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

II. Gaseous diffusive resistances, photosynthesis and transpiration in the leaves as influenced by atmospheric humidity, and air and soil temperatures.

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Abstract

With the purpose to obtain necessary plant data for constructing a simulation model for photosynthesis and growth of rice plant, measurements were made on rice leaves with a leaf chamber method, of the diffusive resistances of stomata (r_s) and mesophyll (r_M) and also of rates of net photosynthesis (P_n) and transpiration (E) in relation to ambient humidity, air and soil temperatures.

Oscillation in P_n , E and also in temperature difference between leaf and air was observed at relative humidity less than 40% at 30°C, which was equivalent to 25 mb in vapour pressure difference (VD) between leaf and air. The period of the oscillation appeared to be 15 minutes and the amplitude increased with VD increase. The oscillation was found to be caused by that of the stomata. At VD less than 15 mb r_s was constant, but above this VD it increased almost proportionally to VD increase, while r_M was unaffected by VD . As a consequence, P_n and E both were suppressed at higher VD to a considerable extent.

With the increase in leaf temperature at a constant relative humidity, r_s seemingly increased. However, the apparent increase in r_s with the temperature was attributable to the increase in VD associated with the temperature increase, and r_s corrected with VD appeared to decrease with the temperature. It was found that r_M decreases with the increase in temperature in negative exponential fashion. A treatment of 10°C soil temperature for 22 hours resulted in an increase in r_s by 30–40% and a reduction in P_n by 7–11% to those at 20°C soil temperature.

Based on these experimental evidences, a numerical evaluation was made for the interacting effects of the air temperature and the humidity on P_n and E . It was suggested that the optimal temperature for P_n may shift upwards with the increase in the humidity and that P_n at the optimal temperature is higher the higher the humidity.

1. Introduction

This series of work has been initiated with the intention to develop a simulation model for rice plant, which may explain and predict the photosynthesis and the growth in relation to the meteorological environments. To obtain necessary data for constructing the model, gaseous diffusive properties of rice leaves in dependence of the

environments have been investigated at first, since very little is known in rice, the main crop in monsoon Asia, about the stomatal and the mesophyll diffusive resistances in relation to meteorological factors and since these resistances play a key role in the plant-environment interactions. In continuation of a previous report about the gaseous diffusive resistances of rice leaves in relation to wind velocity and radiation intensity (Horie, 1978), this report concerns the effects of atmospheric humidity and air and soil temperatures upon the

diffusive resistances of the leaves.

The effects of atmospheric humidity and air temperature on the stomatal diffusive resistance to water vapour and CO₂ transfer, and hence on the photosynthesis and the transpiration, appear to be still conflicting. For example, Lange et al. (1971), Schulze et al. (1972) and Aston (1976) reported that the stomatal resistance changed to a considerable extent with the change in the atmospheric humidity, while Barrs (1973) and Rawson and Begg (1977) reported no stomatal response to the humidity. As for temperature effect, Meidner and Mansfield (1968) reviewed literature thoroughly and reported that the temperature effects on stomatal aperture were also conflicting. They made an attempt to explain the seemingly conflicting temperature effects by introducing the CO₂ factor in the leaf intercellular spaces.

The rice plants are grown in flooding water conditions in most growing period and hence the water environment, which gives the largest influence on the stomatal resistance, is greatly different from other crops, so that the stomatal responses to the environments are expected to be different from other crops. Ishihara et al. (1971 a and b) made measurements of degree of the stomatal aperture in rice leaves under field conditions with an infiltration method, and found that the stomatal aperture was affected to a marked degree with the humidity condition at the field. If the stomatal resistance is sensitive to the atmospheric humidity, then the conflicting temperature effects on the stomatal resistance might be explained, at least partly, from the humidity factor, because the saturation vapour pressure deficit in leaves is a function of temperature. Moreover, it would also be the case that the humidity condition affects the temperature-photosynthesis relationships.

To make the above mentioned points much clearer, measurements were made on rice leaves of the diffusive resistances of the stomata and the mesophyll and also of the rates of net photosynthesis and transpiration in relation to the humidity and air and soil temperatures. This paper describes the effects of the ambient humidity, air and soil temperatures on the stomatal and the mesophyll resistances and also on the rates of net photosynthesis and transpiration of rice leaves.

2. Material and Methods

Most measurements were made on a rice variety of "Nipponbare", a most popular rice cultivar in Japan. In the measurements of photosynthesis-temperature relation, a rice cultivar "Reimei", a variety only raised at northern district of Japan, was also used for comparison. The growing conditions of these rice plants were same as have been described in a previous report (Horie, 1978).

