Depression of Photosynthesis in Rice Plant with Low Root Activity Following Soluble Starch Application to the Soil*

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Received January 30, 1994

Abstract : Soluble starch was applied to soil in a pot where rice plant grew at the 10th leaf stage and the initial heading stage. When root activity and leaf bleeding rate were lowered in the treated plant, photosynthesis and stomatal conductance were investigated in the morning. Immediately after that initial Rubisco carboxylation activity and Rubisco content were determined to elucidate what was predominantly responsible for the depressed photosynthesis due to low root activity. Accompanied by a decrease in root activity and leaf bleeding rate during 2–9 days after soluble starch application, the photosynthesis and stomatal conductance in the treated plants were all lowered while the initial Rubisco carboxylation activity and Rubisco content in their leaves were approached or even higher than that in the control plant. The photosynthesis was an extremely significant positive curvilinear correlation with the stomatal conductance. These results show that the depression of photosynthesis in the low-root activity plant introduced by soluble starch application is due to lower stomatal conductance in the treated plants and not due to a lower internal CO₂ assimilation capacity. The decline of photosynthesis in the treated plants, however, was mitigated, in whole or in part, with prolonging the time after soluble starch application -- perhaps through absorbing the additional nitrogen, which was supplied with the soluble starch.

Key words : Bleeding rate, Initial Rubisco carboxylation activity, Photosynthesis, Rice plant, Rubisco content, Root activity, Soluble starch, Stomatal conductance.

根の生理的活性の減少に伴う水稻葉身の光合成速度低下の要因について：蔣 徳安・平沢 正・石原 邦（東京農工大学農学部）

要 旨：根の生理的活性の低下に伴う光合成速度低下の要因を明らかにするため、ポットに生育させた水稻を用いて、第10葉抽出期および出穂開始期に可溶性デンプン 15 gまたは 30 gを土壌中に加える処理を行った（処理水稻）。この際、土壌中の微生物の作用によって一次的に葉身の窒素含量が低下するのを防ぐため、同時にそれぞれ硫酸 2.5, 5 gを施用した。処理水稻と対照水稻について、根の活性を表す葉身基部からの出液速度、根の α -ナフチルアミン酸化力および午前中の最大光合成速度、拡散伝導度、Rubisco 初期活性および Rubisco 含量を測定した。可溶性デンプン処理後、処理水稻の根の α -ナフチルアミン酸化力、葉身基部の出液速度が減少し、葉身の光合成速度および拡散伝導度は小さくなったが、Rubisco 初期活性および Rubisco 含量は対照水稻とほぼ同じかやや大きかった。また光合成速度と拡散伝導度との間には有意な正の相関関係があった。これらの結果より、可溶性デンプン処理によって生じる根の生理的活性の低下による光合成速度の低下は、葉内の CO₂ 固定能力の低下ではなく、拡散伝導度が低下し、葉内への CO₂ 供給量が減少したためであると考えた。さらに、処理水稻の光合成速度の減少は、日数の経過とともに小さくなるか、みられなくなったのは、可溶性デンプンとともに施用した窒素が吸収され、葉内の窒素含量が高くなったことが関係していると推察した。

キーワード：拡散伝導度、可溶性デンプン、光合成、出穂速度、水稻、根の活性、Rubisco含量、Rubisco 初期活性。

In the study of the relationship between photosynthesis in rice leaf and the environmental factors, the researchers have focused more on the nutritional elements^{3,10,14,15,19}) as

well as atmospheric factors^{7,8,11}). Only a few publications, however, are available which have investigated the relationship between photosynthesis in leaf and physiological activity of root. Photosynthesis was decreased by 10–15% with addition of H₂S and Fe⁺⁺, or with reduction of oxygen supply to root in rice plant, and fell to 60–70% of the control as long as the plant root was soaked in boiling water for 30 s²³). The photosynthesis and root

* Research was supported by the Bao Yu-Kong and Bao Zhao-Long Scholarship for Chinese Students Studying Abroad and a grant from Ministry of Education, Science and Culture, Japan.

