Stomatal Resistance of Rice Leaves as Influenced by Radiation Intensity and Air Humidity

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Abstract

This paper describes results of field experiments of relationships between meteorological conditions and stomatal resistance of rice leaves. The magnitude of stomatal resistance of rice leaves was measured by a porometer at important three developmental stages of rice plants. Stomatal resistance ($r_s$) changed very clearly throughout sunny days in relation to diurnal variation in solar radiation intensity ($S_t$) and leaf-air vapor concentration deficit ($HD$).

Stomatal resistance of the adaxial surface of rice leaves was found to be the same to that of the abaxial surface in the magnitude, indicating that the water vapor fluxes at the both surfaces of rice leaves are equal with each other. The dependence of non-dimensional stomatal resistance [$r_s/r_m\cdot k(HD)^2$] on solar radiation intensity ($S_t$) was well approximated by a hyperbolic function. The relationship between $HD$ and [$r_s/r_m(1+S_t/m/S_t)$] was expressed by a quadratic function of $HD$.

1. Introduction

As well known, solar radiation and air humidity are most important factors controlling stomatal aperture of plants (Meidner and Mansfield 1968, Maotani and Machida 1977, Ackerson and Krieg 1977, Horie 1978). Turner and Begg (1973) have measured stomatal resistance of leaves at different levels in canopies of maize, sorghum and tabaco, and found that the magnitude of $r_s$ increases monotonically with increment of distance from the surface of the each crop canopy. This is concluded to be because of the decrease of solar radiation intensity and the increase of the aged leaves in the lower part of the crop canopy. Ishihara et al. (1971) have studied the influence of the age of leaves and the position of leaves within rice canopy on the stomatal aperture of rice leaves.

Almost all studies of effects of meteorological elements on stomatal aperture and/or resistance of plant leaves have been made in growth chambers or houses, mainly due to the instrumental difficulty, excepting for Kanemasu and Tanner (1969) and Brown and Rosenberg (1973), and Inoue et al. (1979). We have measured the stomatal resistance of rice leaves by using porometer.

A part of these experimental results were used to built a simulation model of microclimate within rice plants (Inoue 1981).

The data obtained in the field observations are analysed in this paper to make clear effects of meteorological elements such as solar radiation and air humidity upon the stomatal resistance of rice leaves. We have also studied the change in stomatal resistance of rice leaves with the developmental growth of plants such as maximum tiller, heading and young ear formation stages.

2. Experimental site and procedure

Microclimatic measurements were made in rice plants (10a) surrounded by the rice fields of the Furukawa Agricultural Experiment Station of Miyagi Prefecture. Rice (cultivar, sasanishiki) was planted with the rate of about 20 stubs per square meters on May 10, 1978. Measurements included...
wind speed \((U)\), dry- and wet-bulb temperatures \((T_d, T_w)\), leaf temperature \((T_f)\), solar radiation \((S_r)\) and net-radiation \((R_n)\), water- and soil-temperatures \((W_T, S_T)\), and stomatal resistance \((r_s)\).

The microclimatic measurements were made continuously for the period from one month after the transplanting of rice plants (June 13th, 1978) to the harvest (Oct. 5th, 1978).

In 1978's experiments, stomatal resistances \((r_s)\) for water vapor transfer were observed on July 5-7 (maximum tiller stage), on July 22-24 (young ear formation stage), and on Aug. 22-24 (ten days after heading stage), respectively. We used the stomatal diffusion porometer (Lamda Ins. Co.) to measure the magnitude of stomatal resistance of rice leaves. The measurements of stomatal resistance for the abaxial and adaxial surfaces of rice leaves were made at the three important stages such as the maximum tiller stage (July 5-7), the young ear formation stage (July 22-24) and the near heading stage (Aug. 22-24), respectively. We have chosen at random two stubbles (Samples A and B) as test samples in the rice field. The stomatal resistance \((r_s)\) was measured for rice leaves positioned in the upper, middle and bottom layers of the canopy. The stomatal resistance of the rice leaves was measured using ten leaflets in the each layer and averaged to obtain the mean stomatal resistance for the each layer. Measurements were made at a interval of about 60 minutes during the period from 0600 to 2000 (JST) on clear days.

Measurements of the plants included plant height and the numbers of stems per hill, and were made five times during the period June 9 to Oct. 5. Seasonal change in plant height and stem numbers per hill is shown in Fig. 1.

