Studies on Photosynthesis and Primary Production of Rice Plants in Relation to Meteorological Environments

III. A model for the simulation of net photosynthesis, transpiration and temperature of a leaf and a test of its validity

Takeshi HORIE

(Division of Meteorology, National Institute of Agricultural Sciences,
P.O. Box 2, Yatabe-machi, Tsukuba-gun, Ibaraki Pref., 305)

Abstract

A semi-empirical model was proposed for the simulation of leaf temperature (T_l), and rates of net photosynthesis (P_n) and transpiration (E) of a single rice leaf in steady-states. The model consisted of two main sub-models: one is for solving the energy balance equations to give E and T_l and another for P_n . In both models the energy and mass transfer processes were expressed in terms of the diffusion resistances, namely, the boundary layer (r_a), the stomatal (r_s) and the overall mesophyll or residual (r_M) resistances. Both the sub-models were thus connected by the resistances and T_l . The diffusion resistances in dependence of wind speed (U), shortwave radiation flux intensity (I_s), the leaf temperature (T_l) and ambient humidity were formulated by means of physical and/or empirical equations. By incorporating experimentally specified parameters into the simultaneous equations thus derived, simulations were made to obtain P_n , E and T_l for various environmental conditions.

The following results were obtained from the simulations. First, with the increase in the radiation intensity (I_s) up to about $0.5 \text{ cal cm}^{-2} \text{ min}^{-1}$, E increased very sharply due to the opening of the stomata, resulting in T_l decrease or only a slight increase, and above this I_s level E and T_l both escaped from the stomatal regulations and increased proportionally to I_s . The leaf-air temperature difference ($T_l - T_a$) was larger the lower the T_a . Second, three types of curves were derived in photosynthesis (P_n)-radiation (I_s) relation, depending on the environmental conditions; a non-saturation type curve at lower T_a , a saturation type curve at near optimal T_a and an optimal type curve at supra-optimal T_a with low humidity. The difference in $P_n - I_s$ curve was attributable to I_s effect on T_l which in turn reflected on r_s and r_M . Third, as a result of the response of r_s to the leaf-air vapour pressure difference, P_n and E at lower humidity were suppressed considerably, resulting in T_l increase. Fourth, with increasing wind speed (U), P_n and E at optimal or above optimal T_a increased, whereas those at sub-optimal T_a decreased. These contradicting effects of U on P_n and E appeared through its effects on r_a and T_l .

The simulation results were compared with measured data on rice leaves by a leaf chamber method and also with data by other workers. Except for T_l at higher I_s and T_a , the model well explained the observed responses in P_n , E and T_l to the environments.

1. Introduction

With the accumulation of knowledge about physiological and physical processes of crop growth, it has become possible to integrate these fragments of knowledge into a functional dynamic model to explain and/or predict crop growth in relation to environmental conditions. Such models may be called crop growth simulation models and are actively being developed in many countries for various crops (e.g., de Wit et al., 1970 and 1978). The crop growth simulation models are being proved to be more mechanistic and explanatory than the traditional regression models in understanding and predicting crop growth and yield from weather conditions. The ultimate objective of this series of work is to develop a simulation model for rice plant growth, which may explain and predict the dynamics of the crop-weather relationships.

Since the primary substance for a crop growth is synthesized through the photosynthetic process, this process plays an essential part of the crop growth. Leaf photosynthetic activity is usually measured under laboratory conditions. The leaf photosynthetic data, thus obtained, can not directly be applied to field conditions, because the environmental conditions are usually greatly different between the laboratory and the field. It is, therefore, necessary to formulate and/or parameterize the laboratory-obtained leaf photosynthetic activities into a general model to be applicable to field environmental conditions. Many models have been proposed for the leaf photosynthetic processes, of which some are theoretical or semi-theoretical (e.g., van Bavel, 1975; Chartier and Prioul, 1976) and some are empirical or semi-empirical (e.g., Takeda and Yajima, 1975; Enoch and Sacks, 1978). These models, however, concern either only limited number of the environmental factors or some particular crops, and any comprehensive model is not yet proposed for the leaf photosynthetic and transpiration activities of rice plants, the main crop in monsoon Asia.

In this paper a semi-empirical steady-state model is proposed for the leaf photosynthesis and transpiration of rice plants in relation to air temperature, radiation flux density, ambient humidity and wind velocity. The model is constructed on

the basis of experimental data on the diffusion resistances to energy and mass transfer on rice leaves, which were reported in previous reports (Horie, 1978 and 1979), and also of information from relevant literatures. Simulation were made with this model to assess the effects of the environments on the leaf energy balance and the net photosynthesis. The validation of the model was made by comparing the simulation results with the observations. This paper describes about the model and the simulation results.

2. Description of The Model

2.1 Outline of the model

The model concerns the rates of net photosynthesis and transpiration in steady-state of a matured leaf of rice plants growing in flooding water condition with sufficient supply of nutrients. The steady-state means that the model does not cover the transient change in these rates caused by delay of the stomatal response to environments. Since the stomata of rice leaves respond to changes in radiation with a time constant of several minutes (Horie, 1978), it may roughly be said that the model gives the rates of net photosynthesis and transpiration after time has elapsed for 20–30 minutes since the change in the environments.

The model consists of two main parts: one is for solving energy balance equations on the leaf to give the boundary layer resistance, the stomatal resistance, the leaf temperature as well as the transpiration rate, because these variables are mutually dependent. Another part of the model is for calculating net photosynthesis by using the diffusive resistances and the leaf temperature derived from the former part.