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α -naphthylamine oxidation capacity were promoted by reasonably draining the water away in the paddy field at the reproductive stage²²⁾. In the afternoon, larger stomatal aperture in the leaf of the rice with a well-developed root system grown on the border of the paddy field¹³⁾ and on the other hand, a smaller stomatal aperture under conditions of high sunlight intensity resulting from the partial excision of root in the rice plant have been reported¹²⁾. The application of soluble starch to soil induced a severe decrease in the photosynthetic rate in rice plant, with an increase in leaf air vapor pressure difference¹¹⁾. The light-photosynthetic curve of rice plant community showed an obvious saturation²⁸⁾. All of those factors suggested that root physiological activity might play an important role in photosynthesis. It still does not explain how low root activity influences photosynthesis and whether it involves the carbon fixation capability associated with Rubisco activity. It is not known if the lowered stomatal conductance derived from soluble starch application^{4,9)} is responsible for depressed photosynthesis. To discover the reason for the low photosynthesis caused by soluble starch treatment, we examined the leaf bleeding and root activity, measured photosynthesis and stomatal conductance simultaneously and rapidly, and then assayed initial Rubisco carboxylation activity and Rubisco content.

Materials and Methods

1. Plant material

Rice (*Oryza sativa* L. cv. Nipponbare) was grown in 1/2000 a Wagner pots filled with mixed soil from the Tama River alluvial and the Kanto diluvial soils (1 : 1, v/v) in submerging conditions. The seedlings at the 4.8 leaf stage were transplanted at the rate of 3 hills with 3 plants per pot on May 26, 1993 after the compound fertilizer (14 : 14 : 14) 7 g/pot was applied as ground fertilizer. Additional fertilizer (14 : 14 : 14) 5, 3 and 5 g per pot were applied on June 12, July 21 and August 4, respectively.

2. Soluble starch application to soil

The application was carried out on two occasions : one at the 10 th leaf stage on June 25 with a control without any additional application, 15 g soluble starch with 2.5 g ammonium sulfate, 30 g soluble starch with 5 g

ammonium sulfate per pot, and the other at the initial heading stage on August 20 with a control, and 15 g, 30 g soluble starch plus 2.5 g ammonium sulfate, respectively. After the application the plants were continuously grown in the submerged conditions. Micro-organism in the soil decomposed soluble starch and consumed oxygen in the soil solution. The soil was strongly reduced and poisonous products such as H_2S etc. to reduce rice root activity accumulated in the soil. In addition, to protect the plant from nitrogen deficiency, ammonium sulfate was applied with soluble starch because of an decrease of available nitrogen in the soil when the micro-organism absorbed the nitrogen.

3. The measurement of photosynthesis and stomatal conductance

Both measurements were performed in the leaf on the main stem with LI-6200 portable photosynthetic and transpiration system (LI-COR) under the outside condition where the plant grew. A supplementary artificial illumination ($1400 \mu\text{mol m}^{-2} \text{s}^{-1}$) was added if necessary and the relative humidity in leaf chamber during measurement for all samples was controlled as high as the atmospheric relative humidity when the first sample was logged. The measurement was undergone between 9 and 11 a. m. with 7 duplications.

4. The assay for initial activities of Rubisco carboxylation

The assay followed the methods described by Lilley et al.¹⁷⁾ and Usuda²⁹⁾. Immediately after photosynthesis was measured, 0.1 g leaf was promptly homogenized in 1.9 ml cooled extraction buffer containing 50 mM Tris-HCl (pH 7.5), 1 mM EDTA (ethylenediaminetetraacetic acid disodium salt), 10 mM $MgCl_2$, 12.5% (v/v) glycerol, 1% PVP-40 (w/v soluble polyvinylpyrrolidone) and 10 mM β -mercaptoethanol, plus about 1% Polyclar AT (insoluble polyvinylpyrrolidone) and acid-washed sand in a chilled mortar with a pestle at 0–4°C. The homogenate was centrifuged at 10,000 g for 10 min. The supernatant diluted properly with the extraction buffer as a crude Rubisco was immediately used to measure the initial activities. The measurement began as soon as 0.1 ml the temperature-balanced enzyme was injected into the 30°C-equilibrated cell with 0.9 ml reaction medium finally consisting of 50 mM HEPES-KOH pH 8.0 1

mM EDTA, 20 mM MgCl_2 , 2.5 mM DTT (dithioerythritol), 1 mM NaHCO_3 , 5 mM ATP, 5 mM phosphocreatine, 0.15 mM NADH, 10 units of phosphoglycerate kinase, 10 units of glyceraldehyde 3-phosphate dehydrogenase, 10 units of phosphocreatine kinase and 0.6 mM RuBP (ribulose-1, 5-disphosphate).

