Injury of Rice Plants Caused by Sulfur Dioxide and Its Mechanism

By YOSHIHIRO MATSUOKA

Agricultural Experiment Station of Chiba Prefecture

Of studies[2)6)7)] on sulfur dioxide injury to crop plants, so-called "invisible injury theory" has been a subject of argument from old time. The reason for that is attributable to the following fact: one of the injurious effects of sulfur dioxide is the inhibition of photosynthesis, and even under slightly contaminated conditions not causing any visible injury a slight inhibition of photosynthesis occurs. However, it has not been known whether such a slight inhibition of photosynthesis can exert adverse effects on plant growth and dry matter production or not. In other words, the critical limit of sulfur dioxide concentration affecting growth and dry matter production is not necessarily made clear.

The present author[3)] has clarified characteristics of sulfur dioxide inhibition of photosynthesis, and made clear the relationship between the inhibition of photosynthesis and dry matter production, by examining the effect of sulfur dioxide on growth and dry matter production at the concentrations not inducing visible injury.

In this experiment, rice seedlings growing in pots were used. An experimental facility to measure photosynthesis of plants being exposed to sulfur dioxide gas under artificial light (Plate 1), and a facility to examine effects of chronic exposure to the gas on plant growth under natural light (Plate 2) were employed.

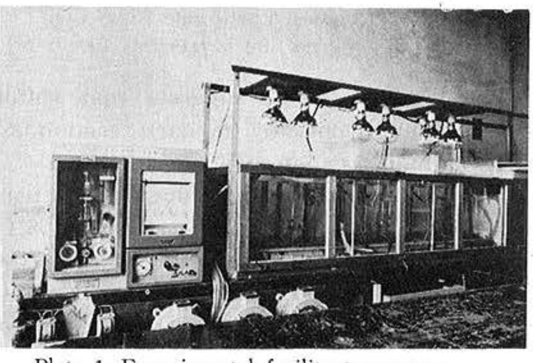

Plate 1. Experimental facility to measure photosynthesis under artificial light with SO_2 gas treatment

Plate 2. Experimental facility to measure plant growth and dry matter production under natural light with chronic exposure to SO_2 gas.

Characteristics and mechanism of inhibition of photosynthesis

At first, to know characteristics of sulfur dioxide inhibition of photosynthesis, preliminary experiments were carried out using both high concentrations of sulfur dioxide which cause marked visible injury and low concentrations inducing no visible injury. The result showed that the inhibition of photosynthesis can be classified into three types: (1) temporary and reversible inhibition occurring only during a period of gas exposure, (2) inhibition which recovers gradually with a certain length of time after the end of gas exposure, and (3) inhibition which can not recover. Based on the fact that only the inhibition of type (1) occurs by the gas exposure at the concentration not inducing visible injury, effects of low concentrations of sulfur dioxide on photosynthesis were further examined.

The change of photosynthetic rate was examined by changing sulfur dioxide concentration in a gas exposure chamber, and it was found that photosynthetic rate changes immediately and in close relation to the change of sulfur dioxide concentration (Fig. 1). This characteristic response was observed even when the exposure period was changed or intermittent exposure was repeated. When

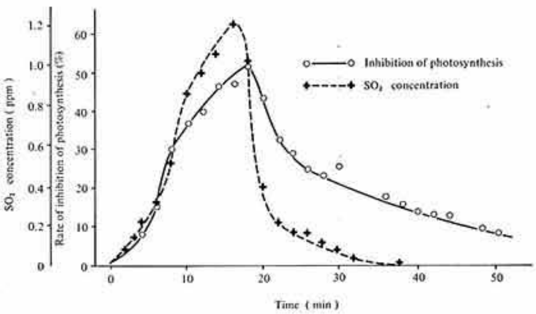

Fig. 1. Relationship between rate of inhibition of photosynthesis and SO_2 concentration

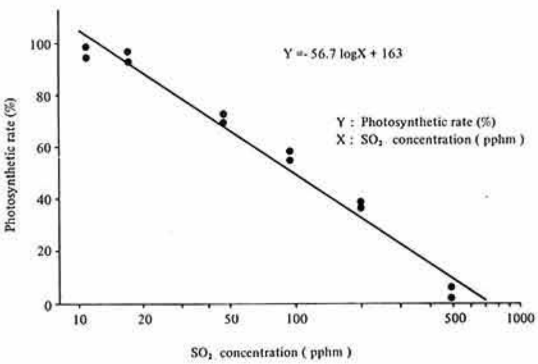

Fig. 2. Relationship between SO_2 concentration and photosynthetic rate

Note: Photosynthetic rate without SO_2 treatment is taken as 100

sulfur dioxide concentration was kept constant, photosynthetic rate was maintained at a certain reduced level until sulfur dioxide was removed.