2.2 Leaf energy balance and transpiration

The energy budget on a leaf may be presented by the following equations:

$$mI_s - I_l - H - LE = 0 \quad (1)$$

$$I_l = 2\lambda_l \sigma \{ (T_l + 273)^4 - (T_a + 273)^4 \} \quad (2)$$

$$H = \frac{2c_p \rho (T_l - T_a)}{r_{ah}} \quad (3)$$

and

$$E = \frac{2 \times 2.17 \times 10^{-4} (e_s(T_l) - e_a)}{(273 + T_a)(r_{av} + r_{sv})} \quad (4)$$

where m is the leaf absorptivity to shortwave radiation; I_s the shortwave radiation flux density ($\text{cal cm}^{-2} \text{sec}^{-1}$); I_l the longwave radiation flux from the leaf ($\text{cal cm}^{-2} \text{sec}^{-1}$); H the sensible heat flux density from the leaf ($\text{cal cm}^{-2} \text{sec}^{-1}$); L the latent heat for evaporation ($=580 \text{ cal g}^{-1}$); E the transpiration rate ($\text{g cm}^{-2} \text{sec}^{-1}$); λ_l the emissivity of longwave radiation of the leaf; σ Stefan-Boltzmann constant ($=13.54 \times 10^{-13} \text{ cal cm}^{-2} \text{sec}^{-1} \text{ } ^\circ\text{K}^{-4}$); T_a and T_l the air and the leaf temperatures ($^\circ\text{C}$); $c_p \rho$ the volumetric heat capacity of air ($=2.91 \times 10^{-4} \text{ cal cm}^{-3} \text{ } ^\circ\text{C}^{-1}$); e_a and $e_s(T_l)$ the water vapour pressures of the air and the leaf (mb); r_{ah} and r_{av} the diffusion resistances at the leaf boundary layer to heat and water vapour transfer, respectively (sec cm^{-1}); r_{sv} the stomatal diffusion resistance to water vapour transfer (sec cm^{-1}).

It is assumed that $e_s(T_l)$, the water vapour pressure at the leaf intercellular spaces, is saturated at the leaf temperature T_l . It is also assumed in eq. (2) that the leaf exchanges the longwave radiation with surrounding bodies of which temperature is equal to air temperature. The factor 2 in eqs. (3) and (4) accounts for the two surfaces of the leaf implying an even stomatal resistance for both surfaces.

The boundary layer diffusion resistance to heat transfer (r_{ah}) at higher wind speed is governed by forced convection and hence a function of wind speed, whereas that at very low wind by free convection and a function of temperature difference between the leaf and the air. At some intermediate of these extreme cases, r_{ah} may be governed both by the free and the forced convections. These aspects may well be formulated by assuming that the resistance due to the forced convection and that due to the free convection are parallel (Haseba, 1973), as:

$$r_{ah} = \frac{r_{fo} r_{fr}}{r_{fo} + r_{fr}} \quad (5)$$

in which r_{fo} and r_{fr} are the boundary layer resistances by forced and free convections, respectively.

Both r_{fo} and r_{fr} are related to Nusselt number Nu , a non dimensional quantity, by,

$$r_{fo} \text{ and } r_{fr} = \frac{d}{\kappa Nu} \quad (6)$$

where κ the thermal diffusivity of air ($=0.215 \text{ cm}^2 \text{sec}^{-1}$) and d the characteristic length of the leaf (cm). In the case of forced convection Nu is given

by

$$Nu = A Re^{1/2} Pr^{1/3} \quad (7)$$

and in free convection by

$$Nu = B Gr^{1/4} Pr^{1/4} \quad (8)$$

where A and B are the proportional constants; Re Reynolds number and equal to Ud/ν with U being wind speed (cm sec^{-1}) and ν the kinematic viscosity of air ($=0.151 \text{ cm}^2 \text{sec}^{-1}$); Pr Prandtl number and equal to ν/κ ; Gr Grashof number. The values of the proportional constants A and B for rice leaves are listed up in Table 1.

The Grashof number taking into account of the humidity factor is given by the following equation (Monteith, 1973);

$$Gr = agd^3 |T_{vl} - T_{va}| / \nu^2 \quad (9)$$

in which a is the thermal expansion coefficient of air ($=1/273^\circ\text{C}^{-1}$); g the gravity acceleration ($=980 \text{ cm sec}^{-2}$); T_{vl} and T_{va} the virtual temperatures of the leaf and the air, respectively. The difference in the virtual temperature is given by

$$T_{vl} - T_{va} = T_l - T_a + \frac{1-\delta}{p} \{ e_s(T_l)(T_l + 273) - e_a(T_a + 273) \} \quad (10)$$

where δ is the density ratio of the water vapour to dry air ($=0.622$) and P the atmospheric pressure ($=1013 \text{ mb}$).

On the basis of experimental data on rice leaves (Horie, 1978 and 1979), the stomatal resistance to water vapour transfer (r_{sv}) in dependence of the shortwave radiation intensity (I_s) and the leaf-air vapour pressure deficit ($VD = e_s(T_l) - e_a$) were formulated as,

$$r_{sv} = \{ r_{s,min} + (r_{s,max} - r_{s,min}) \times \exp(-\beta I_s) \} f(VD) \quad (11)$$

in which $r_{s,min}$ and $r_{s,max}$ are the minimum and the maximum resistances respectively at higher radiation level and in dark without any constraint due to water deficit; β a parameter characterizing the light dependence of the resistance; $f(VD)$ a factor to give VD effect on r_{sv} . $f(VD)$, in turn, was approximated by the following function:

$$f(VD) = 1.0, \text{ for } VD \leq 15 \text{ mb} \quad (12)$$

$$f(VD) = 0.04 VD + 0.4, \text{ for } VD > 15 \text{ mb}$$

In this model effect of the leaf water potential on r_{sv} is not considered, but instead the humidity effect is considered. This is based on the idea that the stomata of rice plants growing in flooding

water conditions may directly respond to the atmospheric humidity without the feedback system resulting from lowered leaf water content, or, in another word, on the new hypothesis of the peristomatal transpiration (Lange et al., 1971; Meidner, 1975; Sheriff, 1977). It is assumed that temperature gives no direct influence on r_{sv} .

The boundary layer diffusion resistance to water vapour transfer (r_{av}) can be calculated from that to heat transfer (r_{ah}) by (Thom, 1968),

$$r_{av} = \left(\frac{\kappa}{D_v}\right)^{2/3} r_{ah} = 0.93 r_{ah}, \text{ for forced convection} \\ r_{av} = \left(\frac{\kappa}{D_v}\right)^{3/4} r_{ah} = 0.92 r_{ah}, \text{ for free convection} \quad (13)$$

in which D_v is the molecular diffusivity of the water vapour ($= 0.242 \text{ cm}^2 \text{ sec}^{-1}$).