5. The quantification of Rubisco

The quantity of Rubisco was done with the single radial immunodiffusion method illustrated by Koide et al.¹⁶⁾ and Sugiyama et al.²⁷⁾ using Rubisco purified from rice seedling according to Makino et al.¹⁸⁾ as a standard.

6. The measurement of bleeding rate and root activity

After the measurement of photosynthesis and Rubisco activity, the bleeding rate of the leaf was determined by an increase in weight of the sanitary cotton which was attached to the cut surface of the base of leaf blade and covered with polyethylene pocket. Then the whole plant was covered with large black polyethylene sack and placed in room at 25°C for 3 h³⁾. Root activity measurement was referred to α -naphthylamine oxidation method²²⁾

except for NaNO_2 instead of NaNO_3 .

Results

1. Root activity and leaf bleeding rate

As illustrated in Table 1, there was a tendency to decrease in the root activity and to dampen the leaf bleeding rate in the plant grown in the pot where soluble starch was applied to the soil. At same time, some black precipitation appeared on the surface of root, and slight odor of H_2S was given off from the treated pot. Although lower root activity of rice plant with application of soluble starch occurred in both stages, the treatment seemed to have a stronger influence on activity at the initial heading stage in relation to slight new root growth. The bleeding rates of the base of the leaf blades were also significantly reduced by the treatment.

2. Photosynthesis and stomatal conductance

When soluble starch was applied at the 10th leaf stage, the photosynthesis of the 10th leaf decreased from $36.23 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ of control to 31.91 of the 15 g soluble starch-treated plant and 30.54 of the 30 g treated

Table 1. The effect of application of soluble starch to soil on root activity and bleeding rate of leaf in rice plant.

Growth stage	Days after treatment	Doze of soluble starch (g pot ⁻¹)	Root activity ($\mu\text{g } \alpha\text{-naphthylamine oxidation g}^{-1} \text{ FW h}^{-1}$)	Bleeding rate* (mg leaf ⁻¹ h ⁻¹)
Maximum tillering stage	2	0	79.93a (100)	91.53a (100)
		15	72.97b (91.3)	83.07b (90.8)
		30	74.93b (94.7)	77.60b (84.8)
	9	0	74.37a (100)	83.90a (100)
		15	69.13b (93.0)	75.26b (89.7)
		30	71.60ab (96.0)	73.70b (87.8)
	21	0	64.50a (100)	21.11a (100)
		15	57.80b (89.6)	15.58b (77.8)
		30	61.20ab (95.5)	18.03ab (85.4)
Heading stage	3	0	53.38a (100)	119.58a (100)
		15	37.95b (65.0)	100.33b (83.9)
		30	37.07b (63.5)	96.20b (80.4)
	16	0	32.66a (100)	65.71a (100)
		15	27.70b (84.8)	45.07b (68.6)
		30	24.04b (73.6)	39.29b (59.8)

The number in parenthesis is percentage taken control as 100.

*The measured leaf is the 10th leaf at the maximum stage and the flag leaf at the heading stage. Different letter shows difference between treatments on the same day at <0.05 level of probability.

Table 2. The effect of application of soluble starch to soil on photosynthesis and stomatal conductance in rice plant.

Leaf position	Days after treatment	Doze of soluble starch (g pot ⁻¹)	Photosynthesis ($\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$)	Stomatal conductance ($\text{mmol m}^{-2}\text{s}^{-1}$)
The 10th leaf	2	0	36.23a (100)	509.3a (100)
		15	31.91ab (88.0)	438.5ab (86.1)
		30	30.54b (84.3)	378.0b (74.2)
	9	0	36.48a (100)	570.1a (100)
		15	32.95b (90.3)	483.0b (84.7)
		30	33.27b (91.2)	454.4b (79.7)
	21	0	27.34a (100)	1013 a (100)
		15	26.88a (98.3)	782 b (77.2)
		30	30.95b (113)	712 b (70.3)
The flag leaf	3	0	36.37a (100)	1285 a (100)
		15	33.92a (93.3)	1055 a (82.1)
		30	33.24a (91.4)	1150 a (89.5)
	16	0	25.87a (100)	731 a (100)
		15	26.22a (101)	728 a (99.6)
		30	25.16a (97.3)	604 a (82.6)

The number in parenthesis is percentage taken control as 100.