3. Results and discussion

3.1 General feature of meteorological conditions and diurnal changes in stomatal resistance

Fig. 2 shows the diurnal variation in microclimatic factors and stomatal resistance of rice leaves to water vapor transfer on three clear and sunny days (6 and 23 July, and 22 Aug. of 1978). The daily totals of solar radiation on 6 and 23 July, and 22 Aug. were 5581y (23.9 MJ m\(^{-2}\)), 6001y (25.7 MJ m\(^{-2}\)) and 4181y (17.9 MJ m\(^{-2}\)), respectively.

The diurnal variation in \(\Delta T\) showing the temperature difference between rice leaves \((T_f)\) and ambient air \((T_a)\) can be characterized by a curve with higher values at midday time and lower values at early morning and late afternoon. The diurnal variation in \(\Delta T\) is in phase with that of solar radiation. This implies that solar radiation impinging on the leaves has substantial effects of temperature conditions of leaves.

The leaf-air vapor concentration deficit \((HD, \mu g cm^{-3})\) affecting the water vapor transfer from leaves to air was evaluated approximately from

\[
HD = a(T_f) - a_a
\]

where \(a(T_f)\) is the saturation absolute humidity at leaf temperature \((T_f)\) and \(a_a\) is the absolute humidity in surrounding air. Leaf temperature of rice plants was measured by a bead thermister set in the sensor cup of the porometer. As a first approximation, the absolute humidity in air measured at a level above the canopy surface was used in replace of \(a_a\).

Fig. 2 shows the daytime variation in \(HD\) calculated for the upper layer of air canopy. The magnitude of \(HD\) for the upper leaf layer changed in a range from 30 \(\mu g\) cm\(^{-3}\) at noon to 3 \(\mu g\) cm\(^{-3}\) immediately before sunset and in early morning. The diurnal change in \(HD\) is also in phase with that of solar radiation, indicating that solar radiation is a most important element controlling transpiration loss of water from plants.
The diurnal variation in $r_s$ of rice leaves changed between the three developmental stages of rice plants. This is mainly due to the change in response of the stomata to microclimatic environment of rice plants. Although in the maximum tiller and near heading stages the stomatal resistance of leaves in the upper layer was smaller than 5 $s$ cm$^{-1}$ during the period with solar radiation above 0.3 $ly$ min$^{-1}$, and the mean value for that period was some 4 $s$ cm$^{-1}$, the stomatal resistance of the leaves in the young ear formation stage showed a peak at the period 1000 to 1400. The midday peak of stomatal resistance is thought to be due to temporary closing of stomata by higher solar radiation and lower air humidity in that time. Quite similar results are reported by Ishihara et al. (1971) on the basis of observations of stomatal aperture of leaves in the well-watered rice plants.

In the maximum tiller stage (July 6) with many young and vigorous leaves, the magnitude of $r_s$ measured in the upper plant layer is lower than that in the other two stages. This means that the young and vigorous leaves can evaporate much water compared with fully matured leaves in those stages.

Transpiration ($E$) from leaf to ambient air is given by

$$ E \approx \frac{HD}{(r_s + r_a)} $$

where $r_a$ is the leaf surface-air resistance ($s$ cm$^{-1}$). In general, under field conditions the magnitude of $r_s$ is considerably larger than that of $r_a$. Therefore it is reasonable to assume that transpiration rate of leaves is mainly controlled by the magnitude of $HD$ and $r_s$.

Fig. 3 is an example showing the diurnal variation in stomatal resistance and solar radiation measured at the three levels within the canopy on a sunny day (July 23). The stomatal resistances of leaves at the heights of 45 cm and 60 cm were smaller than that at the height of 20 cm throughout the day. This is mainly because of the lower intensity of solar radiation at the 20 cm-level. After 1500, values of the stomatal resistance at the height of 20 cm increased considerably with decrease of solar radiation intensity. The increase of stomatal resistance of leaves in the top layer started at 1900 after sunset. The results shown in Fig. 3 indicate that values of stomatal resistance of rice leaves is strongly affected by solar radiation.
Fig. 3. Diurnal changes in stomatal resistance and radiation intensity at three strata of rice plants in well-watered rice field.

It is known that values of stomatal resistance of plant leaves are affected not only by solar radiation intensity but also by numbers of stomatal pores on the leaf surface. Kumura and Hoshikawa (1971) have reported that the numbers of stomata per unit area of rice leaves is nearly equal between adaxial and abaxial surfaces. This results implies that stomatal resistance is also approximately equal between adaxial and abaxial surfaces of rice plants. We have measured the stomatal resistance of adaxial and abaxial surfaces of rice leaves by the diffusion porometer to check the expectation mentioned above. The measurements were made on 6 and 23 July, and 22 Aug. The results obtained are presented in Fig. 4. Fig. 4 indicates clearly that there is no meaningful difference in stomatal resistance between adaxial and abaxial surfaces of rice leaves.