As is apparent from so far described, the leaf temperature (T_l), the transpiration rate (E) and the diffusion resistances (r_a and r_s) are inter-dependent each other. A unique set of solutions for these variables can only be obtained by solving the eqs. (1) through (13) simultaneously for each external environmental condition. This was done by an iteration technique of Newton-Raphson method. The applicability of this method to agro-meteorological problems was described by Takami (1977).

2.3 Net photosynthesis

From solving the energy balance equations in the previous section, the gaseous diffusion resistances and the leaf temperature are given, and then it becomes possible to simulate the net photosynthetic rate of the leaf by an equation analogous to electric circuit which is similar to Gaastra (1963). The basic equation to simulate the net photosynthetic rate (P_n) of the leaf is,

$$P_n = \frac{C_a - \Gamma}{\frac{1}{2}(r_{ac} + r_{sc}) + r_M} \quad (14)$$

where C_a and Γ are the CO_2 concentration of the external air and the compensation CO_2 concentration of photosynthesis (g cm^{-3}), and r_{ac} , r_{sc} and r_M the diffusive resistances to CO_2 transfer at the boundary layer, at the stomata and at the mesophyll, respectively.

The boundary layer and the stomatal diffusive resistances to CO_2 transfer (r_{ac} and r_{sc}) can easily be obtained from those to water vapour (r_{av} and r_{sv}) by similar equations as eq. (13) with taking

into account of the difference in the molecular diffusivity between the two gases. The mesophyll resistance r_M in eq. (14) is not only a physical diffusion resistance, but also inclusive of biochemical carboxylation and photochemical excitation resistances. The 'overall' mesophyll or the residual resistance r_M may be presented by (Monteith, 1963),

$$r_M = r_m + r_c + r_e \quad (15)$$

in which r_m , r_c and r_e are the purely physical CO_2 diffusion resistance at the mesophyll, the carboxylation and excitation resistances, respectively. At higher radiation level of saturating photosynthesis, r_e is practically zero and the photosynthetic rate (P_n) is limited by $r_m + r_c$ (Gaastra, 1963 and Jarvis, 1971), so that $r_m + r_c$ can be determined from P_n at saturating or near saturating radiation level. It is, however, difficult to separate $r_m + r_c$ into its two constituents without introducing any assumption, although an attempt was made to separate it (Chartier et al., 1970).

From the measurements of P_n of rice leaves at near saturating radiation levels, Horie (1979) showed that $r_m + r_c$ can be described by,

$$r_m + r_c = r_{M,min} \{1 + c \exp(-k_m T_l)\} \quad (16)$$

where $r_{M,min}$ is the minimum mesophyll resistance at saturating radiation intensity at higher temperature, and c and k_m are the parameters characterizing the temperature dependence of the resistance. By assuming that the excitation resistance r_e is inversely proportional to the radiation intensity, the dependence of r_e on I_s may be given by (Monteith, 1963),

$$r_e = \frac{\epsilon}{I_s - I_{sc}} \quad (17)$$

where I_{sc} is the compensation radiation intensity of P_n and ϵ a parameter relating to the maximum energy conversion efficiency of the photochemical reaction (cal cm^{-3}).

The compensation CO_2 concentration Γ is related to both photo- and dark respirations and hence is a function of the leaf temperature and the radiation intensity. Whiteman and Koller (1967), however, showed that Γ is affected by radiation only at very low intensity and otherwise is only affected by temperature. In this model Γ is formulated as a function of only T_l . As was shown in a previous report (Horie, 1979), the relation be-

tween Γ and T_l can be well approximated by,

$$\Gamma = \Gamma_{30} Q_{10g}^{(T_l-30)/10} \quad (18)$$

in which Γ_{30} is the value of Γ at $T_l=30^\circ\text{C}$ and Q_{10g} the temperature coefficient of Γ .

Eq. (14) is valid when radiation intensity is equal to or above the compensating intensity (I_{sc}). At $I_s=0$, P_n should be equal to the dark respiration rate R_d . The P_n at this radiation intensity may be given by an equation similar to eq. (18) as,

$$P_n = R_d = R_{d30} Q_{10d}^{(T_l-30)/10}, \text{ for } I_s = 0 \quad (19)$$

where R_{d30} is the dark respiration rate per unit leaf area at $T_l=30^\circ\text{C}$ ($\text{gCO}_2 \text{ cm}^{-2} \text{ sec}^{-1}$) and Q_{10d} the temperature coefficient. From the expressions of eqs. (14) and (17), the slope of the photosynthesis-radiation response curve at the compensation radiation intensity ($I_s = I_{sc}$) is equal to $(C_a - \Gamma)/\epsilon$. Provided that this slope can be extrapolated to zero radiation flux density, then I_{sc} is given by,

$$I_{sc} = R_d \cot \left(\frac{C_a - \Gamma}{\epsilon} \right) \quad (20)$$

2.4 Parameters used for the simulation

Eqs. (1) to (20) suffice to simulate the leaf temperature and the rates of net photosynthesis and transpiration of the rice leaf under various environmental conditions, when an appropriate and consistent set of data is given for the param-

eters. The experimental data for most of these parameters for rice leaves were given in previous reports (Horie, 1978 and 1979) and some other data are available in literature. Trial simulations were made with the direct use of the experimentally determined values for the parameters, and small modifications were made for the values of the parameters by comparing the simulation results with the observation data. Table 1 summarizes the values of the parameters which were finally adopted. All the simulation results given in the subsequent chapter are for 330 vol. ppm in CO_2 concentration of the air (C_a).

