Relationship between Leaf Water Potential and Photosynthesis in Rice Plants

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Photosynthesis of crop plants is markedly influenced by a decrease of leaf water content. Photosynthetic rate is determined by changes in the rate of CO_2 diffusion into leaves through stomata and in the photosynthetic activity in mesophyll cells. In the past, the effect of leaf water content on photosynthesis has been studied by paying attention mainly to stomatal aperture. The authors also assumed that the photosynthetic rate in leaf blades of rice plants begins to decrease at the leaf water potential lower than about −2 bar, and becomes almost nil at −13 bar,[6] based on the experimental results on the relation between leaf water potential and stomatal aperture,[7] and the relation between stomatal aperture and photosynthetic rate.[8] Recently it was pointed out by Boyer,[4] Plaut,[11] Jones[9] and others that photosynthetic activity itself is directly involved in the lowering of photosynthetic rate associated with the decrease of leaf water potential.

In the present study, the effect of the decrease of leaf water potential on photosynthesis of rice leaf blades was investigated by separating it into two factors: stomatal aperture and photosynthetic activity, by employing both the usual gasometric method and the oxygen electrode method.[8] The latter method makes it possible to measure photosynthesis under a condition free from the effect of stomatal aperture (diffusive conductance).

Method of measuring photosynthesis

By the gasometric method, photosynthetic rate is determined by the difference of CO_2 concentration (measured by the infrared gas analyzer) between an inlet and an outlet of an assimilation chamber, in which air temperature, wind velocity and quantity of air stream are kept constant, and is expressed in terms of mg $CO_2\ dm^{-2}\ hr^{-1}$. Transpiration rate is determined by the difference of absolute humidity, converted from dewpoint measured by dewpoint hygrometer, between an inlet and outlet of the above assimilation chamber. Diffusive conductance is calculated by the method of Gaastra[5] from the transpiration rate, air humidity and leaf temperature. Transpiration rate and diffusive conductance are expressed in terms of $gH_2O\ dm^{-2}\ hr^{-1}$ and $cm\ sec^{-1}$, respectively.

Measurements by the gasometric method were done under the condition of 30°C of air temperature, 65–70% of relative humidity, and 60 klux of light intensity.

The oxygen electrode method is as follows: A piece of a leaf blade with an area exactly measured was cut into small pieces of about 1 mm^2, and placed into a buffer solution, containing 0.5 mM of $CaSO_4$, with pH adjusted to 7.2 (the standard medium). After the pre-illumination treatment, $NaHCO_3$ was added to the solution so as to make its concentration to 20 mM, and O_2 evolution rate was measured at water temperature of 25±1°C under 50 klux of light intensity. The rate was expressed in terms of μ mole $O_2\ dm^{-2}\ hr^{-1}$. Water potential of the medium was varied by adding sorbitol to the medium.

Leaf water potential was measured by thermocouple psychrometer (Wescor Co.), immediately after the photosynthesis measure-

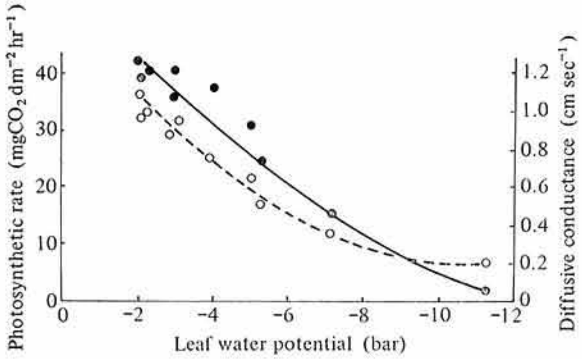

Fig. 1. Effect of leaf water potential on diffusive conductance (open circles) and photosynthetic rate (solid ones)

ment by the gasometric method or immediately before the measurement by the oxygen electrode method.

Measurements by the gasometric method

Rice plants used for the study were grown in flooded pots as usual. Prior to the photosynthesis measurement, plants were exposed to different soil moisture contents for several days, and changes in diffusive conductance and in photosynthetic rate occurring with the lowering of leaf water potential were examined. When the leaf water potential decreased to less than $-2 \sim -3$ bar, the diffusive conductance was decreased, and, almost in parallel to it, the photosynthetic rate decreased, becoming almost zero at about -12 bar (Fig. 1). A close positive correlation between diffusive conductance and photosynthetic rate was recognized.

