Effects of Elevated Atmospheric Carbon Dioxide Concentration on Silica Deposition in Rice (*Oryza sativa* L.) Panicle

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Abstract : The effects of elevated carbon dioxide concentration ([CO2]) on silica deposition on husk epidermis of rice (*Oryza sativa* L. cv. Akitakomachi) during the flowering stage were investigated in this study. The study was motivated by the concept that the rice yield maybe affected by global warming as a result of elevated [CO2] environment since sterility of rice is related to the panicle silica content that influences transpiration, and elevated [CO2] could affect plant transpiration. Silica deposition analysis was focused on the flowering stage of the rice crop grown hydroponically under two [CO2] conditions: 350 μmol mol\(^{-1}\) (ambient) and 700 μmol mol\(^{-1}\) (elevated). Silica deposition on the husk epidermis from three parts of the panicle at four flowering stages were examined using a scanning electron microscope (SEM) combined with an energy dispersive X-ray microanalyzer (EDX). The results demonstrated that elevated [CO2] significantly suppressed silica deposition on the husk epidermis at the lower part of the panicle, and at the early flowering stage when 1/3 of the panicle emerged from the leaf sheath. In the transverse section analysis of the husk, silica deposition on the husk epidermis under elevated [CO2] was less than that under ambient [CO2] at the late flowering stage. The less silica deposition observed on the husks at the late flowering stage under elevated [CO2] might be related to the suppressed transpiration from the panicle by elevated [CO2] found in a previous study.

Key words : Elevated [CO2], *Oryza sativa* L., Panicle, SEM, Silica, Transpiration, X-ray microanalysis.

According to the Intergovernmental Panel on Climate Change (IPCC), atmospheric carbon dioxide concentration ([CO2]) is increasing year by year and it is predicted that the [CO2] at the end of this century may reach 540 to 970 μmol mol\(^{-1}\) (Prentice et al., 2001). Numerous studies suggested that the predicted increase in [CO2] will promote the growth and yield of rice (Kimball and Idso, 1983; Imai et al., 1985; Ziska and Teramura, 1992; Keeling et al., 1995; Baker et al., 1997b). However, elevated [CO2] reduces transpiration and other researchers predicted a decrease in rice yield in the event of a severe drought at a particularly sensitive growth stage such as anthesis and grain filling (Baker et al., 1997a). Rice yield, in particular, is adversely affected by water stress during the flowering stage when the rice panicles emerging from the leaf sheaths are susceptible to water loss (Ekanayake et al., 1993). Even though there are stomata on the panicle rachis and rachis branches, approximately 75% of the panicle is covered by the husk that has only a few stomata at the tip (Kaneko et al., 1988). Ishihara et al. (1990) found that panicle hardly transpires through the stomata. This means that the glumes and anthers are particularly prone to desiccate severely resulting in impaired flower development and high panicle sterility (Ekanayake et al., 1989).

Rice plants accumulate relatively large amounts of silica on the epidermis of their husks or leaves compared with other crops (Takahashi et al., 1990). Silica is absorbed by plants in the form of silicic acid and is transported along with the transpiration stream (Takahashi and Hino, 1978). Jones and Handreck (1967) reported that the overall uptake of silica by rice plants was independent of transpiration, but that the subsequent translocation of silica toward the panicle or the leaf is affected by transpiration. Unlike leaves, the panicle transpires primarily through the thin cuticle layer of the husk epidermis. Silica is polymerized as silica gel (insoluble silica) and forms a layer under the cuticle where water has been lost by transpiration. This water loss at the husk occurs through two layers (Yoshida et al., 1962a, 1962b). Silica deposition on the husk epidermis decreases transpiration from the panicle by approximately 30% (Ma et al., 2001). Yoshida et al. (1962b) proposed that silica deposition on the husk epidermis contributes to maintenance of the water content of the panicle by reducing transpiration. In addition, Seo and Ota (1982a) demonstrated that sterility is related to silica content of the panicles and that the silica content of fertile
rice panicles was always markedly higher than that of sterile panicles. These authors also demonstrated that fertile panicles were better adapted to conserving water compared to sterile panicles and suggested that this ability was related to the high silica content of the fertile panicle (Seo and Ota, 1982b). Since panicle transpiration reaches maximum at the flowering stage, the suppression of transpiration from the panicle by silica deposition on the husk is considered to play an important role in maintaining the water content of the panicle (Miyagawa et al., 1999).