3. Simulation Results and Model Validation

3.1 Leaf temperature, transpiration and photosynthesis in relation to air temperature and radiation intensity

Fig. 1 gives the simulation results on the leaf temperature (T_l), the net photosynthetic rate (P_n) and the transpiration rate (E) in relation to the shortwave radiation flux intensity (I_s) and the air temperature (T_a). The simulation results show that T_l in the dark is slightly lower than T_a . With the increase in the radiation I_s , T_l at higher T_a initially decreases, whereas that at lower T_a slightly increases, and after I_s reached about $0.5 \text{ cal cm}^{-2} \text{ min}^{-1}$, T_l at all T_a increases proportionally to I_s . The shape of the response curve of T_l to I_s at

Table 1. Values of parameters used for the simulations.

parameter	explanation	value
A	constant for Nusselt number in forced convection	0.86
B	constant for Nusselt number in free convection	0.52*
β	parameter for radiation dependence of r_s	$780 \text{ cal}^{-1} \text{ cm}^2 \text{ sec}$
c	parameter for temperature dependence of r_M	107
d	effective leaf width	0.9 cm
ϵ	parameter for radiation dependence of r_M	$0.0208 \text{ cal cm}^{-3}$
Γ_{30}	compensation CO_2 concentration at 30°C	$8.6 \times 10^{-8} \text{ gCO}_2 \text{ cm}^{-3}$
k_m	parameter for temperature dependence of r_M	0.226°C^{-1}
m	leaf absorptivity to short-wave radiation	0.5
Q_{10d}	temperature coefficient of r_d	2.0
Q_{10g}	temperature coefficient of Γ	1.62
R_{d30}	dark respiration rate at 30°C	$8.3 \times 10^{-9} \text{ gCO}_2 \text{ cm}^{-2} \text{ sec}^{-1}$
$r_{M,min}$	minimum of overall mesophyll resistance	1.6 sec cm^{-1}
$r_{s,max}$	maximum stomatal resistance	45 sec cm^{-1}
$r_{s,min}$	minimum stomatal resistance	1.7 sec cm^{-1}

* quoted from Takechi (1968)

higher T_a is, thus, a concaved curve with minimum value at about $0.4 \text{ cal cm}^{-2} \text{ min}^{-1}$. The simulated pattern of the response at higher T_a agrees well with the observation on rice leaves by Ito and Haseba (1975).

The non-linear response in T_l to the radiation at lower level of I_s reflects the stomatal response to the radiation. Namely, the stomatal resistance (r_s) of the rice leaves decreases exponentially with I_s up to about $0.4 \text{ cal cm}^{-2} \text{ min}^{-1}$ and thereafter it becomes a constant value (Horie, 1978), so that the increase in the radiation energy at the lower I_s level is mainly consumed for the transpiration. The sharp increase in the transpiration rate (E) with I_s at the lower radiation level shown in Fig. 1 illustrates this fact in another way.

Another important point from the simulation results on T_l given in Fig. 1 is that the rise of T_l from T_a is larger the lower the T_a . In conditions where I_s is low and T_a is high, T_l is considerably lower than T_o . The upper part of Fig. 2 shows this fact in another way. This is derived from the fact that the slope of the saturation vapour pressure curve increases more and more steeper with T_a .

The temperature and the radiation effects on T_l so far described reflect on the rates of net

photosynthesis (P_n) and transpiration (E). The photosynthesis-radiation response curve at higher T_a exhibits a typical saturation curve or even an optimal type curve, whereas that at lower T_a a non-saturation type curve. These simulation results on P_n-I_s curves are reflecting the following aspects. Namely, at higher I_s and lower T_a , P_n is photochemically saturated, but is restricted by the sum of the mesophyll and carboxylation resistances (r_m+r_c), and in such a situation the increase in I_s leads to a rise of T_l resulting in the reduction in r_m+r_c and the increase in P_n . At near optimal T_a , r_m+r_c is nearly at its minimum value, and further rise of T_l associated with the I_s increase does not reduce r_m+r_c significantly, so that the photosynthesis-radiation response curve shows a saturation type curve. At much higher T_a , the rise of T_l associated with the I_s increase no longer gives any influence to r_m+r_c , but instead it operates to increase both the compensation CO_2 concentration Γ and the stomatal resistance due to increased leaf-air vapour pressure difference, so that in such a case P_n-I_s response curve may exhibit an optimal type curve.

As has already been described, the increase in

Fig. 1. Simulated relationships of leaf temperature (T_l) and rates of net photosynthesis (P_n) and transpiration (E) against shortwave radiation intensity (I_s) for different air temperatures (T_a). Simulations are for 70% relative humidity (RH) and 50 cm sec^{-1} wind velocity (U), and T_a is denoted with numerals on each curve.

Fig. 2. Simulation results on the relation of leaf temperature (T_l), rates of net photosynthesis (P_n) and transpiration (E) against air temperature (T_a) for different radiation intensities (I_s). Simulations are for 70% in relative humidity (RH) and 50 cm sec^{-1} in wind speed, and I_s is denoted with the numeral on each curve.

the transpiration rate (E) with the radiation is sharp at lower I_s level and it becomes less so at I_s above $0.5 \text{ cal cm}^{-2} \text{ min}^{-1}$. The initial rapid increase of E is associated with the reduction in the stomatal resistance, whereas the later slower increase is associated with the increase in T_l .

The simulated leaf temperature, net photosynthesis and the transpiration are plotted against air temperature (T_a) for different radiation levels (Fig. 2). The results shown in Fig. 2 indicates that, with the increase in I_s , the effect of T_a on P_n becomes more and more larger and optimal T_a for P_n shifts upwards. With the increase in T_a , E increases initially exponentially and as T_a becomes larger it tends to levell off. The slower increase in E at higher T_a is reflecting the fact that the increase of T_a at a constant relative humidity leads to an increase in the leaf-air vapour pressure difference which in turn increases the stomatal resistance (r_s).

3.2 Leaf temperature, transpiration and photosynthesis in relation to humidity

Fig. 3 gives the simulation results on the relationships of the leaf temperature (T_l) and rates of net photosynthesis (P_n) and transpiration (E) against ambient humidity for different T_a and I_s conditions. The left hand side of the figure concerns the results for high ($1.2 \text{ cal cm}^{-2} \text{ min}^{-1}$) radiation intensity and right hand side for low ($0.4 \text{ cal cm}^{-2} \text{ min}^{-1}$) radiation.