Different letter shows difference between treatments on the same day at <0.05 level of probability.

plant on the second day, and from 36.48 of the control to 32.95 of the 15 g soluble starch-treated plant and 33.27 of the 30 g treated plant on the 9th day after the treatment (Table 2). No depression, and even promotion of photosynthesis in the treated plant, occurred on the 21st day after soluble starch application. When applied at the initial heading stage, 15 g and 30 g soluble starch, respectively, resulted in a fall in 6.7 and 8.6% of photosynthesis of flag leaf in comparison with control $36.37\mu\text{mol m}^{-2}\text{s}^{-1}$ on the 3rd day (Table 2) after the treatment in spite of the same photosynthetic rate just before the treatments (data not shown). But the difference in the photosynthesis almost disappeared on the 16th day. The results in Table 2 indicated that the more soluble starch was applied, the lower the photosynthesis in the early period after the treatments, and that the stomatal conductance was lower in the treated plants than in the control plant at any time. In comparison with stomatal conductance, the degree of the decrease in photosynthesis in the treated plant was lower. Stomatal conductance, in particular, showed a significant difference in the 10th leaf between the 30 g soluble starch applied plant and the control plant on the 2nd day

and between all treated plants and the control plant on the 9th and 21st days after treatment (Table 2). This difference in stomatal conductance was exactly similar to the difference in photosynthesis, except for the 21st day. Those results suggested that low root activity governed stomatal conductance more directly than photosynthesis.

3. Rubisco activity and content

Table 3 showed the initial activity of Rubisco carboxylation hardly decreased and somewhat increased in the treated plant when photosynthesis was significantly lower. The ratio of the initial activity of Rubisco to photosynthesis was significantly lower in the treated plants than in the control plant on the 2nd and 3rd day after the treatment was carried out at the 10th leaf stage and the initial heading stage, respectively.

4. The relationship between photosynthesis and stomatal conductance

Fig.1 is all data of photosynthesis and stomatal conductance in every determined leaf except for the 21st day, when photosynthesis in the treated plant was recovered by increase in Rubisco activity and content due to simultaneous application of nitrogen. The results demonstrated that there was an extremely

Table 3. The effect of application of soluble starch to soil on initial RuBPCase activity, RuBPCase content and ratio of the activity to photosynthesis.

Leaf Position	Days after treatment	Doze of soluble starch (g pot ⁻¹)	RuBPCase activity (μ mol CO ₂ m ⁻² s ⁻¹)	RuBPCase content (g m ⁻²)	RuBPCase/Photosynthesis
The 10th leaf	2	0	32.1a (100)	5.612a (100)	0.89a
		15	34.1a (106)	5.916a (105)	1.07b
		30	37.6a (102)	5.513a (98.2)	1.23b
	9	0	42.0a (100)	4.994a (100)	1.15a
		15	40.7a (96.9)	5.350ab (107)	1.23a
		30	37.8a (90.0)	5.504b (110)	1.14a
	21	0	32.0a (100)	3.019a (100)	1.17a
		15	29.4a (91.9)	2.887a (95.1)	1.08a
		30	41.9b (131)	3.659b (122)	1.35b
The flag leaf	3	0	37.3a (100)	4.728a (100)	1.03a
		15	46.1b (124)	6.106b (129)	1.36b
		30	42.1b (113)	5.155a (109)	1.27b
	16	0	26.5a (100)	4.403a (100)	1.02a
		15	30.1a (114)	5.466b (124)	1.45a
		30	25.5a (96.2)	4.196a (95.3)	1.01a

The number in parenthesis is percentage taken control as 100.

Different letter shows difference between treatments on the same day at <0.05 level of probability.

Fig. 1 The relationship between photosynthesis and stomatal conductance under the condition of soluble starch treatment. ●, ○ and + indicate 0 (control), 15 and 30 g soluble starch treatment, respectively.