In the leaves, elevated [CO₂] decreases stomatal conductance, which reduces transpiration (Kimball, 1983). However, few reports have addressed the effects of elevated [CO₂] on transpiration from the panicle during the flowering stage. We demonstrated previously that the transpiration rate and total silica content (soluble and insoluble) of the panicle decreased at elevated [CO₂] (700 μmol mol⁻¹) at the flowering stage (Takahashi and Kurata, 2007), suggesting that elevated [CO₂] may affect silica deposition on the husk in response to decreased transpiration from the panicle. However, it is not clear how elevated [CO₂] affects silica deposition (i.e., deposition of insoluble silica) on the husk epidermis during the flowering stage.

In addition, silica deposition on the epidermis of the old leaves was higher than that observed in younger leaves (Yoshida, 1962a), and Takeoka et al. (1984) demonstrated that considerably more silica was deposited at the top of leaves compared to their bases. These findings strongly suggested that silica deposition on the husk also depends on the flowering stage and/or at the site of the panicle. We hypothesize that if elevated [CO₂] affects silica deposition on the husk epidermis during the flowering stage, silica deposition may vary with the flowering stage and/or part of the panicle. The objective of the present study was therefore to investigate the effects of elevated [CO₂] (700 μmol mol⁻¹) on silica deposition on the husk epidermis at different flowering stages and at different parts of the panicle.

Materials and Methods
1. Plant material and growth conditions

Three weeks after germination, rice seedlings (Oryza sativa L. cv. Akitakomachi) having three expanded leaves were transplanted to 2-L plastic pots (1 seedling/pot). Eight seedlings were grown hydroponically in two artificially illuminated chambers (MIR-553, Sanyo Electric Biomedical Co. Ltd., Tokyo, Japan) (4 seedlings/chamber). The [CO₂] in the chambers was maintained at either 350±50 or 700±20 μmol mol⁻¹ by controllers (ZEPI9, Fuji Electric Systems Co., Ltd., Tokyo, Japan). Day/night air temperature was maintained at 35±1°C/28±1°C under a 12-h day/12-h night cycle. Relative humidity was maintained at 50±10% and the photosynthetic photon flux density from the fluorescent lamps in the chambers at the top of the plant was 1040 μmol m⁻² s⁻¹.

The culture solution was prepared following a receipt described by Mae and Ohira (1981). The basal nutrient solution contained: NH₄NO₃, NaH₂PO₄·2H₂O, K₂SO₄, CaCl₂·2H₂O, MgCl₂·6H₂O, EDTA-Fe, H₃BO₃, MnSO₄·5H₂O, CuSO₄·5H₂O, ZnSO₄·7H₂O, and Na₂MoO₄·2H₂O. In each chamber, the silica concentration in the culture solution was adjusted to 100 mg L⁻¹. The solution was renewed weekly. The silica solution used in this study was prepared by passing Water Glass through an ion-exchange resin (DOWEX 50W-X8), which eliminated the Na⁺ for adjusting Na⁺ level in each silica application and for eliminating the effects of additional Na⁺.

Flowering occurred approximately 63 and 70 days after germination in the plants cultivated at elevated [CO₂] and ambient [CO₂], respectively. The panicles for SEM/EDX investigation were obtained at different times in each treatment to ensure that they were at the same developmental stage. In each [CO₂] treatment, panicles at the same level of emergence from the sheath were used.

2. Sample preparation and SEM/EDX

A scanning electron microscope (SEM) (S-4000, Hitachi Co. Ltd., Tokyo, Japan) equipped with an energy dispersive X-ray microanalyzer (EDX) (EMAX-5770X, Horiba Ltd., Kyoto, Japan) was used to determine silica deposition on the husk epidermis in this study.

The dried husks were cut in half with a razor blade. In the case of the transverse sections of the husk, the dried husks were fixed with ethanol and frozen in liquid nitrogen before cutting with a razor blade at the center of the husk. These samples were dried in a vacuum oven for 24 hr (EVELA VOS-300SD, Tokyo Rikakikai Co. Ltd., Tokyo, Japan) before being coated with platinum-palladium (Pt-Pd) using an ion-sputter-coater (E-1030, Hitachi Co. Ltd., Tokyo, Japan). This coating method was described by Motomura et al. (2000, 2004, 2006) and was used successfully for the SEM/EDX quantitative determination of aluminum. Using Pt as an internal standard, the aluminum contents determined by SEM/EDX, the X-ray fluorescence analysis, and absorption spectroscopy were in good agreement (Kato et al., 1998). The same X-ray microanalysis was also used previously to determine the distribution and deposition of Si in leaves and root tissues in rice (Lux et al., 1999), sorghum (Lux et al., 2002) and bamboo (Lux et al., 2003). Measuring conditions for SEM/EDX were as follows: 15 mm working distance, 6 kV accelerating voltage, 0° tilt angle, 30° take-off angle, and 10 μA emission current.