The simulation results given in Fig. 3 show that, with the decrease in the humidity, T_l decreases and E increases in all environmental conditions. When T_a is low, both T_l and E are shown to change linearly with the humidity, indicating that the rates of change of these variables with the humidity are constant. When T_a is high, however, the rates of the change in T_l and E with the humidity become slower as the humidity decreases. If the stomatal resistance r_s would not be affected by the humidity, the rates of the changes in T_l and E should almost be constant for entire humidity range. The non-linear responses in E and T_l to the humidity at higher T_a are derived from the built-in hypothesis that the stomatal resistance (r_s) of the rice leaves increases with the increase in the leaf-air vapour pressure difference (VD) after it exceeds a threshold value. Namely, lower humidity together with a higher T_a leads to a larger value of

Fig. 3. Simulated relationships of leaf temperature (T_l), rates of net photosynthesis (P_n) and transpiration (E) to relative humidity (RH) for different temperature (T_a) and radiation (I_s) conditions. Left for high ($1.2 \text{ cal cm}^{-2} \text{ min}^{-1}$) right for low ($0.4 \text{ cal cm}^{-2} \text{ min}^{-1}$) radiation intensities. T_a is denoted with the numeral on each curve.

VD and, hence, to a larger value of r_s , and in such a condition E is suppressed to a considerable degree resulting in T_l increase. When T_a is low, VD does not take larger value, even though the humidity is low, and in such a case both T_l and E change practically linearly with the humidity. The net photosynthetic rate P_n also decreases with lowering the humidity, and the degree of the reduction of P_n is more pronounced at higher T_a and I_s conditions. The reduction in P_n with lowering the humidity at higher T_a is due to the increase in r_s caused by the excessive transpiration demand, whereas that at lower T_a is not due to the increase in r_s but to the increase in $r_m + r_c$, the sum of the mesophyll and the carboxylation resistances, caused by the decrease in T_l . Thus, the mechanisms for the reduction in P_n with lowering the humidity are different between high and low T_a conditions. The reductions in P_n and suppression in E in conditions of higher T_a and I_s and lower humidity are well known phenomena in upland crops, and are often called 'midday depression' or 'midday closure'. Ishihara et al. (1971 a and b) found that similar phenomena as midday closure occurred also in rice plants, although the plants were growing in a field with flooding water of abundant available water. The simulation results here demonstrated may give an explanation to the mechanism through

which the midday depressions in P_n and E occur in well watered rice plants.

3.3 Leaf temperature, transpiration and photosynthesis in relation to wind speed

In Fig. 4 are given the simulation results on the relations between the wind velocity (U) and the leaf temperature (T_l) and the rates of net photosynthesis (P_n) and transpiration (E) for different air temperature (T_a) and radiation (I_s) conditions. T_l at higher I_s and lower wind speed (U) is considerably higher than T_a for all T_a conditions, whereas, at lower I_s , T_l is either higher or lower than T_a depending on T_a levels. With the increase in U , T_l in all environmental conditions approaches to T_a due to the decrease in the boundary layer resistance (r_a).

Fig. 4. Simulation results on the relationships between wind speed (U) and leaf temperature (T_l) and rates of net photosynthesis (P_n) and transpiration (E) for different air temperature (T_a) and radiation (I_s) conditions. Left for high ($1.2 \text{ cal cm}^{-2} \text{ min}^{-1}$) and right for low ($0.4 \text{ cal cm}^{-2} \text{ min}^{-1}$) radiation intensities. Numerals on each curve denote T_a .

Pronounced effects of the wind (U) on P_n can be seen when I_s is high (the left hand side of the figure). At optimal or supra-optimal T_a , the increase in U results in an increase of P_n , whereas at sub-optimal T_a it reduces P_n . The positive effect of the wind at higher T_a is derived partly from the decrease in r_a and partly from the reduction in T_l , while the negative effect solely from the reduction in T_l . The positive effect of U on P_n or E of crop leaves is often reported (e.g., Yabuki and Miyagawa, 1970). The present simulation results,

however, do suggest that a pronounced positive effect of the wind can appear only in conditions where T_a is at near or above optimal, I_s is high and r_a is limiting P_n to a considerable extent, and in other environmental conditions, the wind gives only a small or negative influence to P_n . In general, P_n of crop leaves is restricted more strongly by the environmental factors which give influences to the overall mesophyll resistance ($r_m + r_c + r_e$) or to r_s than that to r_a . This is more so in narrow leaves like rice in which r_a is much smaller than $r_m + r_c + r_e$ or r_s .

3.4 Model validation

In order to verify the model, the simulation results on the leaf temperature, the net photosynthesis and the transpiration were compared with the actual data measured by a leaf chamber method. Such validations are necessary for this sort of simulation model, because simplifications and parameterizations are unavoidably introduced for modelling the processes. The objectives of this chapter are, therefore, to check whether the processes and the parameters are adequately modelled and suitably specified. The rice cultivar used for the comparison was Nipponbare and the growing conditions of the plants and the measuring procedures for T_l , E and P_n were similar to those which have been described in Horie (1978).

Fig. 5 gives comparisons between the observa-

Fig. 5. Comparisons between the simulation and the measurements in leaf temperature (T_l), net photosynthetic rate (P_n) and transpiration rate (E) of a single rice leaf for different radiation (I_s) and air temperature (T_a) conditions. Circles denote the measurements and solid curves the simulation. Left at low air temperature (16.5°C) and right at high (29°C).

tions and the simulations in T_l , E and P_n for different air temperature (T_a) and radiation (I_s) conditions. The left hand side of the figure shows the relations between I_s and these physiological quantities at 16.5°C T_a , and the right hand side the relations at 29°C T_a . Although small discrepancies may be seen between the simulations and the observations in the absolute values of T_l , E and P_n , it may be concluded that the model well explains the patterns of responses in T_l , E and P_n of rice leaves to the radiation and the air temperature. Namely, both the model and the measurements show that, with the increase in I_s , T_l at lower I_s increases very slowly or decreases, and at I_s above about $0.5 \text{ cal cm}^{-2} \text{ min}^{-1}$ it increases almost proportionally to I_s . The model and the observations agree also in that the increase in E with I_s is sharp at lower levels of I_s and is less so at higher I_s levels. Furthermore, the experimental data given in Fig. 5 appear to show that the photosynthesis-light response curve at higher T_a level is a saturation type curve and the curve at the lower T_a is a non-saturation type curve. This seems to justify the simulation results. As has already been explained, this difference in the photosynthesis-radiation curve is derived from the radiation effect on T_l , which reflects itself on the mesophyll and the carboxylation resistances.