Measurements of net photosynthesis and transpiration were made with the leaf chamber method on intact leaves of potted rice plants at the maximum tillering stage. The setup used for the simultaneous measurements of the net photosynthesis and the transpiration has already been described in the previous report. Namely, the setup allows the measurements under controlled conditions of air temperature, humidity and radiation intensity at any desired level. The rate of net photosynthesis or transpiration was determined by multiplying the air flow rate through the chamber to the difference in CO₂ concentration or in water vapour concentration between the inlet and outlet of the chamber. The CO₂ concentration difference was measured with a differential type infrared CO₂ analyser (Beckman, model 865) and the water vapour with a dew-point hygrometer (EG & G, model 880). Average leaf temperature over the leaves in the chamber was measured with four pairs of copper-constantan thermocouples of 0.1 mm in diameter, which were stuck on the abaxial surfaces of the leaves.

Most measurements were made under a constant conditions of short-wave radiation intensity being $0.64 \text{ cal cm}^{-2} \text{ min}^{-1}$ ($=0.28 \text{ cal cm}^{-2} \text{ min}^{-1}$ in PAR) and CO₂ concentration in the chamber about 330 ppm, with the exception of those for CO₂ compensation points of photosynthesis. The CO₂ compensation points were determined by measuring photosynthesis under different CO₂ concentration in the chamber, including CO₂-free air. The CO₂ concentration was controlled at a given level by changing the mixing ratio of normal air and CO₂-free air produced with soda lime. Soil temperature treatments were given by placing the pot in a temperature-controlled water bath. On each measurement, 6 or more leaves from different nodes and tillers of a plant were inserted into the

chamber. Thus, the rates of net photosynthesis and transpiration gave averaged values over the leaves per plant.

The total diffusive resistance to water vapour transfer between the air and the intercellular spaces in the leaf was calculated from the following equation:

$$r_a + r_s = \frac{2 \times 2.17 \times 10^{-4}}{E} \left\{ \frac{e_s(T_l)}{273 + T_l} - \frac{e_a}{273 + T_a} \right\} \quad (1)$$

in which $r_a + r_s$ is the total diffusive resistance in sec cm^{-1} ; E the rate of transpiration in $\text{gH}_2\text{O cm}^{-2} \text{sec}^{-1}$; T_l and T_a the leaf and the air temperatures in centigrade; $e_s(T_l)$ the saturation vapour pressure (mb) at T_l ; e_a the vapour pressure in the air (mb). The factor 2 accounts for an even stomatal distribution on both surfaces of the leaf. The boundary layer resistance (r_a) on the leaves in the chamber, as determined with model rice leaves made of a filter paper, was shown to be given by the following equation (Horie, 1978):

$$r_a = 2.1 d^{1/2} U^{-1/2} \quad (2)$$

where 2.1 is a proportional constant; d the effective leaf length along the wind direction; U the wind speed in cm sec^{-1} . By subtracting r_a from the total diffusive resistance given by eq. (1), the stomatal diffusive resistance r_s can be evaluated.

The mesophyll resistance r_M was calculated by the following equation, which is derived from Holmgren, Jarvis and Jarvis (1965):

$$r_M = \frac{C_a - \Gamma}{P_n} - \frac{r_{ac} + r_{sc}}{2} \quad (3)$$

in which C_a is the ambient CO_2 concentration; Γ the compensation CO_2 concentration in photosynthesis; P_n the rate of net photosynthesis; r_{ac} and r_{sc} the diffusive resistances to CO_2 transfer at the boundary layer and at the stomata. r_{ac} and r_{sc} were calculated from those to water vapour transfer, as (Thom, 1968 and Jarvis, 1971):

$$\begin{aligned} r_{ac} &= r_a \left(\frac{D_H}{D_C} \right)^{2/3} \\ \text{and} \\ r_{sc} &= r_s \left(\frac{D_H}{D_C} \right) \end{aligned} \quad (4)$$

where D_H and D_C are the molecular diffusivities of water vapour and carbondioxide, respectively. According to Slatyer and Jarvis (1966), 1.68 was adopted for the ratio D_H/D_C .

As has already been described in the previous report, the mesophyll resistance r_M , thus determined, is not purely physical resistance to CO_2 transfer in the liquid phase in the mesophyll, but also inclusive of carboxylation resistance. For this reason, r_M in this context has only a value of representing the relative degree of contribution of the residual processes, other than the purely physical CO_2 transfer process in the air phase, to net photosynthetic rate.

