

A Simulation Study of Surplus Productivity as Influenced by the Photosynthesis and Respiration Rates of a Single Leaf

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Abstract

A microcomputer simulation was used to demonstrate the overall behavior of surplus production, which was calculated from Kuroiwa's (1966) production formula, as influenced by the photosynthesis rate (p_0) at the saturated light and dark respiration rate (r_A) for a single leaf.

The effect of p_0 and r_A upon surplus production (P_s) was illustrated as a contour map and three-dimensional diagram as a function of leaf area index (A) and light attenuation coefficient (K). A maximum in this type of A - K - P_s relation was a common feature, that is, there existed an optimum light attenuation coefficient (K_{opt}) at which the highest surplus production ($P_{s, top}$) could be obtained among the maximum surplus productions ($P_{s, max}$).

Being independent of any combination of p_0 and r_A values, it emerged from the simulation that the value of $P_{s, top}$ remained constant as long as the r_A/p_0 ratio was held constant. The significance of the constancy predicted here is discussed in relation to crop and pasture production.

Introduction

The productivity of crop plants is the cumulative end result of various physiological and biochemical events such as photosynthesis, respiration and partition of assimilates among the organs of the plant concerned. Most of these events are influenced by numerous weather variables in different ways and at different times during the growth cycle. Moreover, these commonly involve highly interactive systems and nonlinear functions with thresholds and other difficult response functions.

In order to analyse such an immense complexity of production processes in a rational manner, mathematical models have played an increasingly important role in the field of crop science since the epoch-making work of Monsi and Saeki (1953). Their work clarified the significance of a canopy structure in relation to light re-distribution within a canopy which is principally determined by leaf inclination angle and leaf spatial arrangement. As

Evans (1975) has pointed out, the above study opened the way to a number of subsequent works on the modeling approach to crop photosynthesis.

The recent advent and rapid propagation of microcomputers for personal use has made it possible to deal much more effectively with such complex production processes occurring in a crop. In the present study, Kuroiwa's (1966) formula for canopy photosynthesis was used to examine, with the aid of a microcomputer, the overall trends of surplus production as a function of leaf area index (LAI) and light attenuation coefficient (K). A simultaneous graphic representation with computation was carried out on the CRT visual display unit of a microcomputer (NEC, PC9801F). All the figures illustrated here were obtained by screen-copying such pictures from the unit.

Kuroiwa's formula employed here has been extended from the original Monsi and Saeki equation so as to give daily surplus production directly by assuming the sinusoidal variation of daily light flux density over a crop canopy, on the basis of the simple assumption that only diffuse light is

irradiated into the canopy as an energy source. The distinction between diffuse and direct light has been omitted for simplicity in this formula, so that it may serve as a potent tool for evaluating the overview of daily surplus productivity, without the need for information about the solar elevation angle and the direct light intensity on each occasion, based on the productive structure of a canopy and on the physiological characteristics of a single leaf. In recent works performed to simulate the carbon dynamics of a tropical rainforest, this approach has been successfully applied to compute forest productivity (Oikawa, 1985; 1986). However, it should be kept in mind that the adverse effect of this simplicity may to a certain extent hinder the strict applicability of this formula to a real plant community, as discussed in a later section. The main objective of the present work was to examine the formula to show qualitatively the effects of changes in any of the variables. Quantitative simulation of a real community was a desirable but secondary objective.

Outline of the model

The P_g values (ton dw/ha/day) were computed using Kuroiwa's (1966) formula as stated above,

$$P_g(A, K) = \frac{2 \cdot D \cdot p_{max} \cdot \kappa}{K} \times \left[\ln \{ 1 + \sqrt{1 + K \cdot \beta \cdot I_{0, max} / p_{max}} \} - \ln \{ 1 + \sqrt{1 + K \cdot \beta \cdot I_{0, max} \cdot \exp(-K \cdot A) / p_{max}} \} \right] \quad (1),$$

where A is the leaf area index (LAI), D is the day-length (hrs), $I_{0, max}$ is the maximum light intensity at the culmination time (klux), p_{max} is the light-saturated photosynthesis rate of a single leaf (mg CO₂/dm²/hr), β is the initial slope of the light-photosynthesis relation (mg CO₂/dm²/hr/klux), K is the light attenuation coefficient of a canopy, and κ is the conversion constant from CO₂ assimilated by photosynthesis into dry matter synthesized ($\kappa=0.60$). In addition, Eq. (1) was modified from the original expression so that we could evaluate the effect of atmospheric CO₂ on canopy photosynthesis; p_{max} was assumed to be proportional to CO₂ concentration in the ambient air C_a as follows:

$$p_{max} = (C_a / 300) \cdot p_0 \quad (2),$$

where p_0 is the light-saturated photosynthesis rate at $C_a=300$ ppm.

Surplus production P_s , which means net production of the productive organ, is expressed as:

$$P_s(A, K) = P_g(A, K) - 24 \cdot \kappa \cdot r_A \cdot A \quad (3).$$

As shown in Eq. (3), Kuroiwa's formula has assumed that foliage respiration is directly proportional to LAI, as in the studies of Davidson and Philip (1958), Saeki (1960), Verhagen *et al.* (1963), and Monteith (1965). This assumption, however, does not strictly hold, because several subsequent experiments showed that it increased roughly asymptotically with increase in LAI (e.g. Ludwig *et al.*, 1965), as reviewed by Yoshida (1972).