Similar comparisons were made for different T_a and humidity conditions (Figs. 6 and 7). Although there may again be seen some discrepancies in the absolute values between the simulations and the observations, it may still be said that the model well explains the general patterns of responses in T_l , E and P_n to T_a and humidity conditions. Namely, the model simulations and the measurements agree in that T_l is considerably higher than T_a at lower T_a , with increasing T_a , $T_l - T_a$ decreases, and at higher T_a , T_l becomes lower than T_a . The agreement can also be seen in that the optimal T_a for P_n of rice leaves is around 25°C (Fig. 6). In addition to the above aspects, the humidity effects on P_n and E can clearly be appreciated both in the simulation and the observations (Fig. 7). As have already been explained, these humidity effects are considered to be reflecting the stomatal response to the leaf-air vapour pressure difference.

From so far described, it may be concluded,

Fig. 6. Comparisons between the simulations and the observations in leaf temperature (T_l), net photosynthetic rate (P_n) and transpiration rate (E) of rice leaves in relation to air temperature (T_a). The circles denote the measurements and solid curves the simulation results.

Fig. 7. Comparison between the simulations and the measurements in leaf temperature (T_l), net photosynthetic rate (P_n) and transpiration rate (E) in relation to ambient humidity. Circles are measured values and solid curves the simulation results.

within the range of the experimental data, that all the related processes and parameters in the model are adequately modelled and specified.

4. Discussion

A considerable amount of work has been made on leaf temperature (T_l) of several crops both theoretically and experimentally. Such work is important in understanding the physiology and metabolisms in leaves in relation to environments, because the metabolic activities in leaves are more directly related to T_l than to the air temperature (T_a) and because it is not unusual in some circumstances that T_l differs from T_a more than 10°C . Recently, the leaf temperature is re-attracting attentions, because it is proved to be a good measure to detect the crop water stress by remote sensings (Jackson et al., 1977).

The leaf temperature and the transpiration rate are determined as the results of the energy partitionings on a leaf, of which processes are partly physical and partly physiological because stomatal actions are involved. Many models have been proposed for predicting T_l in relation to the environmental conditions (Drake et al., 1970; Gates and Papian, 1971; Haseba and Ito, 1975). Only a few models, however, dealt with the stomatal functionings properly with experimentally specified functions and parameters. In this paper is proposed a model to explain and predict T_l of a rice leaf together with the experimentally specified functions and parameters for the stomatal activities. Moreover, the energy partitioning model is combined with the leaf photosynthesis model in terms of T_l and the gaseous diffusive resistances to explain the leaf photosynthetic activity in relation to the environmental conditions. Within the range of the experimental data for the comparisons, the model was shown to behave reasonably.

The simulated T_l of the rice here obtained, however, is somewhat different from the data on various crops reported by other workers. One of the different point is that the temperature difference between leaf and air ($T_l - T_a$) at low T_a is considerably smaller in the rice than that in other broad leaf crops. For example, Drake et al. (1970) measured T_l of a *Xanthium* leaf with the maximum width of 6.4 cm. Their data show that $T_l - T_a$ at

10°C in T_a , 90 cm sec^{-1} in wind speed, 70% in relative humidity and at $1.25\text{ cal cm}^{-2}\text{ min}^{-1}$ in photosynthetically active radiation was about 10°C . The value of $T_l - T_a$ of the rice leaf, simulated for the same condition, is 4.8°C and thus $T_l - T_a$ of the *Xanthium* leaf is approximately two times as large as that of the rice leaf. The difference in $T_l - T_a$ between the *Xanthium* and the rice may be attributable to smaller stomatal resistance of rice and to smaller boundary layer resistance due to narrower width of rice leaves.

Another different point of the present simulation results on T_l from the measurements by other workers is on T_l at higher T_a and radiation conditions. Linacre (1964) collected the leaf temperature data for various crops from literatures, most of which were the data taken in fields under high irradiance, and plotted them against T_a . He showed that the regression line was linear and it crossed the line of equality at about 35°C T_a , indicating that, below this T_a , T_l is higher than T_a and, above this, T_l is lower than T_a . Drake et al. (1970), studying on the T_l of the *Xanthium* leaf at radiation intensity on the leaf being $1.25\text{ cal cm}^{-2}\text{ min}^{-1}$, found that T_l and T_a cross at about 35°C T_a . The present simulation results, however, show that T_l at 35°C T_a and at $1.2\text{ cal cm}^{-2}\text{ min}^{-1}$ is somewhat higher than T_a (c.f. Figs. 2, 3 and 4), although the values of $T_l - T_a$ change with the wind speed and the humidity. Ito and Haseba (1975), measuring T_l of potted rice plants at outdoors in a mid-summer day in Japan, reported that T_l of the rice is a little bit lower than T_a even at a higher radiation.

The T_l data taken in fields, however, can not directly be compared with the present simulation results, because in the simulation the radiation intensity refers to that on the leaf surface, whereas the intensity in fields means that on a horizontal sensor, so that the intensity on the leaf in outdoor conditions is considerably lower than the global radiation intensity, especially in erect leaves like rice. The T_l data taken in fields must, therefore, be put out of the present discussion, but the data by Drake et al. (1970) still remain as a matter of the discussion, because their data were taken under a comparable condition with the present simulation.

Drake et al. attributed their observation data

with *Xanthium*, that T_l became lower than T_a from 35°C T_a , to the reduction in the stomatal resistance (r_s) at higher T_a . There are some reports showing reduction of r_s at higher T_a (Raschke, 1970; Schulze et al., 1974). Raschke reported that the stomatal conductance of a maize leaf increased with T_a above 35°C T_a , escaping from the CO₂ control of the stomata. The pure temperature effect on r_s of the rice leaf was not clear within T_l up to 35°C, although a weak tendency of its decline with T_l was observed (Horie, 1979). In fact, the temperature effect on r_s of the rice was overcome by the humidity effect, because the increase in T_a at a constant relative humidity leads to an increase in the leaf-air vapour pressure difference which in turn increases r_s .