Using EDX, distributions of silica on six parts of the
husk epidermis shown in Fig. 1 were examined. The size of the section from each part was approximately 1140 μm × 840 μm. The spectrum of the husk epidermis was detected using the EDX (Fig. 2). The relative silica concentration (RSC) was determined by comparing the intensity of the Si peak relative to that of the Pt peak. The method was described by Takahashi et al. (2006) for determining silica distribution on the husk of rice plants grown in the ambient [CO2] condition.

3. Silica distribution on the husk epidermis at different flowering stages

The rice husks were obtained from the upper part of the four panicles at all four flowering stages: (1) booting stage, when the panicle just emerged from the leaf sheath; (2) early flowering stage, when approximately 1/3 panicle emerged; (3) middle flowering stage, when approximately 2/3 of the panicle emerged, and the (4) late flowering stage, when the panicle emerged completely from the leaf sheath. The panicles at the late flowering stage were sampled from the main stem, and those at other stages from the remaining tillers in each pot. The RSC on the husk epidermis at the four flowering stages was determined by the spectrum analysis using EDX with a scanning time (total detecting time) of 200 s.

At the late flowering stage, silica distributions on the husk epidermis were detected by the mapping analysis using the EDX. Four husks from each panicle were used for both [CO2] treatments. Silica distributions on the transverse section of the husk were examined by the line and mapping analyses using the EDX. SEM photographs were obtained as digital images of 256 × 256 pixels in the mapping and line analyses. In the line analysis, scanning was carried out on areas measuring 27 × 256 pixels at the palea. The scanning time (total detecting time) employed was 900 s in the line analysis and 500 s in the mapping analysis. The transverse sections for replications were obtained from different husks and examined at the same point on the palea.

4. Silica distribution on the husk epidermis at different parts of the panicle

Four panicles were obtained from the main stem of the rice plant at the late flowering stage. The husks were obtained from the upper, middle, and lower parts of the four panicles (Fig. 3). The RSC on the husk epidermis was determined at parts of the husk epidermis using the spectrum analysis function attached to the EDX and the scanning time (total detecting time) of 200 s.
5. Statistical analysis

The effects of elevated [CO$_2$] on silica distribution were investigated by determining the RSC at each part of the husk epidermis (Fig. 1, a-f) using t-tests. Differences in RSC on the husk epidermis between ambient [CO$_2$] and elevated [CO$_2$] were statistically analyzed using a t-test with JMP software (SAS Institute, version 3.2.6, NC, USA).

Results

We analyzed the effect of elevated [CO$_2$] on the silica deposition on the husk epidermis. In general, less silica deposition was observed in the elevated [CO$_2$] condition compared with ambient [CO$_2$]. Further analyses showed that the silica deposition on the husks varied with the flowering stage, and site of the panicle.

1. Effect of elevated [CO$_2$] at different flowering stages

RSC was lower in the elevated [CO$_2$] condition at all flowering stages and all parts of the husk (Fig. 4) with two exceptions: 1) during the booting stage (Fig. 4A), and 2) at the tip of the husk in the late flowering stage (Fig. 4D, e-f). At the early flowering stage, RSC was significantly decreased by elevated [CO$_2$] ($p<0.05$ at c, d, and f; $p<0.01$ at b; $p<0.001$ at a; Fig. 4B). However, at the late flowering stage only minor differences in RSC that were not statistically significant were observed at each part of the husk (Fig. 4D).

The RSC in ambient [CO$_2$] increased as flowering progressed from the booting to the middle flowering stage. However, in the elevated [CO$_2$] condition, no increase in RSC was observed from the booting to the early flowering stage (Figs. 4A, B).