When Eq. (3) is acceptable for an approximate relation, then there must be an optimum leaf area index A_{opt} , i.e. the LAI that gives the maximum surplus production $P_{s, max}$ at any value of K as:

$$A_{opt}(K) = \frac{1}{K} \ln \frac{K \cdot \beta \cdot I_{0, max}}{p_{max} \{ (p_{max} \cdot D / (p_{max} \cdot D - 24 \cdot \kappa \cdot r_A)) - 1 \}} \quad (4).$$

Thus, substituting A_{opt} in Eq. (4) for A in Eq. (3) yields $P_{s, max}$ as:

$$\begin{aligned} P_{s, max}(K) &= P_s \{ A_{opt}(K) \} \\ &= P_g \{ A_{opt}(K) \} - 24 \cdot \kappa \cdot r_A \cdot A_{opt}(K) \end{aligned} \quad (5).$$

However, the appearance of A_{opt} in a real crop will be considered in more detail later, in connection with the proportionality of foliage respiration against LAI.

Results

Surplus production P_s of a plant canopy, which was calculated from Eq. (3), is displayed on a contour map and three-dimensional diagram in Figs. 1 and 2. In both figures, the x-axis represents LAI (A) values from 0 to 10, and the y-axis values of the light attenuation coefficient (K) from 0.2 to 1.2. The surplus production (P_s) in terms of ton dw/ha/yr is illustrated by a contour plot with an interval of 10 ton dw/ha/yr for each graph of the series in the left-hand column and P_s is further plotted against the z-axis in the right-hand column. Fig. 1 shows the effect of the unit respiratory rate of a single leaf (r_A) on P_s values, where r_A is 1.6 in [A], 2.0 in [B] and 2.4 mg CO₂/dm²/hr in [C],

and where the light-saturated photosynthesis rate (p_0) is fixed at a standard value of 20 mg CO₂/dm²/hr. Fig. 2 shows the effect of single-leaf light-saturated photosynthetic rate (p_0) on P_s values, where p_0 is 10 in [A], 20 in [B] and 30 mg CO₂/dm²/hr in [C], and where the unit respiratory rate (r_A) is set at 10% of each p_0 value (i.e. $r_A/p_0=0.1$). The values of the other five parameters included in Eqs. (1)–(3), namely the maximum light intensity at culmination time

($I_{0,max}$), day-length (D), CO₂ concentration in the air (C_a), initial slope of the photosynthesis-light relation (β) and the conversion factor from CO₂ to carbohydrate (κ) were fixed, respectively, at 100 klux, 12 hrs, 330 ppm, 2.0 mg CO₂/dm²/hr/klux and 0.60 g dw/g CO₂.

As previously reported (Oikawa, 1985), each maximum P_s value is shown as a triangle mark in all the contour maps and three-dimensional diagrams of Figs. 1 and 2. This means that there