The 10th leaf and the flag leaf were measured under $40 \pm 1\%$ and $60 \pm 1\%$ initially relative humidity in leaf chamber, respectively.

positive curvilinear correlation between the photosynthesis and stomatal conductance in both leaves. In addition, it showed lower photosynthesis and lower stomatal conductance of the 10th leaf in the soluble starch-applied plants (the white circles and crosses

in Fig.1) compared with those in the control plants (the black circles in Fig.1).

Discussion

Our results confirmed that the root activity of rice plant was depressed by soluble starch

application to the soil, causing a low rate of leaf bleeding (Table 1). It can be considered that the low root activity was poisoned by H_2S and Fe^{++} under the fermentation condition in which oxygen in soil solution was exhausted by microorganism. The decline of photosynthesis in the plant with low root activity occurred a few days after soluble starch treatments (Table 2), while the initial Rubisco activity and Rubisco content were not lower in the treated leaf than in the control (Table 3). The Rubisco content in the soluble starch applied plants was as high as that in the control plant and was even a little higher than that in the control plant, which meant that an additional nitrogen available kept the treated plants from nitrogen deficiency⁹⁾. The results that low photosynthesis in soluble starch treated plants did not contribute to decrease in Rubisco activity and Rubisco contents are similar to the report in which the low photosynthesis in wheat treated with soil drying was not mainly involved in those⁶⁾. The reports^{4,10,19)} that nitrogen increased in leaf photosynthesis very well explain our result on the recovered photosynthesis in the treated plant in late period, because of an increase in Rubisco carboxylation activity and Rubisco content; maybe by its taking in more nitrogen which was applied to the soil with soluble starch.

Our results coincided with reports in which soluble starch caused the stomatal conductance to fall^{4,9)}. The extremely positive curvilinear correlation between stomatal conductance and photosynthesis was not only supported by other reports^{5,25)}, but also provided convincing evidence to explain why photosynthesis was reduced by soluble starch treatments (Fig.1).

It is still not certain why soluble starch application induces a lower stomatal conductance and how the plant leaf senses this low root activity and leads a lower stomatal resistance to avoid the damage of losing too much water. Although there is no doubt that potassium plays an important role in stomata movement and it was known early that among mineral elements, potassium uptake was inhibited most severely by respiratory inhibitors such as H_2S , NaCN and NaN_3 ^{20,21)} and a very low Eh in the soil resulted from the treatment⁹⁾ also easily produced H_2S and Fe^{++} which poisoned rice root as we observed a black root in the treated plant in this experiment, there

are some reports in which the photosynthesis of the leaf did not decrease in the young expanded leaf^{14,24)} and the leaf usually possessed higher transpiration even if leaf potassium content dropped to as low as 1% based on dry matter weight²⁴⁾. It is unimaginable that leaf potassium content was reduced to less than 1% in such a short time by the soluble starch treatment in our experiment. Therefore, the possibility can be excluded that the soluble starch treatment reduced stomatal conductance owing to potassium deficiency. Recently it has been reported that less cytokinin in the xylem exudation of rice cultivar with poorly-developed root system was detected²⁶⁾ and that free ABA concentration in the xylem increased¹⁾ when only a part of the root system was located in drying soil. It has been reported that ABA in the xylem, as a signal synthesized in root, regulated stomatal behaviour and plant growth under soil drying²⁾. Our experiments do not exclude the probability that soluble starch plus nitrogen application results in a lower soil water potential in a short time.

The curvilinear correlation between the photosynthesis and stomatal conductance elucidated that soluble starch treatment did not obviously drop in photosynthesis when photosynthesis was measured in high air humidity where stomatal conductance was larger, for example, in the flag leaf or in the 10th leaf on the 21st day after soluble starch application to the soil in our experiment, even if the plants have low root activities. If the stomatal conductance is dominant in controlling the depression in photosynthesis after soluble starch application, we can reasonably presume that an acceleration in the depression of photosynthesis will take place in the low root activity plants treated with soluble starch when transpiration rises in the middle of day with higher sunlight intensity and temperature, and lower relative humidity and that the depression will still be attributed to the decrease in stomatal conductance even if photosynthesis in the morning has been increased due to higher Rubisco activity and content caused by additional nitrogen. It is necessary to investigate the diurnal changes in the plants with different root activities to verify this hypothesis.

Acknowledgements

We would like to thank Dr.T. Ookawa and graduate student Y.F. Xu for their help in this experiment.

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