Similar humidity effect on r_s of rice was observed by Ishihara et al. (1971) in a field with flooding water under conditions of high T_a and radiation and low humidity. For the above reasons, the humidity effect on r_s is taken into consideration in this model, but it is assumed that r_s of the rice is temperature neutral within T_l up to 35°C. The stomatal response to much higher temperature and its implications to T_l , net photosynthesis and transpiration of rice leaves are the problems for further studies.

In this model long-term adaptative responses of the leaves to the radiation and the temperature are not considered. Evidences are reported, however, that leaf photosynthetic responses to radiation and temperature are affected by these environmental conditions under which the plants have grown (Murata, 1961; Björkman and Holmgren, 1963; Raschke, 1970; Ludlow and Wilson, 1971).

Data by Murata (1961) on rice leaves show that the effect of one-week shading of the plants on the photosynthesis-radiation response curve was small when the shading percentage was less than 50% of a summer radiation in Japan, and above this shading percentage, the net photosynthesis at higher radiation level was considerably suppressed. The effect of the growth temperature on the photosynthesis-temperature relation of the rice could not be found in literature, but many evidences are reported for other plants. Ludlow and Wilson (1971) found with several tropical grasses and legumes that the growth temperature affects the photosynthesis-temperature relationships of

the plants to a considerable extent and that its effect appears through the changes both in r_s and the overall mesophyll resistance (r_M). Moreover, they found that the growth temperature effects can be diminished by a 15-hour acclimatization, indicating that time constants required for r_s and r_M to adapt to a new growth temperature condition are about 15 hours.

The above mentioned adaptative responses of leaf photosynthesis to the temperature and the radiation conditions can only be explained by a dynamic model in which the adaptative processes are incorporated in proper manners. To expand the present model to such a dynamic model, more experimental work is needed on the rice plants about the adaptations in the photosynthetic activities to the growth environments.

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Literature Cited

- 1) Björkman, O. and Holmgren, P., 1963: Adaptability of the photosynthetic apparatus to light intensity in ecotype from exposed and shaded habitats. *Physiol. Plant.*, **16**, 889-914.
- 2) Chartier, P., Chartier, M., and Čatský, J., 1970: Resistances for carbon dioxide diffusion and for carboxylation as factors in bean leaf photosynthesis. *Photosynthetica*, **4**, 48-57.
- 3) Chartier, P. and Prioul, J. L., 1976: The effect of irradiance, carbon dioxide and oxygen on the net photosynthetic rate of the leaf: a mechanistic model. *Photosynthetica*, **10**, 20-24.
- 4) Drake, B. G., Raschke, K., and Salisbury, F. B., 1970: Temperatures and transpiration resistances of *Xanthium* leaves as affected by air temperature, humidity, and wind speed. *Plant Physiol.*, **46**, 324-330.
- 5) Enoch, H. Z., and Sacks, J. M., 1978: An empirical model of CO₂ exchange of a C₃ plant in relation to light, CO₂ concentration and temperature. *Photosynthetica*, **12**, 150-157.
- 6) Gaastra, P., 1963: Climatic control of photosynthesis and respiration. In: *Environmental control of plant growth*, ed. by L. T. Evance,

- 113-40. Academic Press, New York.
- 7) Gates, D. M. and Papian, L. E., 1971: *Atlas of energy budgets of plant leaves*. Academic Press, New York.
- 8) Haseba, T., 1973: Studies of transpiration in relation to the environment (5). Influence of short-wave radiation and air temperature on transpiration. *J. Agr. Met., Tokyo*, **29**, 189-197.*
- 9) Haseba, T. and Ito, D., 1975: *ibid.* (7). Variation of transpiration rate and leaf temperature with meteorological elements. *J. Agr. Met., Tokyo*, **30**, 173-82.*
- 10) Horie, T., 1978: Studies on photosynthesis and primary production of rice plants in relation to meteorological environments. I. Gaseous diffusive resistances, photosynthesis and transpiration in the leaves as influenced by radiation intensity and wind speed. *J. Agr. Met., Tokyo*, **34**, 125-36.
- 11) Horie, T., 1979: *ibid.* II. Gaseous diffusive resistances, photosynthesis and transpiration in the leaves as influenced by atmospheric humidity, and air and soil temperatures. *J. Agr. Met., Tokyo*, **35**, 1-12.
- 12) Ishihara, K., Ishida, Y. and Ogura, T., 1971a: The relationship between environmental factors and behavior of stomata in the rice plant. 2. On the diurnal movement of the stomata. *Proc. Crop Sci. Soc. Japan*, **40**, 497-504.*
- 13) Ishihara, K., Ishida, Y. and Ogura, T., 1971b: *ibid.* 3. On the aperture of the stomata and their diurnal movement in the leaf at different position on the stem. *Proc. Crop Sci. Soc. Japan*, **40**, 502-12.*
- 14) Ito, D. and Haseba, T., 1975: Leaf temperature and transpiration of rice plants. *Proc. of The Annual Meeting of Agr. Met. Soc. Japan*, Dec. 4-6, 1975, pp. 14.**
- 15) Jackson, R. D., Idso, S. B., Reginato, R. J. and Ehrlir, W. L., 1977: Crop temperature reveals stress. *Crops and Soils Magazine/June-July '77*, 10-13.
- 16) Jarvis, P. G., 1971: The estimation of resistance to carbon dioxide transfer. In: *Plant photosynthetic production, manual of methods* (ed. by Šesták, T., Čatský, P., and Jarvis, P. G.) pp. 556-631. Dr. W. Junk N. V. Publishers, The Hague.
- 17) Lange, O. L., Lösch, R., Schulze, E. D. and Kappen, L., 1971: Responses of stomata to change in humidity. *Planta (Berl.)*, **100**, 76-86.
- 18) Linacre, E. T., 1964: A note on a feature of leaf and air temperatures. *Agr. Meteorol.*, **1**, 66-72.
- 19) Ludlow, M.M. and Wilson, G.L., 1971: Photosynthesis of tropical pasture plants. II. Temperature and illuminance history. *Aust. J. Biol. Sci.*, **24**, 1065-75.
- 20) Meidner, H., 1975: Water supply, evaporation and vapour difference in leaves. *J. Exp. Bot.*, **26**, 666-73.
- 21) Monteith, J. L., 1963: Gas exchange in plant communities. In: *Environmental control of plant growth* (ed., L. T. Evance), pp. 95-112. Academic Press, London.
- 22) Monteith, J. L., 1973: *Principles of environmental physics*. 147 pp. Edward Arnold Publishers, London.
- 23) Murata, Y., 1961: Studies on the photosynthesis of rice plants and its culture significance. *Bull. Nat. Inst. Agr. Sci., Ser. D*, 1-170.
- 24) Raschke, K., 1970: Temperature dependence of CO₂ assimilation and stomatal aperture in leaf sections of *Zea Mays*. *Planta (Berl.)*, **91**, 336-63.
- 25) Sheriff, D. W., 1977: Evaporation sites and distillation in leaves. *Ann. Bot.*, **41**, 1081-82.
- 26) Schulze, E.-D., Lange, O. L., Evenari, M., Kappen, L. and Buschbom, U., 1974: The role of air humidity and leaf temperature in controlling stomatal resistance of *Prunus armeniaca* L. under desert condition. I. A simulation of the daily course of stomatal resistance. *Oecologia (Berl.)*, **17**, 159-170.
- 27) Takami, S., 1977: A modelling approach to the mass and energy transfer through the soil-plant atmosphere system. *J. Agr. Met., Tokyo*, **32**, 209-16.**
- 28) Takechi, O., 1968: Leaf temperature and energy balance in plants. *J. Agr. Met., Tokyo*, **24**, 95-102.**
- 29) Takeda, T. and Yajima, M., 1975: An improvement of semi-empirical method for estimating the total photosynthesis of the crop population. I. On light-photosynthesis curve of rice leaves. *Proc. Crop Sci. Soc. of Japan*, **44**, 343-49.*
- 30) Thom, A. S., 1968: The exchange of momentum, mass, and heat between an artificial leaf and the air flow in a wind-tunnel. *Qurt. J. Roy. Meteor. Soc.*, **44**, 44-55.
- 31) van Bavel, C. H. M., 1975: A behavioral equation for leaf carbon dioxide assimilation and a test of its validity. *Photosynthetica*, **9**, 165-76.
- 32) Whiteman, P. C., and Koller, D., 1967: Interactions of carbon dioxide concentration, light intensity and temperature on plant resistances to water vapour and carbon dioxide diffusion. *New Phytol.*, **66**, 463-73.