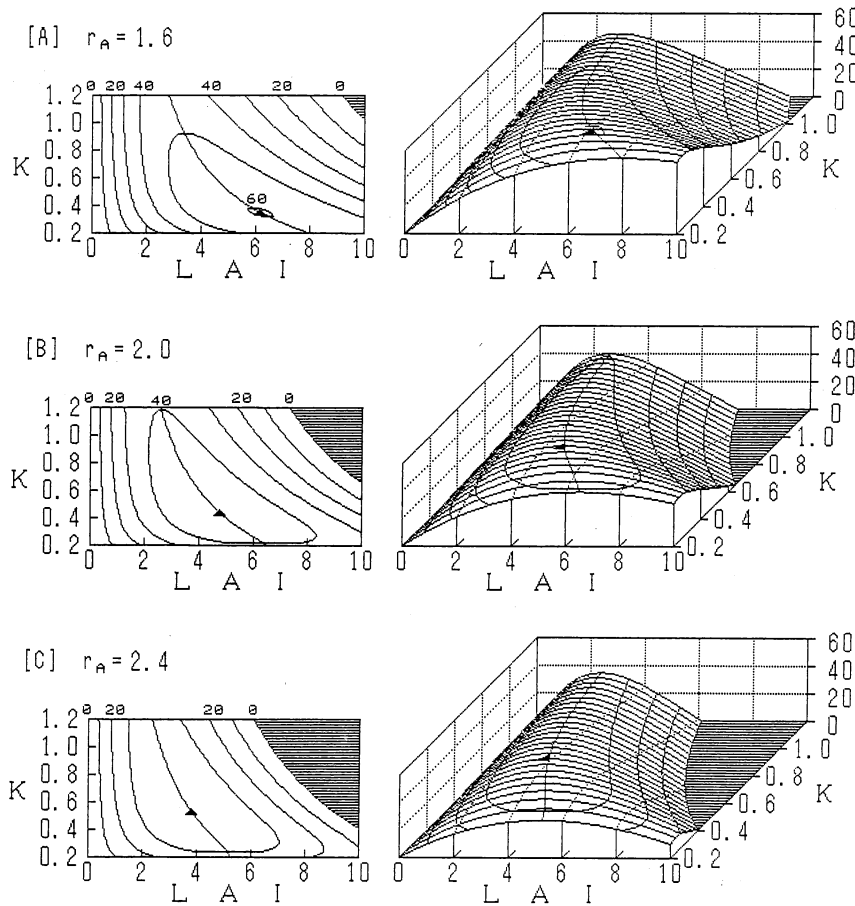


Fig. 1 Rates of surplus production (P_s) of a plant canopy under sunny conditions ($I_{0,max}=100$ klux) calculated at three rates of dark respiration of a single leaf. A, $r_A=1.6$ mg CO₂·dm⁻²·hr⁻¹; B, $r_A=2.0$; C, $r_A=2.4$. Rates are illustrated as a function of leaf area index (LAI) and attenuation coefficient of light (K) by a contour plot with an interval of 10 ton dw·ha⁻¹·yr⁻¹ for each graph of the series in the left-hand column and are further three-dimensionally plotted against the z -axis in the right-hand column. p_0 is fixed at 20 mg CO₂·dm⁻²·hr⁻¹. The rates of maximum surplus production ($P_{s,max}$) are illustrated by the ridge of a solid line, and the highest rate among them ($P_{s,top}$) is marked by a triangle in each graph.

exists an optimum light attenuation coefficient (K_{opt}) at which the highest surplus production ($P_{s, top}$) can be obtained among the $P_{s, max}$ values deduced from Eq. (5).

The effect of r_A on P_s values is clearly shown in Fig. 1, i.e. P_s becomes smaller with increasing r_A . For instance, the $P_{s, top}$ values are 60.1 ton dw/ha/yr at $r_A = 1.6$ mg CO₂/dm²/hr (Fig. 1A), 48.8 at $r_A = 2.0$ (Fig. 1B) and 39.9 at $r_A = 2.4$ (Fig. 1C), respectively. In addition, an increase in r_A shifts the position of $P_{s, top}$ in the A - K coordinate system gradually from a high A_{opt} and low K_{opt} coordinate to a low A_{opt} and high K_{opt} . This means that the superiority of relatively low K values for community production, which has been generally emphasized since the work of Monsi and

Saeki (1953), may be pronounced in a community with a relatively low single-leaf respiration rate, especially when sufficient leaf area is available to intercept the incident light. The A_{opt} line gradually becomes approximately parallel to the y -axis (i.e., independent of K values), as r_A increases, $P_{s, top}$ likewise shifts to the left.

The effect on P_s of changing p_0 under a constant r_A/p_0 ratio (Fig. 2) is similar to that of changing r_A under a constant p_0 value (Fig. 1). Namely, an increase of p_0 proportional to r_A brings about a shift of $P_{s, top}$ position from a high A_{opt} and low K_{opt} coordinate to a low A_{opt} and high K_{opt} ; the shift is similar to that in Fig. 1. We can conclude from this response that the overall pattern of P_s behavior in the A - K coordinates is