Rate of inhibition of photosynthesis showed a close relation to sulfur dioxide concentration (Fig. 2). The relationship between photosynthetic rate as expressed in percentage (Y) of that in normal air and sulfur dioxide concentration (X pphm) is shown as follows:

$$Y = -56.7 \log X + 163$$

This equation suggests that sulfur dioxide inhibits mainly the dark reaction of photosynthesis.

Effect of light intensity, ranged from 5 klux to 50 klux, on sulfur dioxide inhibition was examined, and it was found that the higher the light intensity the more the inhibition was, but the inhibition occurred even under 5 klux, a weak light limiting photosynthetic rate

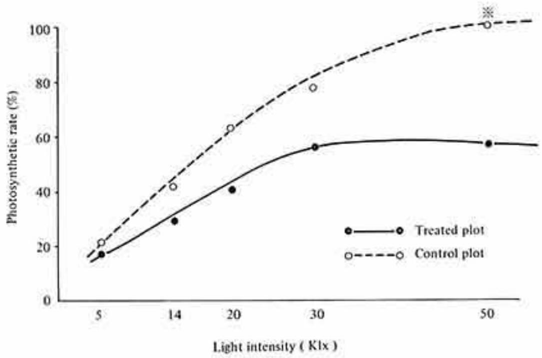

Fig. 3. Light-photosynthesis curve as affected by SO_2.

Note: *: Photosynthetic rate (52.6 CO_2 mg/pot/hr) is taken as 100

(Fig. 3). This result suggests that sulfur dioxide inhibits not only the dark reaction but also the light reaction of photosynthesis.

The inhibition was also influenced by temperature. Within a range from 17°C to 38°C, the higher the temperature, the less was the rate of inhibition (Fig. 4).

Whenever the inhibition of photosynthesis occurred, transpiration was also reduced, suggesting the effect of sulfur dioxide on stomatal aperture.

Based on these findings, the mechanism of

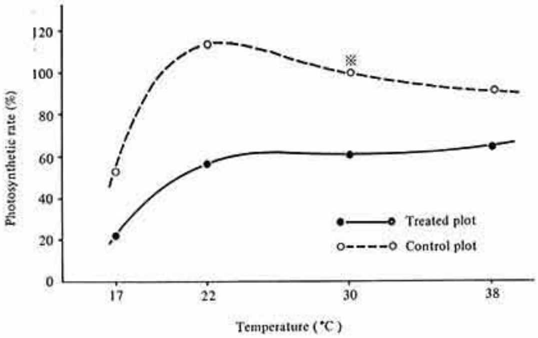

Fig. 4. Temperature-photosynthesis curve as affected by SO_2.
Note: *: Photosynthetic rate (62.3 CO_2 mg/pot/hr) is taken as 100.

sulfur dioxide inhibition of photosynthesis is considered to be multiple, i.e., sulfur dioxide inhibits both stomatal movement and photosynthetic reaction, effecting both of the light reaction and the dark reaction. As to the inhibition to the dark reaction, it can be presumed that the major mechanism is the inhibition of photophosphorylation[11] and RuDP carboxylase[10] rather than glycolate oxidase,[8] by taking into account the characteristic that the inhibition is closely related to the change of sulfur dioxide concentration.

The reason for the reduced inhibition at high temperature is presumed as follows, based on reports of Tanaka et al. (1972)[5] and Zelitch (1959).[9] Sulfur dioxide absorbed by leaves produces α-hydroxysulfonates, which may inhibit photo-respiration.

Factors effecting sulfur dioxide absorption by leaves

Rate of sulfur dioxide absorption by leaves varied not only with sulfur dioxide concentration but also with temperature, light intensity, wind, and stomatal aperture. The rate of absorption was measured at different temperatures and light intensities. At a given concentration of sulfur dioxide the higher the temperature and the higher the light intensity, the higher was the rate of absorption by leaves.

Similarly the higher the wind velocity, up to 2 m/sec, the more was the absorption. However, at the wind velocity higher than 2 m/sec the rate of absorption was lower than the above case, and in the range of 2 — 5 m/sec no apparent difference in absorption was observed, irrespective of wind velocities.

When the stomatal aperture was changed by changing concentrations of oxygen and carbon dioxide in the air or by spraying phenylmercuric acetate solution, the absorption of sulfur dioxide showed a high correlation with the stomatal aperture, without showing no relation with photosynthetic and respiration activities of leaves.

Microscopic examinations of the necrotic injury of leaf mesophyll caused by sulfur dioxide confirmed that the necrosis began to appear in the mesophyll tissues adjacent to the sub-stomatal cavity and spread to neighbouring tissues.