- 33) Wit, C. T. de, Brouwer, R., and Penning de Vries, F. W. T., 1970: The simulation of photosynthetic systems. In: *Proc. of the IBP/PP Technical meeting, Trebon, 14-21, September 1969*, pp. 47-60. PUDOC, Wageningen.
- 34) Wit, C. T. de et al., 1978: *Simulation of assimilation, respiration and transpiration of crops*. 141 pp. PUDOC, Wageningen.
- 35) Yabuki, K. and Miyagawa, H., 1970: Studies on the effect of wind speed upon the photosynthesis (2). The relation between wind speed and photosynthesis. *J. Agr. Met., Tokyo*, **26**, 137-41.*
- * in Japanese with English summary and
** in Japanese without English summary.

気象環境とイネの物質生産に関する研究

III. 個葉の光合成, 蒸散および葉温のシミュレーションモデルとその妥当性の検証

堀 江 武

(農業技術研究所気象科, 茨城県筑波郡谷田部町観音台 3-1-1)

要 約

定常状態におけるイネ個葉の光合成, 蒸散および葉温と気象環境との関係を説明・予測するための半経験的なシミュレーションモデルが提出された。このモデルは, 葉面の熱収支式を解いて拡散抵抗, 葉温そして蒸散速度をもとめるサブモデルと, このようにして得られるガス拡散抵抗と葉温を用いて光合成速度をもとめるサブモデルとから成立っている。葉面境界層抵抗(r_a), 気孔抵抗(r_s)および包括葉肉抵抗(r_M)と風速, 日射, 葉温および湿度との関係は物理学的な関係式あるいは経験式によって与えられている。実験データに基づいて決められた諸パラメータの値を用いて, 光合成, 蒸散および葉温に及ぼす気象環境の影響を評価するためのシミュレーションが行なわれた。シミュレーション結果はつぎのように要約される。

第一に, 全短波放射強度が $0.5 \text{ cal cm}^{-2} \text{ min}^{-1}$ 附近までは, 光の増加につれて気孔が開くので, 蒸散は急激に増加し, 一方葉温は減少するかごくわずかに増加しない。この光強度以上では蒸散, 葉温とも気孔の制御を外れて, 日射に比例して増加する。この場合葉-気温差は気温が低いほど大きくなる。第二に, 光-同化曲線の形は, 低気温下では不飽和型, 適温に近い気温条件下で

は飽和型, そして適温以上に気温が高くかつ湿度が低いときには最適値型の曲線になることが予測された。このように環境条件によって光-同化曲線の形が異なるのは, 日射が葉温に影響しそれがさらに r_s と r_M に反映し, その影響の現われ方が温・湿度条件によって異なるためである。第三に, r_s が葉-空気間の水蒸気張力差によって変化することにより, 湿度の低下につれて光合成は著しく減少し, 蒸散の増加と葉温の低下が抑制された。第四に, 気温が適温以上のときには, 風速の増加につれて光合成, 蒸散はともに増加するが, 気温が低いときには逆に風速とともに減少する。このような風速の複雑な効果は, 風速が r_a と葉温の両者に及ぼす影響を介して表われたものである。

このようなシミュレーション結果は, ガス収支法によって測定された光合成と蒸散, 葉温の実測値および他の研究者の実測データと比較検討された。気温が高くかつ日射が強い条件下での葉温のシミュレーション値が実測データよりも幾分高くなることを除いては, モデルは光合成, 蒸散および葉温の気象環境に対する反応の実測データをよく説明した。