3. Results and Discussion

3.1 Influence of atmospheric humidity

Fig. 1 shows changes with relative humidity in the rates of net photosynthesis (P_n) and transpiration (E), the diffusive resistances of stomata (r_s) and mesophyll (r_M), and also in the temperature difference between leaves and air ($T_l - T_a$). Fig. 1 is derived from continuous measurements of P_n , T_l and T_a , and discontinuous measurements of E and r_s , when the humidity was progressively decreased from 80% to 23% and thereafter it was increased again up to 64%. In general, the decrease in the humidity resulted in the increase in E and the decrease in the leaf temperature. The mesophyll resistance was unaffected by the humidity treatments, while the stomatal resistance r_s increased gradually with the decrease in the humidity from 60% downwards. The photosynthetic rate P_n showed maximum rate at 80–60% relative humidity, and with the further reduction in the humidity it tended to decrease as r_s increased.

In the humidity range from 40 to 80%, small fluctuations may be appreciated in P_n and also in $T_l - T_a$, but the fluctuations were not periodical and the amplitudes were small. For these reasons, the fluctuations observed at humidity range above 40% may not be regarded as the oscillation. With the further reduction in the humidity from 40% at 30°C T_a (= 25 mb vapour pressure difference between leaf and air) downwards, the fluctuations became very periodical and the amplitudes of them larger. Moreover, a clear parallelism can be seen in the phase of the fluctuations of P_n , $T_l - T_a$, E and also in r_s , although the latter two quantities were less frequently measured than the former two. Hence, the fluctuations observed at relative humidity below 40% may be regarded as the oscillations caused by the stomatal movements, as

Fig. 1. Changes with relative humidity (RH) in rates of net photosynthesis (P_n) and transpiration (E), diffusive resistances of stomata (r_s) and mesophyll (r_m), and temperature difference between leaf and air ($T_l - T_a$) in rice leaves at 30°C T_a .

was reported in many plant species under certain environmental conditions (Ehrler et al., 1965, and Shirazi and Stone, 1976).

Fig. 1 also shows that the period of the oscillations at 33% relative humidity was approximately same as that at 23% and about 15 minutes, while the amplitudes were larger at the lower humidity. The amplitudes in $T_l - T_a$, P_n , E and in r_s at 33% relative humidity were 0.5°C, 1.9 mgCO₂ dm⁻² hr⁻¹, 0.2 gH₂O dm⁻² hr⁻¹ and 0.34 sec cm⁻¹ respectively, while those at 23% relative humidity were 0.83°C, 2.3 mgCO₂ dm⁻² hr⁻¹, 0.25 gH₂O dm⁻² hr⁻¹ and 0.47 sec cm⁻¹.

Since the oscillations, appeared at lower humidity, diminished with the subsequent increase in the humidity (Fig. 1), it is considered that the oscillation of the stomatal resistance was caused by the increased transpiration demand as imposed by lowering the humidity. With respect to the mechanism of the stomatal oscillation, two hypotheses were proposed respectively by Stålfelt (1956) and Raschke (1965). Stålfelt's hypothesis is such that, under conditions of high transpiration demand, a water deficit develops in leaves, causing the stomatal closure, and then the reduction in transpiration follows, which in turn corrects the water deficit, and the stomatal opening occurs again. While the hypothesis by Raschke is that the

stomata are operating as an oscillating regulator effecting a constant CO₂ supply to the leaves. In Raschke's case, the period of the oscillation is of 5–6 minutes, while that caused by the water balance was reported to be 20–30 minutes (Ehrler et al., 1965; Meidner and Mansfield, 1968; Shirazi and Stone 1976). The period of the oscillation here observed with rice leaves was about 15 minutes, which value is much closer to the latter than the former. For this reason, the oscillation observed in the rice leaves under low humidity may be considered to be caused by the change in water status in the leaves. However, the possibility that CO₂ is also involved in this process can not perfectly be denied, since it has been shown in a previous report with rice (Horie, 1978), that stomata may stabilize the CO₂ concentration in the leaf intercellular spaces on a constant level over a wide range of the radiation intensity.

To analyse quantitatively the effect of the humidity on the stomatal resistance (r_s), the transpiration rate (E) and the net photosynthetic rate (P_n), difference in water vapour pressure between leaf and air, or in another word the saturation vapour pressure deficit (VD), was calculated for each case of the measurements, because VD is more directly related to E than the relative humidity. Moreover, data of P_n , E , r_s and the mesophyll

resistance r_M at a given VD condition were divided by the values of these quantities at 10 mb VD for each series of the measurements, to give the relative effects of VD on these quantities. The relative photosynthesis, transpiration, and stomatal and mesophyll resistances, thus determined, were plotted against the vapour pressure deficit VD (Fig. 2).