All these results suggest that the main entrance for sulfur dioxide into leaves is the stomata. Effects of various external and internal factors on the absorption of sulfur dioxide seem to be explained by their effect on the stomatal aperture.

Effects of low concentration of sulfur dioxide on growth and dry matter production

At a low concentration not inducing visible injury, sulfur dioxide treatment was given intermittently over a long period to examine its effect on growth and dry matter production of rice plants. Seedlings at 2.8 to 5.5 leaf stage, growing in pots, were used. The experiment was run for a period of 31 days. Sulfur dioxide concentration was 0.5 ppm (which causes 30% inhibition of photosynthetic rate) in an average. The exposure of 5 hrs/day was done in 21 days.

During the experimental period, no visible injury was recognized at all. However, in the treated plot the leaf emergence rate and

Table 1. Comparison of calculated dry weight with actual dry weight measured

Growth stage	Dry weight (mg) in treated plot		Dry weight (mg) in control plot	W_1/W_2	$W-W_1/W-W_2$
	Measured (W_1)	Calculated (W_2)	Measured (W)		
3.0 leaf stage	109.4	105.5	117.2	1.028	0.752
4.8 leaf stage	174.0	164.7	183.0	1.056	0.492
5.5 leaf stage	309.7	290.8	319.0	1.065	0.330

number of tillers were somewhat decreased. Particularly the difference in the total leaf area per plant between the treated and control plots was increased as the gas exposure was repeated. As no difference was recognized in the leaf area of individual leaf fully developed, the difference in the total leaf area is due to the difference in leaf emergence rate and in number of tillers.

Photosynthetic rate and dry weight were measured at 3.9, 4.5, and 5.5 leaf stages. Although the photosynthetic rate per unit leaf area showed no difference between plots, the photosynthesis per plant was lower in the treated plot. Dry weight of treated plants was less than that of control plants at any time of measurement, indicating the inhibited dry matter production without any visible injury. Decrease in dry weight was most remarkable with leaf sheath portion.

If the effective sunshine hours per day in this experiment is taken as 10 hrs, the photosynthesis in the treated plot is estimated to have been inhibited by about 9% of the photosynthesis of control plants for a whole period. By multipling this value to the dry weight (W) of the control plot, the dry weight of the treated plot (W_2) can be calculated. The calculated dry weight (W_2) and the actual dry weight (W_1) determined in the treated plot are compared in Table 1, which indicates that the decrease in dry weight due to sulfur dioxide was smaller than the quantity of photosynthesis inhibition.

References

1) Asada, K. et al.: Effect of α-hydroxy sulfonates on photochemical reactions of spinach chloroplasts and participations of glyoxylate in photophosphorylation. *Plant Cell Physiol.*, **6**, 615-629 (1965).

2) Katz, M. & Ledingham, G. A.: Experiments on yield of barley and alfalfa. In effect of sulfur dioxide on vegetation. National Research Council Canada, 332-368 (1939).

3) Matsuoka, Y.: Experimental studies of sulfur dioxide injury to rice plant and its mechanism. *Spec. Bull. Chiba Agr. Exp. Sta.* No. 7, 62-63 (1978) [In Japanese with English summary]

4) Silvius, J. E., Ingle, M. & Baer, C. H.: sulfur dioxide inhibition of photosynthesis in isolated spinach chloroplasts. *Plant Physiol.* **56**, 434-437 (1975).

5) Tanaka, H., Takanashi, T. & Yatazawa, M.: Experimental studies on sulfur dioxide injuries in higher plants. (1) Formation of glyoxylate-bisulfite in plant leaves exposed to sulfur dioxide. Water Air Soil Pollution **1**, 205-211 (1972).

6) Taniyama, T.: Studies on the development of symptoms and the mechanism of injury caused by sulfur dioxide in crop plants. *Bull. Fac. Agr. Mie Uni.*, No. 44, 11-130 (1972) [In Japanese with English summary].

7) Thomas, M. D. & Hill. G. R.: Relation of sulfur dioxide in the astmosphere to photosynthesis and respiration of alfalfa. *Plant Physiol.* **12**, 309-383 (1937).

8) Zelitch. I.: α-Hydroxysulfonates as inhibitors of the enzymatic oxidation of glycolic and lactic acids. *J. Biol. Chem.*, **224**, 251-260 (1957).

9) Zelitch. I.: The relationship of glycolic acid to respiration and photosynthesis in tabacco leaves. *J. Biol. Chem.*, **234**, 3077-3081 (1959).

10) Ziegler, I.: The effect of SO_3^{--} on the activity of ribulose-1, 5- diphosphate carboxylase in isolated spinach chlorolpasts. *Planta*, **130**, 155-163 (1972).