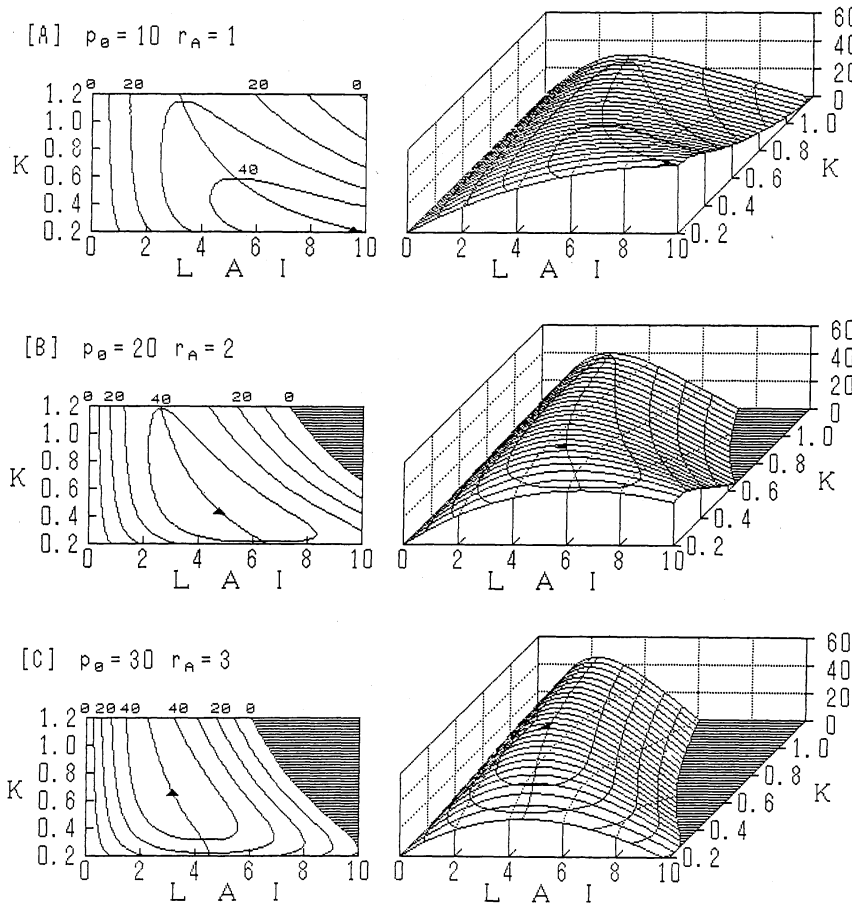


Fig. 2 Rates of surplus production (P_s) of a plant canopy under sunny conditions ($I_{0, max} = 100$ klux) calculated at three rates of light-saturated photosynthesis and dark respiration of a single leaf. A, $p_0 = 10$ and $r_A = 1$ mg CO₂·dm⁻²·hr⁻¹; B, $p_0 = 20$ and $r_A = 2$; C, $p_0 = 30$ and $r_A = 3$. Other explanations are the same as for Fig. 1. cf. Figs. 3B and 5A.

primarily determined by the value of r_A rather than that of p_0 . However, special attention should be paid to the values of $P_{s, top}$ drawn in Fig. 2; as it is obvious that they are identical to each other, i.e. a value of 48.8 ton dw/ha/yr is independent of the p_0 or r_A values, although their positions shift as mentioned above.

This startling result emerging from Fig. 2, showing the constancy in $P_{s, top}$ value, was confirmed for a wide combination of p_0 and r_A values at each K_{opt} . Fig. 3 shows examples of this constancy in the A - P_s coordinates, where $P_{s, top}$ remains the

same at any combination of p_0 and r_A values as long as the r_A/p_0 ratio is held constant. In Fig. 3, three levels of the r_A/p_0 ratio, corresponding to the three graphs in Fig. 1, have their respective constant $P_{s, top}$ values unchanged by the p_0 and r_A values, $P_{s, top}$ being greater with a low r_A/p_0 ratio. The value of $P_{s, top}$ decreases from 60.1 ton dw/ha/yr at $r_A/p_0 = 0.08$ (Fig. 3A) to 39.8 at $r_A/p_0 = 0.12$ (Fig. 3C). This range of $P_{s, top}$ belongs to a group of high net production recorded among various crops and natural grasses as summarized by Murata (1980).

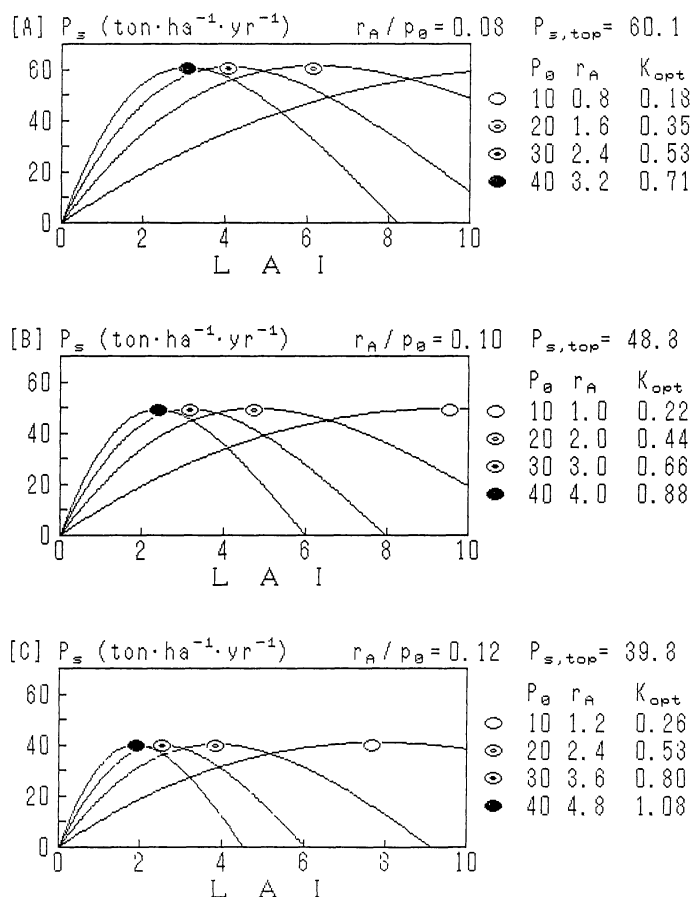


Fig. 3 Relation between leaf area index (LAI) and surplus production (P_s) at the optimum light attenuation coefficient (K_{opt}). The effect of different r_A/p_0 ratios on P_s is illustrated in the three graphs. A, r_A/p_0 ratio equal to 0.08; B, r_A/p_0 ratio equal to 0.10; C, r_A/p_0 ratio equal to 0.12. The lower the r_A/p_0 ratio, the higher the $P_{s, top}$ value (circle mark on each curve), and *vice versa*. Notice the constancy of the $P_{s, top}$ value in each graph, independent of the combination of p_0 and r_A .