However, stomatal resistance of dicotyledonous crops is known to be different between adaxial and abaxial surfaces of leaves. For example, Kanematsu and Turner (1969) have found with snap bean that the stomata of its adaxial surface need much light to open compared with the stomata on its abaxial surface. Inoue et al. (1979) have also observed with cucumber crop that the stomata on the abaxial surface of its leaves are more sensitive to solar radiation and air humidity than the stomata on its adaxial surface.

3.2 Stomatal resistance as influenced by solar radiation and air humidity

We have studied effects of solar radiation and air humidity on stomatal resistance of rice leaves. By assuming the following relationship between stomatal resistance \( r_s \) and solar radiation \( S_t \), the independent effect of solar radiation on the stomatal resistance was separated from simultaneous effects of solar radiation and air humidity on stomatal resistance

\[
r_s/r_m (1 + S_{r,m}/S_t) = k f(HD)
\]

where \( f(HD) \) is an unknown function of \( HD \), \( r_m \) and \( S_{r,m} \) the minimum stomatal resistance and the solar radiation at 2 \( r_m \), and \( k \) the proportionality constant, respectively.

The following steps for successive approximation were adapted to evaluate separately the effects of solar radiation and air humidity on the stomatal resistance of rice leaves.

1) The value of \( f(HD) \) is estimated by values of \( r_s/r_m (1 + S_{r,m}/S_t) \) and \( HD \) using initial appropriate values of \( r_m \) and \( S_{r,m} \).
2) By substituting the value of \( f(HD) \) so obtained into Eq. (3), \( r_s/r_m f(HD) \) is determined.
3) New values of \( r_m \) and \( S_{r,m} \) are calculated by making use of the value of \( r_s/r_m f(HD) \)
f(HD) is again estimated from \( \frac{r_s}{r_m} \left(1 + \frac{S_{t,m}}{S_t}\right) \) and using new values of \( r_m \) and \( S_{t,m} \). By substituting \( \frac{r_s}{r_m} f(HD) \) newly evaluated into Eq. (3), the value of \( r_m \) is again determined.

The decrease in stomatal resistance of rice leaves with increasing solar radiation was very rapid in a range of radiation intensity lower than some 0.3 ly min\(^{-1}\) (139 W m\(^{-2}\)). After that, it approximated to its minimum \( (r_m) \). The above relation between \( r_s \) and \( S_t \) can be approximated by a hyperbolic function as shown in Fig. 5. The values of \( r_m \) and \( S_{t,m} \) evaluated for the three developmental stages of rice plants were 0.34 and 0.35 on July 6, 0.92 and 0.67 on July 23 and 24, and 1.39 s cm\(^{-1}\) and 0.45 ly min\(^{-1}\) on Aug. 22 and 23, respectively. The value of \( S_{t,m} \) was smaller at the maximum tiller stage (July 6) than at the young ear formation stage (July 23, 24) and the near heading stage (Aug. 22, 23). This results indicate that young and vigorous leaves of rice plants can adapt to more intensive solar radiation than matured rice leaves.

The dependence of stomatal resistance \( (r_s) \) on radiation intensity \( (S_t) \) has been found to vary with crop species and ages of crop leaves. Horie (1978) has reported that the values of \( r_s \) and \( S_{t,m} \) of leaves of potted rice plants are lower at the maximum tiller stage than other growing stages.

As shown in Fig. 6, the value of \( \frac{r_s}{r_m} \left(1 + \frac{S_{t,m}}{S_t}\right) \) increases very rapidly with increment of leaf-air vapor concentration deficit \( (HD) \). This means that an unknown function of \( f(HD) \) can be approximated by

\[
f(HD) = k (HD)^2
\]

It is reasonable to assume from Eq. (4) that the stomatal resistance of rice leaves goes up markedly with increasing leaf-air vapor concentration deficit \( (HD) \).

The very rapid increase in stomatal resistance of...
rice leaves in a higher range of HD is caused by closing of stomatal aperture due to the imbalance of leaf water state under that conditions. This is in good agreement with results obtained by Ishihara et al. (1971) using potted rice plants. By considering Eq. (4), the relationship between leaf-air vapor concentration deficit (HD) and dimensionless stomatal resistance \( r_s/r_m (1+S_{t,m}/S_t) \) was found to be expressed by the following quadratic function of HD on independently of the growing stage of rice plants.

\[
\frac{r_s}{r_m} (1+S_{t,m}/S_t) = k (HD)^2
\]  

(5)

The proportionality constant \( k \) was found to be \( 9 \times 10^{-3} (\mu g \ cm^{-3})^{-2} \).