Secondly, by making use of the phenomenon[10] that stomata are opened temporarily by a hydropassive opening when the leaf blades have been excised from their leaf sheaths during the course of measuring photosynthesis, relation between leaf water potential and photosynthetic rate was examined with leaf blades which had open stomata. At varying times after the excision, the excised leaf blades were taken out from the assimilation chamber after measuring their diffusive conductance and photosynthetic rate, and then their leaf water potential was measured immediately. In Fig. 2, changes of these values with the time after the excision are given, by taking each of these values shown before the leaf excision as 100. Fig. 2 indicates that the leaf water potential decreased rapidly reaching lower than -12 bar in two min after the excision, while the diffusive conductance and photosynthetic rate were kept almost unchanged up to 3 min after the excision, but then they decreased rapidly. The

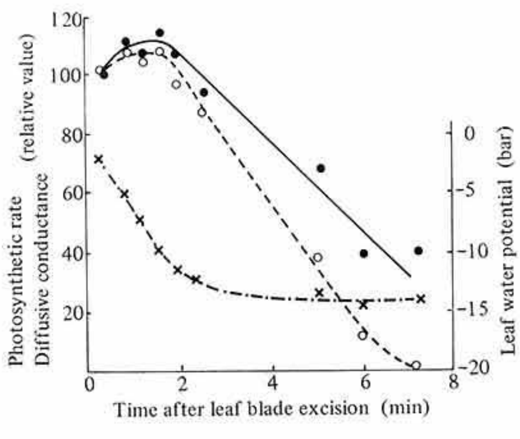

Fig. 2. Changes of leaf water potential (crosses), diffusive conductance (solid circles) and photosynthetic rate (open ones) after leaf blade excision from leaf sheath

photosynthetic rate decreased to almost nil after 7 min. The diffusive conductance and photosynthetic rate both plotted against the leaf water potential, are illustrated in Fig. 3. It can be seen that the photosynthetic rate was hardly changed over a range of leaf water potential from −2 bar to about −12 bar, as far as the stomata were open. From this result, it was assumed that the photosynthetic activity in mesophyll cells is not reduced even when the leaf water potential is lowered to −12 bar, provided that the exposure of the photosynthetic apparatus to the lowered leaf water potential is of short time.

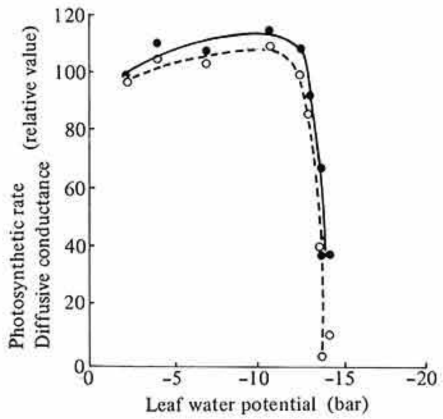

Fig. 3. Relation between leaf water potential and diffusive conductance (solid circles) and photosynthetic rate (open ones) after leaf blade excision from leaf sheath

Measurements by the oxygen electrode method

Leaf blades sampled from rice plants growing under flooded condition were dried gradually under a low light intensity in the laboratory to prepare leaf blades with various leaf water potentials, and O_2 evolution rate was measured with them. By this method, relation between leaf water potential and photosynthetic rate free from the effect of stomata was obtained. The water potential of the medium was adjusted to be almost equal to the leaf water potential.

Leaf blades began to roll at about −6 bar of leaf water potential, both edges of leaf blade contacted each other at about −12 bar, and the blades wilted in needle-like form at about −15 bar. However, the O_2 evolution rate was hardly changed up to the potential of −25 bar, keeping the value higher than 400 μ mole O_2 dm^{-2} hr^{-1}. At the lower potential than −25 bar it decreased rapidly as shown in Fig. 4. From this result, it was assumed that the photosynthetic activity in mesophyll cells is not affected until the leaf water potential is decreased considerably and leaf water content decreases.

It was examined whether or not, as a simple method for comparing different kinds of crops

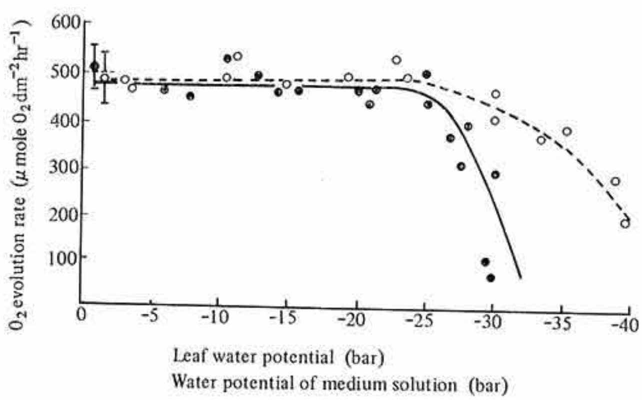

Fig. 4. Effects of leaf water potential (solid circles) or water potential of medium solution (open ones) on O_2 evolution rate