Common to the three graphs in Fig. 3, the higher the photosynthesis (p_0) and respiratory rate (r_A), the lower the leaf area at which the $P_{s, top}$ value is achieved. In short, A_{opt} , giving rise to $P_{s, top}$, is attainable with a lower investment in leaf area as the p_0 and r_A values increase. The merit of the high physiological activities of a single leaf is reversed, however, by a sharp decline in surplus production (P_s) when a plant canopy exceeds its A_{opt} value.

Fig. 4 illustrates, for three combinations of p_0 and r_A , P_s contour maps and three-dimensional diagrams as in Figs. 1 and 2. The values of all independent variables except $I_{0, max}$ are identical with those of Fig. 2; $I_{0, max}$ is lowered from 100

klux in Fig. 2 to 60 klux in Fig. 4. Thus Fig. 4 represents the P_s patterns on a cloudy day, whereas Fig. 2 represents those on a sunny day. Although the overall patterns in Fig. 4 are similar to those in Fig. 2, the reduction in available light energy reduces the P_s values at any value of LAI or K . The $P_{s, top}$ decreases from 48.8 ton/ha/yr at 100 klux to 29.3 ton/ha/yr at 60 klux. The position of $P_{s, top}$ shifts with the decrease of the incident light to a greater K and lower LAI at every combination of p_0 and r_A in Fig. 4. For example, a comparison of Fig. 4A with Fig. 2A shows that the reduction in the level of incident light from 100 klux to 60 klux increases K_{opt} from 0.22 to 0.37 and decreases A_{opt} at K_{opt} from 9.5 to 5.7

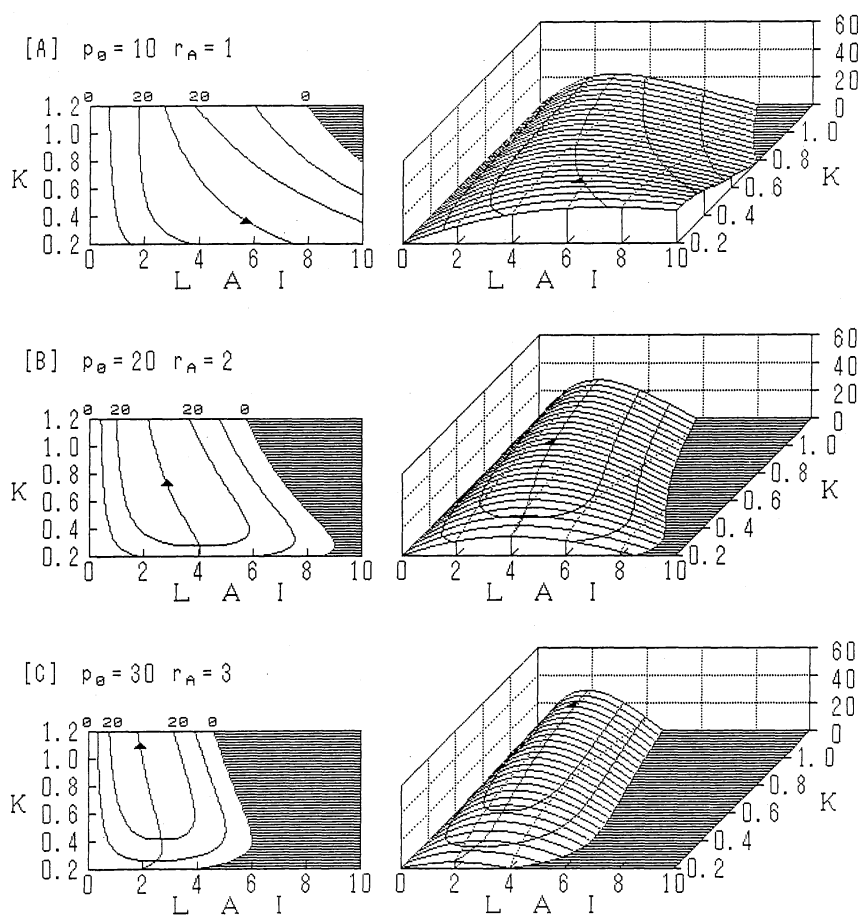


Fig. 4 Rates of surplus production (P_s) of a plant canopy under cloudy conditions ($I_{0, max} = 60$ klux) calculated at three rates of light-saturated photosynthesis and dark respiration of a single leaf. A, $p_0 = 10$ and $r_A = 1$ $\text{mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$; B, $p_0 = 20$ and $r_A = 2$; C, $p_0 = 30$ and $r_A = 3$. Other explanations are the same as for Fig. 2. cf. Fig. 5C.

when $p_0=10$ and $r_A=1$ mg CO₂/dm²/hr. The three graphs of Fig. 4 also show that the law of constant $P_{s, top}$ under conditions of constant r_A/p_0 ratio holds as in Fig. 2.

A better understanding of the importance of incident light energy in determining surplus production was obtained by comparing the production under different $I_{0, max}$ levels. Fig. 5 summarizes the effect of incident light energy on the P_s values in K_{opt} foliage; $I_{0, max}=100$ klux in [A], 80 klux in [B], and 60 klux in [C]. As incident light

energy decreased, P_s values including $P_{s, top}$ decreased, as did the optimum LAI value at which $P_{s, top}$ occurred (Fig. 5). Fig. 5 also reveals the law of constant $P_{s, top}$ for each light level.