At all flowering stages in both [CO$_2$] treatments, the RSC in the epidermis tended to increase gradually from the base to the top of the husk. In the ambient [CO$_2$] condition, the differences in RSC between the base and the tip of the husk were relatively small at the early flowering stage, but RSC at the base was approximately half that at the tip in the middle and late flowering stages. Conversely, in the elevated [CO$_2$] condition, the RSC at the base of the husk was less than half that at the tip of the husk at any of
the flowering stages except for the booting stage. In particular, the difference in RSC between the base and the tip of the husk was large at the late flowering stage. The range of RSC in different parts of the husk was 0.22 to 1.62 in ambient [CO$_2$] and 0.18 to 1.74 in the elevated [CO$_2$] condition.

The differences in RSC between the two [CO$_2$] treatments at the base of the husk epidermis were larger than those at the tip of the husk at all flowering stages. Interestingly, at the late flowering stage, the RSC at the tip of the husks subjected to elevated [CO$_2$] treatment tended to be slightly higher than those in ambient [CO$_2$] (Fig. 4D). The differences in RSC between the base and the tip of the husk at the late flowering stage in both [CO$_2$] treatments were reconfirmed by the mapping analysis using the EDX (Fig. 5). As shown in Fig. 5B2, 4, the images used for mapping silica distribution on the epidermis revealed that the amount of silica deposition was larger at the base than that at the tip of the husk, and more uniform within the husks in ambient [CO$_2$] than in the elevated [CO$_2$] condition. At the tip of the husk, however, silica deposition on the trichomes and papillae was heavier under the elevated [CO$_2$] conditions compared with that in ambient [CO$_2$] (Fig. 5A2, 4). A large number of trichomes were observed at the tip of the husk epidermis (data not shown). Because silica accumulated on the trichomes at the tip of the husk, there may be no significant differences in RSC in the husk epidermis other than the trichomes between the two [CO$_2$] treatments. The greater silica deposition on the trichomes under the elevated [CO$_2$] condition than in ambient [CO$_2$] may contribute to the slightly higher RSC in the tip of the husk.

To further evaluate the RSC in the husk epidermis other than the trichome, we investigated the transverse section of the husk and determined the effect of elevated [CO$_2$] treatment at the late flowering stage. Fig. 6 shows the transverse section of a husk composed of the palea and lemma with trichomes. silica distribution in the transverse sections at point A of the palea (Fig. 6) was determined using the mapping analysis using the EDX (See Fig. 7). Rice seedlings were grown hydroponically under either ambient [CO$_2$] (350 μmol mol$^{-1}$; A1, A2, B1, B2) or elevated [CO$_2$] (700 μmol mol$^{-1}$; A3, A4, B3, B4).

The husks were obtained from the upper part of the panicle at the late flowering stage after complete heading. Rice seedlings were grown hydroponically under either ambient [CO$_2$] (350 μmol mol$^{-1}$; A1, A2, B1, B2) or elevated [CO$_2$] (700 μmol mol$^{-1}$; A3, A4, B3, B4).
the rice grown in ambient [CO\textsubscript{2}]. As shown in Fig. 7, heavy silica deposition was observed around the husk epidermis regardless of [CO\textsubscript{2}] treatment, while the amount of silica deposited on the husk epidermis in ambient [CO\textsubscript{2}] was more than that in the elevated [CO\textsubscript{2}] condition (Fig. 7C, D). A similar pattern of silica deposition was found in all transverse sections (four husks in each [CO\textsubscript{2}] treatment) examined in this study. While no significant differences were observed in the RSC in the middle region of the husk epidermis between the two [CO\textsubscript{2}] treatments at the late flowering stage (Fig. 4D), the mapping analysis through the transverse section of the husk demonstrated that silica deposition on the epidermal area other than trichomes in the elevated [CO\textsubscript{2}] condition was less than that in ambient [CO\textsubscript{2}].

2. Effects of elevated [CO\textsubscript{2}] at different parts of the panicle

The effects of elevated [CO\textsubscript{2}] on the silica deposition at upper, middle, and lower parts of the panicle were examined. With the exception of the tip of the husk obtained from the upper part of the panicle (Fig. 8A, e-f), the RSC in the epidermis of the husk exposed to elevated [CO\textsubscript{2}] was less than that in ambient [CO\textsubscript{2}] (Fig. 8B, D). In particular, at the lower part of the panicle, the RSC in the husk epidermis of the plants grown in the elevated [CO\textsubscript{2}] condition was significantly lower \((p<0.05\) at a, b, d, e, and f; \(p<0.01\) at c; Fig. 8C). The RSC in the husk at the lower part of the panicle cultivated in the elevated [CO\textsubscript{2}] condition was approximately half, or less than half of that in ambient [CO\textsubscript{2}].