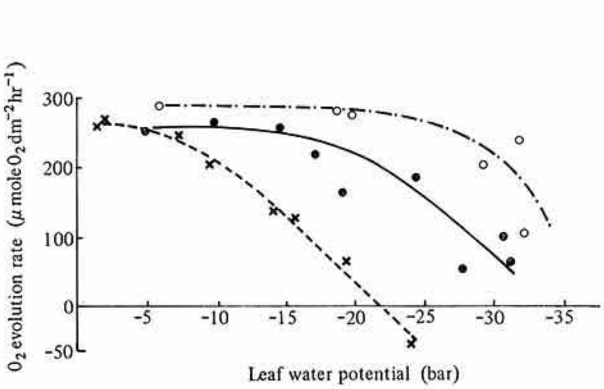

Fig. 5. Effects of leaf water potential on O_2 evolution rate in high humidity (crosses), control (solid circles) and dry soil (open ones) plots

or different growth conditions of a crop, it is possible to estimate the relationship between leaf water potential and photosynthetic activity from the relation between water potential of medium solution and O_2 evolution rate, which can be obtained simply by changing water potential of the medium instead of changing leaf water potential. The result (Fig. 4) shows that the medium water potential at which O_2 evolution begins to decrease (although somewhat gradually) is almost similar to the level of leaf water potential.

It is known with various crops that leaf water potential at which diffusive conductance and photosynthetic rate begin to decrease is different with different growth conditions.[3] However, it is not completely made clear whether or not the response of photosynthetic activity itself to the lowering of leaf water potential differs according to growth conditions.

Therefore, three different growth conditions were prepared: (1) high humidity plot, where plants were grown in a humid green house, (2) dry soil plot, where watering was made only when leaf blades began to roll, and (3) the control plot, which was kept flooded like the high humidity plot, but placed outdoors like the dry soil plot. Plants in the (1) plot were tall with less tillers and long, thin leaves, showing a spindly growth and shade type. On the contrary, plants in the (2) plot were short with short, thick leaves, and showed xeromorphism.

With plants of (1) plot, O_2 evolution rate began to decrease at -5 bar of leaf water potential, and showed a negative value at -25 bar (Fig. 5). Whereas that of (2) plot began to decrease at the leaf water potential lower than -20 bar, but it was still 200 μ mole O_2 dm^{-2} hr^{-1} even at -30 bar. The control plot (3) was intermediate between the both plots.

Results of the measurements done by changing the water potential of the medium also showed the same trend as above: water potential of the medium at which the O_2 evolution began to decrease was plot $(1) > (3) > (2)$, although it was slightly lower than corresponding leaf water potential.

Osmotic potential of leaf blades containing enough water and with high leaf water potential was -9.1 ± 0.3, -9.8 ± 0.3 and -11.8 ± 0.5 bar for the plot (1), (3) and (2), respectively. Namely, the lower the leaf water potential at whcih O_2 evolution rate began to decrease, the lower was the osmotic potential. Thus, the osmotic adjustment to the photosynthetic apparatus was recognized.

Discussion

It was recognized from this study that the stomata of leaf blades of rice plants are closed sensitively in response to the lowering of the leaf water potential, but the photosynthetic activity was not affected even when the leaf water potential decreased to a considerable extent. Based on this fact, it can be considered that the reduction of photosynthetic rate occurring with the lowering leaf water potential is entirely caused by a decrease of CO_2 supply into leaves due to stomatal closure.

As for sunflower and soybean, diffusive conductance and photosynthetic rate begin to decrease at $-8\sim-12$ bar or lower than that of leaf water potential, and the decrease takes a S-shape curve.[1,2] For sunflower it was also recognized that the leaf water potential, which induces beginning of stomatal closure, also induces beginning of the reduction in the photosynthetic activity in mesophyll cells.[4] Namely, it is assumed that, when the photosynthetic rate decreases due to lowered leaf water potential, not only stomatal closure occurs, but also photosynthetic activity is considerably affected.

Thus, it is considered that rice and sunflower differ from each other in their responses to dry condition. In rice, the photosynthetic rate is decreased by the stomatal closure, but at the same time transpiration is also reduced, so that water content in plants is not reduced so much. As a result, photosynthetic activity is not affected by water deficiency. On the other hand, in sunflower, even when the leaf water potential is lowered to some extent, the photosynthetic rate is kept high without a change, and at the same time transpiration also goes on intensively resulting in a further reduction of soil moisture, which in turn accelerates the lowering of leaf water potential. Thus, the photosynthetic rate comes to be reduced, and at this time, the photosynthetic activity is also reduced. Which of these different characters is advantageous for growth or survival of plants under dry conditions may depend on a severity and duration of dryness.

Not consistent with the past result,[9] it was found in the present study that the photosynthetic activity of rice leaves was not affected by leaf water potential down to about -25 bar. On the contrary, in C_4 plants including corn, which are regarded to be highly efficient in water utilization for photosynthesis and hence adaptable to arid regions the photosynthetic activity begins to decrease about -10 bar.[12]

This fact indicates interestingly that rice plants, which grow under flooded condition and are regarded to be less resistant to drought, have a photosynthetic apparatus more resistant to water deficiency. It seems to be necessary to carry out physiological and ecological studies on plant characters responsible for lowering drought-resistance of rice plants.

The present study is a part of Special Scientific Research funded by the Ministry of Education, Science, and Culture.

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(Received for publication, December 11, 1982)