Discussion

Although a high potential for dry-matter production is by no means the only determinant of economic yield in crop plants, it gives a definite foundation upon which other improvements may be based. High economic yield is dependent on

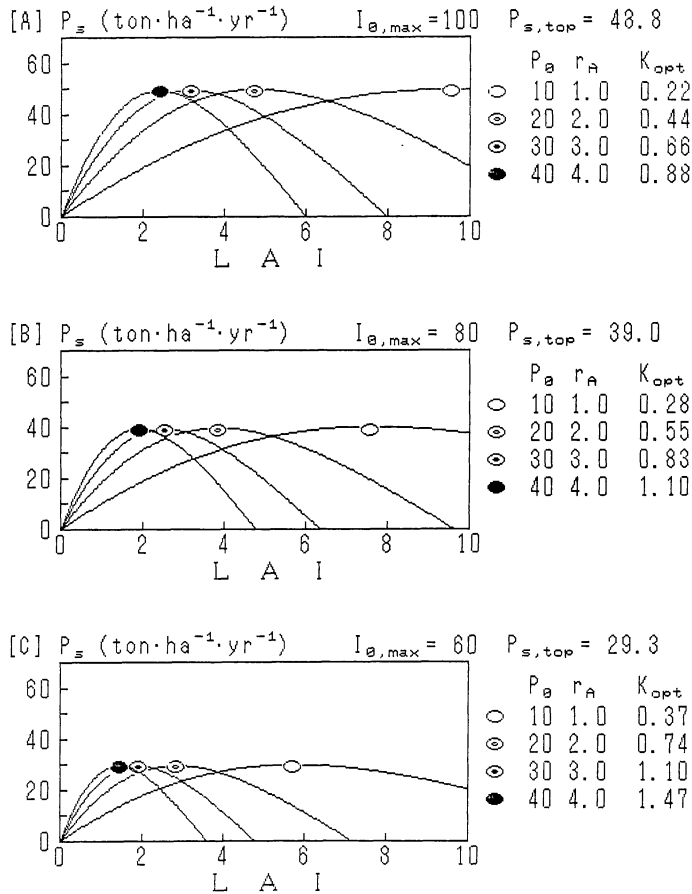


Fig. 5 Relation between leaf area index (LAI) and surplus production (P_s) at the optimum light attenuation coefficient (K_{opt}). The effect of different weather conditions on P_s is illustrated in the three graphs. A, $I_{0, max}=100$ klux (sunny conditions); B, $I_{0, max}=80$ klux (slightly cloudy conditions); C, $I_{0, max}=60$ klux (cloudy conditions). The higher the $I_{0, max}$ value, the higher the $P_{s, top}$ value (circle mark on each curve), and *vice versa*. Notice the constancy of the $P_{s, top}$ value in each graph, independent of the combination of p_0 and r_A . cf. Fig. 3.

sustained high levels of crop surplus production. If the rate of photosynthesis of a single leaf increased linearly with increased light intensity, it would not matter how the available light was distributed among the leaves in a foliage. However, because of the diminishing return response of individual leaf photosynthesis to increasing light flux, the amount of light received by each leaf needs to be known in order to accurately model the surplus production of a foliage canopy.

The present simulations using Kuroiwa's (1966) formula have clearly predicted that the surplus production, as fully described in the preceding section, is closely dependent upon the photosynthetic and respiratory capabilities of the individual leaves and upon the light distribution pattern in a foliage determined mainly by their spatial arrangement. As is well known from both theory (e.g. Monsi and Saeki, 1953) and experiment (e.g. Rhodes, 1971), Figs. 1 and 2 demonstrated that canopies with erect leaves and low values of light attenuation coefficient ($K=0.3$ to 0.5) are more productive than canopies with more horizontal leaves ($K=0.7$ to 1.0 or more) under sunny conditions and large values of LAI, where erect leaf canopies intercept virtually all incident light. However, it is worth noting that the superiority of lower K values gradually disappears as the leaf respiratory rate (r_A) increases (cf. Figs. 1C and 2C). For example, the optimum light attenuation coefficient (K_{opt}) becomes 1.08 in the case of $p_0=40$ and $r_A=4.8$ mg CO₂/dm²/hr (Fig. 3C). When the leaf respiratory rate lies within such a high range, canopies composed of horizontal leaves would make it possible to attain maximum production even under favorably sunny conditions.

Either an increase of p_0 or a decrease of r_A should bring about the enhancement of surplus productivity unless it is strongly associated with other physiological characteristics so as to offset the enhancement of productivity. Manipulation of the rate of dark respiration is potentially a very promising approach to varietal improvement in yield, because many plant species consume a significant portion (40–60%) of the carbon fixed daily in dark respiration. In a glasshouse experiment using *Lolium perenne* L. (perennial ryegrass) lines with contrasting rates of mature leaf dark respiration, Wilson (1982) found that populations

of a slower-respiring line had a faster net assimilation rate, greater phytomass and larger LAI than those of a faster-respiring line. The populations of the slower line showed a significant (up to 13%) increase in the annual yield, where the greatest advantage occurred mostly over mid-to-late summer when the temperature would be expected to be highest and the respiratory activity therefore greatest. Robson (1982) also obtained a similar result in a growth room experiment with two selected lines of *L. perenne*, where the slower line had a 22–34% lower rate of dark respiration per unit dry weight. These results cited here are in agreement with the computation shown in Fig. 1.