We can obtain from Eq. (5) the following two conclusions. First is that stomatal resistance of rice leaves is more sensitive to solar radiation than to other factors under conditions that radiation flux density \( S_T \) is lower than \( S_{t,m} \). Second is that the stomatal resistance is mainly controlled by the magnitude of HD under conditions that \( S_T \) is higher than \( S_{t,m} \) and HD is above about 16 \( \mu g \ cm^{-3} \).

Several researchers (Ackerson and Krieg 1977, Camaco et al. 1974, Hall and Kaufman 1975, Horie 1978) have studied with sesame, rice, sunflower and cucumber the influence of HD on the magnitude of \( r_s \). Our results presented in Fig. 6, and approximated by Eq. (5) agreed well with their results. Meidner (1975) has pointed out the peristomatal transpiration as a main cause for the response of stomatal opening to the change in surrounding air humidity. Hall and Kaufman (1975), Ackerson and Krieg (1977) and Camacho et al. (1974) have reported that the stomatal resistance of tested plant leaves increases so curvilinearly with increment of HD, as approximated by a quadratic function of HD. On the other hand, Horie (1981) showed that the stomatal resistance of rice, sunflower and cucumber plants is retained at a nearly constant level in a range of leaf-air vapor pressure deficit (VD) below some 15 mb and thereafter increases linearly with the increment of VD.

### 3.3 Transpiration rate of rice leaves

As already pointed out, transpiration rate \( (T_r) \) of plant leaves can be expressed by

\[
T_r = C\Delta e / (r_a + r_s)
\]  

(6)

where \( \Delta e \) is the leaf-air vapor pressure deficit (mb), \( C \) is a conversion factor from water vapor pressure to absolute humidity \( (7.15 \times 10^{-7} g \ cm^{-3} \ mb^{-1}) \), \( r_a \) is approximated by \( r_a = 1.3(d/U)^{1/2} \), \( d \) is the effective leaf length along the wind direction (cm), \( U \) is the mean wind velocity (cm s\(^{-1}\)).

By using measured values of HD, U, d, and Eq. (6), transpiration rate of rice leaves in the upper layer was calculated and presented as a function of HD in Fig. 7. Although there is somewhat large scatter of points, we can conclude that transpiration rate of rice leaves increases first nearly proportionally, reached the maximum at HD of some 16 \( \mu g \ cm^{-3} \) and thereafter decreases very slowly with increasing values of HD. Non-linear relationship between HD and \( T_r \) illustrated in Fig. 7 is attributed to the rapid increase of \( r_s \) of rice leaves with increasing HD as shown in Fig. 6. The results obtained with rice leaves are in good agreement with results reported by Ackerson and Krieg (1977) with maize leaves. The decrease in \( T_r \) in a higher range of HD seems to be an example of the regulation of water loss from plant leaves by the control of stomatal opening.

Fig. 7. Transpiration rate \( (T_r) \) as a function of leaf-air vapor concentration deficit (HD). Data were obtained at maximum tiller, young ear formation, and heading stages of rice plants.

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Literature Cited


出穂後には水稲稈のなかで上葉の割合が卓越するので群落上層頬の気孔抵抗は幼穂形成期頃の値より小さくなった。しかし、下層の老化した葉の気孔抵抗はかなり大きくなった。

2. 水稲稈を上・中・下層に分け、各々の供試葉の気孔抵抗を測定した結果、一般に下層葉ほど気孔抵抗値は大であった。これは下層での低い日射強度と老化葉の増大のためである。

水稲葉の表・裏面の気孔抵抗値は生育時期に無関係にほぼ等しいことがわかった。

3. 気孔抵抗に影響する日射強度と葉－気水蒸気濃度差との複合効果を図式解法により分離した結果、日射強度（$S_t$）と無次元気孔抵抗 $[r_s / r_m k (HD)^2]$ との関係は直角双曲線で良く近似でき、これは現在までの結果と一致した。この手法で処理した生育期別の気孔抵抗から求めた特徴値 $S_{t, m}$ と $r_m$ は水稲稈の生育特性をある程度反映したものであることがわかった。

同様に、無次元気孔抵抗は葉－気水蒸気濃度差（$HD$）のおよそ2乗に比例して増大し、次式で近似できた。

$$r_s = r_m (1 + S_{t, m} / S_t) k (HD)^2.$$  

4. 水稲群落の上層葉の蒸散速度（$T_i$）は、葉－気水蒸気濃度差の増加につれて最初直線的に増加するが、$HD \approx 15-20 \mu g \cdot cm^{-2}$ で最大に達し、その後は逆に僅かに減少することがわかった。これは $HD$ の増大に伴う気孔抵抗の急激な増大によるもので、蒸散による水損失の一種の抑制作用ということができる。