As can be seen in Fig. 2, the stomatal resistance r_s was constant until VD reached about 15 mb, but thereafter it increased almost proportionally to VD , so that the value of r_s at 30 mb VD was almost twice of that at 10 mb VD . The transpiration rate (E) at 30 mb VD was about twice of that at 10 mb VD . If r_s would not be affected by VD , this ratio should be threefold, and hence 34% reduction of E resulted in with about twofold increase in r_s as VD increased from 10 to 30 mb. The net photosynthetic rate (P_n) at 30 mb VD was about 75% of that at 10 mb VD , and hence the degree of the reduction was about 25%. This reduction ratio was smaller than that in E . This is because, not only the diffusive resistances of the stomata and the boundary layer, but also the mesophyll resistance r_M is included in photo-

synthesis, and r_M was unaffected by VD .

Ishihara et al. (1971 a and b) measured the degree of stomatal aperture of rice plants under field conditions, and reported that the stomatal aperture reduced at middays with high temperature and radiation intensity and low humidity. Moreover, they found that the depressed stomatal aperture under the conditions of high transpiration demand could be re-opened with a high humidity treatment given by enclosing the plant with a plastic cover. The present results together with those findings by Ishihara et al. lead to the following conclusion. That is, even in rice plants which are growing under paddy field conditions of abundant supply of water, the aerial environments of excessive transpiration demands may cause the depression of the stomatal opening to a considerable degree, which in turn reduces the rate of net photosynthesis to a marked extent.

The generality, that r_s increases with the increase in the evaporatory demand as imposed by lowering ambient humidity, is supported by the wide range of plant species (Ludlaw and Wilson, 1971; Schulze et al., 1972; Lange et al., 1971; Hall and Kaufman, 1975; Aston, 1976; Yabuki and Kiyota, 1978). Lange et al. (1971) found that stomata respond to atmospheric humidity directly without the feedback system resulting from lowered leaf water content. This was confirmed also by Aston (1976) with sunflower. With respect to the mechanism with which the stomata respond to the atmospheric humidity, attentions are recently being paid to the peristomatal transpiration (Meidner, 1975; Sheriff and Meidner, 1975; Sheriff, 1977). The peristomatal transpiration is, contrary to classical views, a view that the inner wall of guard and adjacent epidermal cells are the major sites of evaporation from the stomatal transpiration. Moreover, evidences have been reported that water flow through the epidermis exists with a certain degree of isolation or with very high resistance from the remainder of leaf tissue (Sheriff and Meidner, 1974 and Meidner, 1975).

In the present experiment with rice plant, measurements were made with the plants growing in pots with flooding water level, and less than one-third of total leaf area per plant was inserted into the leaf chamber and the remainder leaves were left in the room in which the evaporatory

Fig. 2. Dependence on saturation vapour pressure deficit (VD) of relative values of rates of net photosynthesis (P_n/P_{n10}) and transpiration (E/E_{10}), and diffusive resistances of stomata (r_s/r_{s10}) and mesophyll (r_M/r_{M10}) in rice leaves. The relative values of these quantities are expressed by setting the absolute values at 10 mb VD to unity.

demand was very low. Hence, it might have not been the case that the lowering humidity imposed an excessive transpiration than the supply of water to give a reduction in leaf water content. For this reason, it would be more realistic to consider that the stomata of the rice leaves responded directly to the atmospheric humidity, presumably by way of the peristomatal evaporation. To confirm this, however, much effort is needed not only to measure the stomatal resistance but also to measure the leaf water potential at same time.

3.2 Influence of temperature

Since the absolute values of P_n , E , r_s and r_M were different among the measurements on different leaves, they were divided by their values at 30°C leaf temperature for each series of the measurements at different temperatures, giving relative effects of the leaf temperature on these physiological quantities. In Fig. 3 are given the relative values of the photosynthesis (P_n), the transpiration (E) and also E/P_n , the transpiration coefficient on a CO_2 basis, as a function of the leaf temperature

Fig. 3. Dependence on leaf temperature (T_l) of the relative rates of net photosynthesis (P_n/P_{n30}) and transpiration (E/E_{30}), and transpiration coefficient on a CO_2 basis (E/P_n). P_n and E are presented as relative values to those at 30°C T_l .

T_l .