Selection for increased photosynthetic ability may be one of the possibilities which will result in increased yields of various crops, because considerable varietal differences in their photosynthetic rate (p_0) per unit leaf area have been found and the enhancement of surplus productivity is theoretically predicted by Eq. 3. Although much experimental effort has been expended in order to confirm the association between p_0 and yield, there is no clear evidence to suggest that increases in crop productivity have been accompanied by a rise in p_0 , and indeed in some cases, the rate has fallen, e.g., Osada (1966) could find no positive correlation between p_0 and grain yield among rice varieties. Ford *et al.* (1983), using 18 lines of soybean, reported that lines selected for higher p_0 may not lead to greater seed or dry matter yields. Babu *et al.* (1985) likewise reported that genotypes which had demonstrably high p_0 did not appear to be high yielders in blackgram. Most of the progress toward greater grain yield seems to be accounted for by improvements in the harvest index. Even in forage plants where any increase in above-ground phytomass is reflected directly in yield, no consistent relationship between p_0 and yield was found in tall fescue (Nelson *et al.*, 1975), in *Lolium perenne* (Rhodes, 1972), or in alfalfa (Delaney and Dobrenz, 1974).

Such paradoxical behavior might be explainable by the present simulation study, where the $P_{s, top}$ value was constant and independent of p_0 if the r_A/p_0 ratio was held constant (Figs. 2–5). A number of reports indicate that the photosynthetic and respiratory processes of plants are closely linked, both metabolically and through environ-

mental control. For instance, the daily total respiratory flux for clover plants grown under constant conditions was formulated by McCree (1970) into a linear function of two components, that is, the dry weight of a whole plant and the total photosynthetic flux during a daytime period. Recently, Koike (1985) found a positive correlation between the light-saturated net photosynthesis rate ($p_0 - r_A$) and r_A in leaves of many deciduous tree species.

As is well known, the r_A/p_0 ratio of a crop is closely associated with its adaptability for heavy manuring. For instance, using 6 rice cultivars, Osada (1966) clearly demonstrated that under heavier manuring conditions, those cultivars with higher adaptability minimize the enhancement effect of respiration rate and thus have a lower r_A/p_0 ratio, and *vice versa*. The heavier manuring conditions may have brought about excessive overshadowing of the foliage of the lower-adaptability cultivars. This suggests that the optimum leaf area index (A_{opt}) exists as deduced from Eq. (4), although McCree and Troughton (1966) have denied this, concluding that the A_{opt} observed in field experiments could be attributed to the failure to include material which died between harvests. Recently, through measurements of the CO_2 exchange rate of bermudagrass swards in a chamber, Morgan and Brown (1983) showed that A_{opt} was 4.7 at 1,600–2,000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$. Despite the low rates of respiration in the lower leaves of the canopy, the optimum leaf area index may exist in a population, although it will be necessary to further investigate experimentally the interrelationship between photosynthesis, respiration and growth.

The present simulation yields valuable information for determining the effect of photosynthesis and respiration parameters on surplus production, and it demonstrates how our knowledge of physiology and micro-meteorology can be integrated realistically. Further refined models will no doubt attempt to analyse such problems as the growth of a crop and of specific organs in relation to the total productivity. However, considerably more biological data will be required before computation of such complex interactions can be undertaken.

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References

- Babu, R. C. P., Srinivasan, S., Natarajaratnam, N. and Rangasamy, S. R. S., 1985: Relationship between leaf photosynthetic rate and yield in blackgram [*Vigna mungo* (L.) Hepper] genotypes. *Photosynthetica*, **19**, 159–163.
- Davidson, J. L. and Philip, J. R., 1958: Light and pasture growth. In *Proc. UNESCO Sympos. Climatology and Microclimatology*. Canberra 1956. Arid Zone Research **XI**, 181–187.
- Delaney, R. H. and Dobrenz, A. K., 1974: Yield of alfalfa as related to carbon exchange. *Agr. J.*, **66**, 498–500.
- Evans, L. T., 1975: The physiological basis of crop yield. In *Crop Physiology* (ed. by L. T. Evans). Cambridge Univ. Press, London. 327–355.
- Ford, D. M., Shibles, R. and Green, D. E., 1983: Growth and yield of soybean lines selected for divergent leaf photosynthetic ability. *Crop Sci.*, **23**, 517–520.
- Koike, T., 1985: Photosynthetic characteristics of various broad-leaved trees. In *Consideration of a natural forest* (ed. by Hokkaido Eirinkyo). Hoppou Ringyoukai, 116–119. (in Japanese).
- Ludwig, L. J., Saeki, T. and Evans, L. T., 1965: Photosynthesis in artificial communities of cotton plants in relation to leaf area. *Aust. J. boil. Sci.*, **18**, 1103–1118.
- Kuroiwa, S., 1966: Dry matter production of plants. In *A Series of Modern Biology Vol. 9, Ecology and Evolution*. Iwanami Shoten, Tokyo, 71–100. (in Japanese).
- McCree, K. J., 1970: An equation for the rate of respiration of white clover plants grown under controlled conditions. In *Prediction and Measurement of Photosynthetic Productivity*. Pudoc, Wageningen, 221–229.
- McCree, K. J. and Troughton, J. H., 1966: Non-existence of an optimum leaf area index for the production rate of white clover grown under constant conditions. *Plant Physiol.*, **41**, 1615–1622.
- Monzi, M. and Saeki, T., 1953: Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Jap. J. Bot.*, **14**, 22–52.
- Monteith, J. L., 1965: Light distribution and photosynthesis in field crops. *Ann. Bot.*, **29**, 17–37.
- Morgan, J. A. and Brown, R. H., 1983: Photosynthesis and growth of bermudagrass swards.

