh, K., 1983: Comparative studies on dry matter production, plant type and productivity in soybean, azuki bean and kidney bean VII. An analysis of the basis of radiation absorption and its efficiency for dry matter accumulation. *Jpn. J. Crop Sci.*, **52**, 49–58.
- Ojima, M., Fukui, J. and Watanabe, I., 1965: Studies on the seed production of soybean II. Effect of three major nutrient elements supply and leaf age on the photosynthetic activity and diurnal changes in photosynthesis of soybean under constant temperature and light intensity. *Jpn. J. Crop Sci.*, **33**, 437–442.
- Pearce, R. B., Brown, R. H. and Blaser, R. E., 1967: Photosynthesis in plant communities as influenced by leaf angle. *Crop Sci.*, **7**, 321–324.
- Saeki, T., 1960: Interrelationship between leaf amount, light distribution and total photosynthesis in a plant community. *Bot. Mag. Tokyo*, **73**, 55–63.
- Sakamoto, C. M. and Shaw, R. H., 1967: Apparent photosynthesis in field soybean communities. *Agron. J.*, **59**, 73–75.
- Sameshima, R., 1995: Estimating the absorptivity of solar radiation in soybean canopies – for use in crop models –. *J. Agric. Meteorol.*, **51**, 37–45.
- Shibles, R. M. and Weber, C. R., 1966: Interception of solar radiation and dry matter production by various soybean planting patterns. *Crop Sci.*, **6**, 55–59.
- Shiraiwa, T. and Hashikawa, U., 1993: Variation analysis of efficiency of intercepted radiation conversion in the accumulation of dry matter by soybean. *Jpn. J. Crop Sci.*, **62**, 1–8.
- Sinclair, T. R. and de Wit, C. T., 1975: Photosynthate and nitrogen requirements for seed production by various crops. *Science*, **189**, 565–567.
- Sinclair, T. R., 1986: Water and nitrogen limitations in soybean grain production 1. Model development. *Field Crops Res.*, **15**, 125–141.
- Sinclair, T. R. and Horie, T., 1989: Leaf Nitrogen, Photosynthesis, and crop radiation use efficiency: a review. *Crop Sci.*, **29**, 90–98.
- Sinclair, T. R., Shiraiwa, T. and Hammer, G. L., 1992: Variation in crop radiation-use efficiency with increased diffuse radiation. *Crop Sci.*, **32**, 1281–1284.
- Wells, R., 1991: Soybean growth response to plant density: relationships among canopy photosynthesis, leaf area, and light interception. *Crop Sci.*, **31**, 755–760.

ダイズ群落による乾物生産速度の解析およびモデリング — 日射強度への曲線的な反応 —

鯨 島 良 次

(国際農林水産業研究センター)

要 約

作物群落による吸収日射量と乾物生産量に比例関係が存在することは既往の多くの測定結果から明らかであり、その比例係数は日射利用効率 (*RUE*) と称されている。*RUE*を用いた生育解析・予測は多く行われているが、通常 *RUE* は日射強度依存性が無く、日射強度 (タイムスケールが一日である場合は日射量, R_S で代表される) と乾物生産速度 (*DMPR*) は比例すると仮定されている。しかし、遮光処理を行うと *RUE* が増大する事、群落光合成速度が日射強度に対して双曲線型の反応を見せる事は既知であり、これらは上の仮定に疑問を生じさせる。そこで、次の形のモデルを仮定して、*DMPR* と *RUE* の日射強度依存性を解析した (ダイズ品種エンレイを供試)。

$$DMPR = DMPR_{\max}(R_S) * g(\alpha)$$

ここで、 $DMPR_{\max}(R_S)$ は完全に日射を吸収する仮想

的な群落 (日射吸収率 = 1.0) の *DMPR*, $g(\alpha)$ は *DMPR* に及ぼす α の影響。既往の文献に見られる結果を参考に、 $DMPR_{\max}(R_S)$ には双曲線、 $g(\alpha)$ には直線を採用した。

遮光試験を含む圃場試験データからモデルのパラメータを決定した。生育初期とその後の期間で異なるパラメータを使用する必要があった。 $DMPR_{\max}(R_S)$ と R_S の明らかな曲線関係が認められた。*RUE* の R_S 依存性を考慮しない従来のモデルでは、連続する低照度下で生育するダイズの生育を再現することが出来ないが、このモデルを使用すれば可能であり、本モデルは寡日照障害解析・予測への応用が可能である。

キーワード：*RUE*, *CGR*, 生長解析, 群落光合成, *Glycine max*(L.) Merr.