For a comparison, the rate of photosynthesis of a rice cultivar "Reimei", a variety cultivated only at the northern part of Japan is also plotted in Fig. 3, in addition to the variety of "Nipponbare", the main cultivar for this experiment. The optimal range of T_l for P_n was between 23–32°C, and below or above this temperature range P_n decreased gradually. In comparison with "Nipponbare", "Reimei" showed a tendency of somewhat smaller decline of P_n at suboptimal T_l and larger decline at superoptimal T_l . To signify these varietal difference observed here, however, more experimentations are needed. E increased almost exponentially with the increase in T_l . This is because the saturation water vapour pressure increases with temperature in an exponential fashion. As a consequence of these characteristics of temperature dependence of P_n and E , the transpiration coefficient E/P_n showed a minimum value at around 23°C T_l , and above this temperature it sharply increased, while at temperature below this it showed a tendency of a slight increase with the decrease in T_l .

To analyse the results given in Fig. 3 based on

Fig. 4. Dependence on leaf temperature T_l of stomatal resistances without (r_s) and with (r'_s) correction with the vapour pressure deficit, and mesophyll resistance (r_M) in rice leaves. r_s , r'_s and r_M are presented as relative values to those at 30°C T_l .

gaseous diffusive properties of the leaves, the relative values of the stomatal (r_s) and the mesophyll (r_M) resistances were calculated in the same way as in P_n and E , and are given in Fig. 4 as a function of the leaf temperature T_l . Fig. 4-a presents the relative stomatal resistance to that at 30°C T_l in dependence of T_l . The average of the absolute values of r_s at 30°C T_l was 1.86 sec cm⁻¹. Although the variation was considerably large, the stomatal resistance showed an increasing tendency with the increase in T_l . The results shown in Fig. 4-a, however, do not give the effect of T_l alone, because increasing temperature, under a constant relative humidity, is necessarily accompanied by the increase in the water vapour pressure difference between leaf and air (VD), of which effect on r_s has already been shown in Fig. 2. To exclude the VD effect, the data shown in Fig. 4-a were corrected with VD using the relation between r_s and VD given in Fig. 2. Fig. 4-b gives the corrected stomatal resistance (r'_s) with VD as a function of T_l . In this case the average of the absolute values of r'_s at 30°C T_l reduced to 1.61 sec cm⁻¹, and the range of the scatter of the points also reduced than that in Fig. 4-a. Moreover, r'_s even showed a reducing tendency of slight reduction with the increase in T_l .

The mesophyll resistance r_M was fairly constant in the temperature range between 27 and 35°C, but below this range it increased exponentially with the decrease in T_l (Fig. 4-c). The dependence of r_M on the leaf temperature T_l may be presented by the following equation with satisfactory accuracy:

$$r_M = r_{M,\min} \{1 + c \exp(-k_m T_l)\} \quad (5)$$

in which $r_{M,\min}$ is the minimum r_M at the optimal leaf temperature, and c and k_m parameters. The values of $r_{M,\min}$ were in the range of 3.6–4.3 sec cm⁻¹ and best estimates for parameters c and k_m were 47.8 and 0.233, respectively. As has already been described, r_M is not a purely physical diffusion resistance in the liquid phase, but it also includes the carboxylation resistance related to the biochemical processes of CO₂ fixation. It is considered that the dependence of r_M on T_l , shown in Fig. 4-c, was reflecting the temperature effect on the carboxylation resistance more strongly than on the purely physical diffusion resistance.

The exponential decrease in r_M with T_l does not

mean that the photosynthetic rate increases in an exponential fashion with T_l , because the compensation CO₂ concentration Γ also increases exponentially (c.f. Fig. 6). The rate of net photosynthesis in relation to r_a , r_s , r_M and Γ , and also to the external conditions of temperature and humidity is more fully analysed in section 3.4.

Meidner and Mansfield (1968) reviewed the effect of temperature on stomatal aperture and reported that the temperature effect was conflicting among workers. Namely, some workers found that temperature had no effect, some found that stomatal aperture decreased with the increase in temperature and some found that it increased with temperature. Meidner and Mansfield gave an explanation to those conflicting results by introducing CO₂ factor in the intercellular spaces. It is well known that a high CO₂ concentration in the intercellular spaces leads to a closure of stomata. The intercellular space CO₂ concentration is closely related to the compensation CO₂ concentration in photosynthesis which is known to increase with temperature (Heath and Orchard, 1957; Akita et al., 1969), so that the intercellular space CO₂ concentration should also increase with temperature. Thus, according to Meidner and Mansfield, the conflicting results of the temperature effect on r_s are derived from difference in the temperature dependence of the compensation CO₂ concentration among species.