1. Carbon dioxide exchange characteristics of swards mowed at weekly and monthly intervals. *Crop Sci.*, **23**, 347–352.
- Murata, Y., 1980: Photosynthesis and Dry Matter Production. In *Photosynthesis and Dry Matter Production*. (ed. by Miyaji, S. and Murata, Y.), Rikougakusya, Tokyo, 475–510. (in Japanese).
- Nelson, C. J., Asay, K. H. and Horst, G. L., 1975: Relationship of leaf photosynthesis to forage yield of tall fescue. *Crop Sci.*, **15**, 476–478.
- Oikawa, T., 1985: Simulation of forest carbon dynamics based on a dry-matter production model. I. Fundamental model structure of a tropical rainforest ecosystem. *Bot. Mag. Tokyo*, **98**, 225–238.
- Oikawa, T., 1986: Simulation of forest carbon dynamics based on a dry-matter production model. II. Effects of dry season upon a tropical rainforest ecosystem. *Bot. Mag. Tokyo*, **99**, 213–223.
- Osada, A., 1966: Relationship between photosynthetic activity and dry matter production in rice varieties, especially as influenced by nitrogen supply. *Bull. Nat. Agr. Sci., Ser. D*, **14**, 117–188. (in Japanese with English summary).
- Rhodes, I., 1971: The relationship between productivity and some components of canopy structure in ryegrass (*Lolium* spp.). 2. Yield, canopy structure and light interception. *J. agric. Sci. Camb.*, **77**, 283–292.
- Rhodes, I., 1972: Yield, leaf-area index and photosynthetic rate in some perennial ryegrass (*Lolium perenne* L.) selections. *J. agric. Sci.*, **78**, 509–511.
- Robson, M. J., 1982: The growth and carbon economy of selection lines of *Lolium perenne* cv. S23 with differing rates of dark respiration. 1. Grown as simulated swards during a regrowth period. *Ann. Bot.*, **49**, 321–329.
- Saeki, T., 1960: Interrelationships between leaf amount, leaf distribution and total photosynthesis in a plant community. *Bot. Mag. Tokyo*, **73**, 55–63.
- Verhagen, A. M. W., Wilson, J. H. and Britten, E. J., 1963: Plant production in relation to foliage illumination. *Ann. Bot.*, **27**, 627–640.
- Wilson, D., 1982: Response to selection for dark respiration rate of mature leaves in *Lolium perenne* and its effects on growth of young plants and simulated swards. *Ann. Bot.*, **49**, 303–312.
- Yoshida, S., 1972: Physiological aspects of grain yield. *Ann. Rev. Plant Physiol.*, **23**, 437–464.

剰余生産力に対する個葉の光合成・呼吸速度 の影響のシミュレーションによる解析

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要 約

黒岩(1966)の物質生産理論式で求められる剰余生産力が、この式に含まれる各種のパラメータの変化に対してどのような振る舞をするかという問題が、コンピュータ・シミュレーションによって検討された。

この黒岩式から得られる剰余生産力を、群落の葉面積指数(A)と吸光係数(K)の関数として表わしたときに、一つの極大値が存在することが、最近報告されている(及川, 1985)。このことは最適吸光係数(K_{opt})と、それに応じた最高剰余生産力($P_{s, top}$)とがあることを意味している。そこで本論文では、剰余生産(P_s)に対する単葉の光飽和したときの光合成速度(p_0)と暗呼吸速度(r_A)

の影響が、新たに開発された等高線・三次元表示法に基づいて、重点的に調べられた。

その結果、 p_0 と r_A の変化に対する K_{opt} と $P_{s, top}$ への影響が系統的に明らかにされた。ここで特に注目される点は、 p_0 と r_A の値が変われば、 K_{opt} や A_{opt} の値は変化するが、 r_A/p_0 比が一定である限り、 $P_{s, top}$ の値は常に一定である、という関係が成り立っていたことである。引き続き、植物の葉の生理特性に基づいて、この $P_{s, top}$ 値の一定であることの、物質生産における意義が論じられた。