The present result of analysis on rice leaves may give an another interpretation to the conflicting temperature effects on r_s . As is shown in Fig. 4-a and b, the humidity effect is always coupled with the temperature experiments, unless care is paid to maintain the vapour pressure deficit at a constant level. Hence, it is very likely that the conflicting temperature effects might have been produced by the differences in water vapour pressure deficit (VD) and also by the difference in the sensitivity to VD among species.

3.3 Influence of soil temperature

Fig. 5 shows results of soil and water temperature treatments. The underground temperature of a rice plant was stepwise changed from 30 to 10°C, and then it was increased back to 30°C. Leaves corresponding to 34% of the total leaf area of a plant were inserted into the assimilation chamber, and the measurements were made under a constant

Fig. 5. Changes with under-ground temperature in rates of net photosynthesis (P_n) and transpiration (E), and diffusion resistances of stomata (r_s) and mesophyll (r_m) in rice leaves. The conditions for the measurements were 30°C in air temperature and $0.64 \text{ cal cm}^{-2} \text{ min}^{-1}$ in short-wave radiation intensity.

aerial environment of $0.64 \text{ cal cm}^{-2} \text{ min}^{-1}$ in short-wave radiation intensity, 30°C in temperature and about 57% in relative humidity. The remainder leaves, stems and the leaf sheaths were in open air under a weak diffuse room light. The experiment was continued for four days.

With the increase in the duration of the sub-optimal temperature treatment at the roots zone, both the rates of P_n and E showed a tendency of decline. The decline in these rates was associated with the increase in r_s , while the mesophyll resistance (r_m) was fairly constant. On the third day of the treatment, in which the root-zone temperature (T_s) was increased back to 30°C from continued 10°C treatment, P_n and r_s both did not fully recover to the levels before the suboptimal T_s treatment. Namely, the values of P_n and r_s at 30°C T_s on the first day were about $26 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ and 2.5 sec cm^{-1} respectively, while those values at the same T_s on the third day were about $24 \text{ mg CO}_2 \text{ dm}^{-2} \text{ min}^{-1}$ and 3.1 sec cm^{-1} , and hence 8% reduction in P_n and 24% increase in r_s resulted in during the three days' treatment of the suboptimal T_s . After T_s was risen back to 30°C the plant was kept under this temperature for one more night,

but neither P_n nor r_s showed any sign of a recovery. Two reasons may be considered for the hysteresis effect of the prolonged T_s treatment. One is that after-effect of the suboptimal T_s treatment continued for considerably long period. Another is that aging of the leaves was accelerated during the experimental period, because the leaves were kept in the assimilation chamber in unnatural form and environments for four days. Probably, both might be the cause of the hysteresis appeared in P_n and r_s with the T_s treatment.

For the above reasons, difficulties may arise to assess the effects of the suboptimal root-zone temperature on P_n and r_s . However, the ratio of P_n and r_s at 20°C T_s , measured before the 10°C T_s treatment, to those at 10°C T_s may be considered the maximum effect of the low T_s treatment, while the ratio of P_n and r_s at 20 or 30°C T_s , measured after the low T_s treatment, to those at 10°C may give the minimum effect. The rate of net photosynthesis (P_n) at 20°C T_s on the first day of the measurement was on average $26.1 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$, the rate at 10°C T_s on the third day, after the continued 22 hours' treatment of 10°C T_s , was $23.1 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$, and the rate at 20°C T_s

just after the 10°C T_s treatment was 24.8 mgCO₂ dm⁻²hr⁻¹. Hence, the treatment of 10°C T_s for 22 hours resulted in the reduction of P_n on maximum 11% and on minimum 7%. In the same way as in P_n , the maximum and the minimum effects of the 10°C T_s treatment on the stomatal resistance r_s was estimated to be 40 and 31% in comparison with r_s at 20°C T_s .

Barlow, Boersma and Young (1977) studied the effect of suboptimal T_s on leaf water potential, net photosynthetic rate and transpiration rate in maize seedlings. They found that the leaf water potential decreased with the decrease in T_s gradually at first, and at T_s below 12.5°C it decreased very sharply. With the decrease in T_s , P_n and E both showed a similar pattern of reduction as the water potential, so that P_n at 10°C T_s reduced to only 20% of that at 28°C. Thus, their data clearly indicate that, with the decrease in T_s , water absorption was suppressed and subsequently a reduction in leaf water potential occurred, which in turn reduced P_n and T_r . An important point in their results is that there exists a critical soil temperature below which the leaf water potential, and hence P_n and E both, decrease very sharply.

In the rice plant of this experiment, the reduction in P_n as T_s decreased from 20 to 10°C was only about 10%. This reduction may probably be associated with a reduced rate of water uptake and the subsequent depression in leaf water potential, which in its turn increase the stomatal resistance r_s . The critical soil temperature as Barlow et al. (1977) found in maize, however, can not be seen in the rice plant, in the range of T_s from 30 to 10°C. If such a critical soil temperature should also exist in rice, it would be lower than 10°C. To clarify the causes for the difference in the response to low soil temperature between the rice and the maize, more efforts are needed of investigating T_s effect in relation to shoot-root ratio and also to the soil water content.

3.4 Evaluation of interacting effects of air temperature and humidity

In the foregoing sections, it has been clarified that excessive transpiration demand as imposed by lowering the humidity increases the stomatal resistance r_s , and hence reduces the rates of net photosynthesis and transpiration in the rice leaves to a marked degree. It was also shown that, in the

relation between temperature and these physiological properties of the leaves, the humidity effect is often included. In this section the interacting effects of air temperature and humidity upon P_n and T_r are numerically evaluated based on the present experimental results.

From eq. (1), the water vapour transfer between the leaves and air may be given by,

$$E = 2 \frac{\frac{2.17 \times 10^{-4}}{273 + T_l} e_s(T_l) - \frac{2.17 \times 10^{-4}}{273 + T_a} e_a}{r_a + r_s} \\ = 2 \frac{2.17 \times 10^{-4}}{273 + T} \frac{VD}{r_s + r_a} \quad (6)$$

where T is the average temperature of leaves (T_l) and air (T_a) and VD the difference in the water vapour pressure between the leaves and air. Similarly, the CO₂ transfer between the leaves and air is, from eqs. (3) and (4), given by,

$$P_n = \frac{C_a - \Gamma}{\frac{1}{2} \{ r_a \left(\frac{D_H}{D_C} \right)^{2/3} + r_s \left(\frac{D_H}{D_C} \right) \} + r_M} \quad (7)$$

In equations (6) and (7), the boundary layer resistance r_a is a function of wind speed, which function has already been given by eq. (2). Although the stomatal resistance r_s showed a slight decline with the increase in the temperature (Fig. 4-b), it is assumed here that r_s is independent of the temperature for the sake of simplicity. r_s in dependence of the vapour pressure deficit (VD), as shown in Fig. 2, may be presented in the form that:

$$r_s = r_{s10} f(VD) \quad (8)$$

in which r_{s10} is the stomatal resistance at 10 mb VD and is equal to 1.61 sec cm⁻¹, and $f(VD)$ is a factor to give the effect of VD on r_s and is shown in Fig. 2. The mesophyll resistance r_M has been shown to be independent of VD but strongly dependent on the temperature, and the temperature dependence of r_M is given by eq. (5).

The compensation CO₂ concentration of photosynthesis Γ of the rice leaves is given in Fig. 6 as a function of the leaf temperature T_l . In Fig. 6 is also cited similar data on rice seedlings reported by Akita, Miyasaka and Murata (1969), although their original data were related to air temperature but not to leaf temperature. In both cases, the

relation between Γ and T_l can be presented by the following equation with a satisfactory accuracy:

$$\Gamma = \Gamma_{30} Q_{10}^{(T_l - 30)/10} \quad (9)$$

where Γ_{30} is the value of Γ at 30°C and Q_{10} the temperature coefficient. The values of these parameters, however, were largely different between the present case of the measurements and that by Akita et al. (1969). The estimated values for Γ_{30} and Q_{10} in the present case were 48.0 ppm and 1.62, respectively, while those from the data of Akita et al. were 118 ppm and 2.01, respectively. Two reasons may be considered for the discrepancy in the values of Γ_{30} and Q_{10} between the present case of measurements and that by Akita et al. Firstly, in the latter case Γ was related to air temperature but not to the leaf temperature, and it is very usual that the leaf temperature is much higher than the air temperature in assimilation chambers. Secondly, in the former case the measurements were made only on the leaves, while in the latter on whole seedlings, and hence the respiration by heterotrophic organs might be included in the latter. In the simulation the estimated values from the present measurements were used for the parameters Γ_{30} and Q_{10} .

It is assumed that the leaf temperature is equal to that of air at higher wind speed. Then, equations (2), (5), (6), (7), (8) and (9) suffice to simulate

Fig. 6. Temperature dependence of compensation CO_2 concentration of photosynthesis (Γ) in rice leaves. Curve 1 is derived from the present measurement and 2 from Akita, Miyasaka and Murata (1969).

Fig. 7. Simulated rates of net photosynthesis and transpiration, and transpiration coefficient on CO_2 basis in dependence of air temperature and humidity.

the rates of net photosynthesis and transpiration at saturating radiation level in relation to air temperature, atmospheric humidity and wind speed. Fig. 7 gives the simulation results for wind speed being 100 cm sec^{-1} . The results shown in Fig. 7 well illustrate how the atmospheric humidity affects the temperature (T_a)-net photosynthesis (P_n) and the T_a -transpiration (E) relationships. The T_a - E relationship should be in a shape of exponential function, if stomatal resistance would not be affected by the vapour pressure deficit VD . In Fig. 7, however, such exponential characters can only be seen at higher humidity or at lower T_a , and at lower humidity or at higher T_a the transpiration rate tends to level off. This is because VD increases with the increase in T_a or the decrease in the humidity, which in turn increases r_s .

Fig. 7 also shows that the humidity affects P_n at higher temperature to a considerable extent and that the optimal T_a for photosynthesis changes with the humidity. In general, the optimum temperature shifts upwards as the humidity increases, and P_n at the optimum T_l increases with the humidity. These phenomena, appeared in the

relation among the temperature, the humidity and the net photosynthetic rate, are again due to the VD effect on the stomatal resistance.

As a consequence of the above mentioned characters of P_n and E , the simulated transpiration coefficient on the CO_2 basis in dependence of the temperature and the humidity is as is shown in Fig. 7-b. As has been shown experimentally (Fig. 3), the simulated relation between the temperature and the transpiration coefficient is also somewhat concaved curve, with the minimum value around 20°C . The concaved nature is more apparent at lower humidity. The transpiration coefficient is, of course, higher the lower the humidity.

The above simulation results strongly suggest that a depression in net photosynthetic rate at superoptimal temperature in laboratory or in field may often be accelerated by increased stomatal resistance due to increased vapour pressure deficit. In such situations, it is suggested that the depressed photosynthetic rate at the superoptimal temperature may be recovered, at least partly, by increasing the ambient humidity. It seems worthwhile to examine this possibility by means of experiments.

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気象環境とイネの物質生産に関する研究

II. 葉面ガス拡散抵抗, 光合成および蒸散 に及ぼす大気湿度と気・水温の影響

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要 約

気象条件からイネの物質生産の動態を説明・予測するシミュレーションモデルを開発することがこの研究の最終的な目的である。このために必要なデータを得る目的で、気孔(r_s)および葉肉(r_M)のガス拡散抵抗, 光合成および蒸散と大気湿度および気・水温との関係が単葉レベルでの同化箱法によってもとめられた。

気温 30℃で相対湿度が 40%以下, したがって葉と空気との間の水蒸気張力差 (VD) が 25 mb 以上で, net の光合成速度 P_n , 蒸散速度 E および葉温 T_l の振動がみとめられた。振動の週期は約 15 分で一定であったが, 振幅は湿度の低下とともに増大した。これらの振動はすべて気孔抵抗が振動することによって引き起されたものであることがわかった。気孔抵抗 r_s と VD の関係についてみると, VD が 15 mb 以下では r_s はほぼ一定であったが, 15 mb 以上になると r_s は VD に比例して直線的に増加した。一方, r_M は VD によってほとんど影響されなかった。

このため, 葉と空気間の水蒸気張力差 VD が高くなると光合成, 蒸散ともかなりの程度まで抑制された。

相対湿度一定の条件下で葉温を高めた場合, 見かけ上 r_s は増加した。しかし, この増加は葉温を高めることに附随する VD の増加によって起ったものであって, 温度の直接的な影響とは考えられない。 VD の影響を加味して補正された r_s は温度の増加とともに逆に減少する傾向がみられた。一方, 葉肉抵抗 r_M は葉温の増加とともに指数関数的に減少した。10℃の水・地温処理を連続して 22 時間行なった場合, 20℃の場合と比較して r_s は 30~40%増加し, 光合成は 7~11%減少した。

以上の実験結果に基づいて, 気温と湿度が P_n と E に与える相互的な影響を評価するための数値計算が行なわれた。 P_n の最適気温は湿度の増加につれて高温側に移行し, また最適気温条件下における P_n は湿度の増加とともに増大することが示唆された。