Independent of [CO\textsubscript{2}], the RSC in the husk epidermis gradually increased from the base to the tip of the husk, and tended to increase from the lower to the upper part of the panicle. The range of the RSC was 0.38 to 1.59 in ambient [CO\textsubscript{2}], and 0.18 to 1.74 in the elevated [CO\textsubscript{2}] condition within the same panicle. Thus, the RSC was found to vary more under the elevated [CO\textsubscript{2}] condition than the ambient [CO\textsubscript{2}]; in agreement with the finding obtained in the analysis of silica distribution at different flowering stages.

Differences in RSC between the upper and lower parts of the panicle at each part of the husk epidermis ranged from 0.26 to 0.36 in ambient [CO\textsubscript{2}], and from 0.25 to 0.92 in the elevated [CO\textsubscript{2}] condition (Fig. 9).
observed. Elevated [CO₂] significantly suppressed silica deposition on the husk epidermis, especially than that in ambient [CO₂] during flowering, except than that observed on the young leaves. In both [CO₂] treatments, silica deposited on the epidermis of the husk was less at the lower part of the panicle than at the upper part. This suggested that the difference in silica deposition between the upper and the lower parts of the panicle is due to the difference in the time of emergence from the leaf sheath (Takahashi et al., 2006).

RSC in the elevated [CO₂] conditions was lower than that in ambient [CO₂] during flowering, except for the booting stage. Because the panicle was covered with the leaf sheath at the booting stage, no difference in RSC between the two [CO₂] treatments might be observed. Elevated [CO₂] significantly suppressed silica deposition on the husk epidermis, especially at the early and the middle flowering stage. While the observation of the husk epidermis revealed no significant differences in RSC between the two [CO₂] treatments at the late flowering stage, the examination of transverse sections using both the mapping and line images of the palea revealed that the silica deposition was less in the husk epidermis of specimens grown in the elevated [CO₂] condition. In our previous study in which we examined the whole panicle silica content by chemical analysis, the silica content of panicle in the elevated [CO₂] condition was significantly less than that in ambient [CO₂]; 0.95 mg SiO₂ g⁻¹ dry weight in the elevated [CO₂] condition and 1.30 mg SiO₂ g⁻¹ dry weight in ambient [CO₂] (Takahashi and Kurata, 2007).

At the lower part of the panicle, the RSC on the husk epidermis in elevated [CO₂] was significantly less than that in ambient [CO₂]. Differences in RSC in the husk epidermis between the upper and lower parts of the panicle in the husk epidermis were similar in each part of the husk in ambient [CO₂], but increased linearly from the base to the tip of the husk in the plants in the elevated [CO₂] condition. These findings suggested that silica was deposited on the husk epidermis more unevenly when grown in the elevated [CO₂] condition than when grown in ambient [CO₂]. Similarly, the results of mapping the images of the husk epidermis showed that silica deposition at the base of the husk for elevated [CO₂] was more uneven than that in the ambient [CO₂] treatment. Soni and Parry (1973) reported that silica distribution on the epidermis of the rice husk was uneven and that heavy silica deposition was observed on the papillae under ambient [CO₂]. Similar results were obtained in the other plants under ambient [CO₂]. For example, in the inflorescence bracts of barley (Hordeum sativum L.), Hayward and Parry (1973) reported heavy silica deposition on the trichomes. Hodson et al. (1982) assumed that the bristles of Setaria italica (L.) Beauv. with their stomata were transpiring organs, but that only the prickles appeared to be characterized by heavy silica deposits. Similarly, heavy silica deposition was observed in the micro hairs and prickles of the leaf blades of Pleioblastus chino (Motomura et al., 2000). Sangster et al. (1983b) reported that the papillae, prickle and macro hairs of glume in the Phalaris canariensis L. accumulated varying amounts of silica. They also showed that bract hairs of Phalaris canariensis contained some silicon prior to extension growth (Sangster et al. 1983a). The finding of marked unevenness in silica deposition observed on the husks of rice grown in the elevated [CO₂] condition in this study suggests that uneven silica deposition in the aforementioned reports may also become more apparent under the elevated [CO₂] conditions. Furthermore, because the silica content of the panicle is related to fertility (Seo and Ota,
uneven silica deposition may even result in an uneven distribution of fertility in the panicle under the elevated [CO2] conditions.

In conclusion, the results of this study showed that elevated [CO2] significantly suppressed silica deposition on the husk epidermis at the early and the middle flowering stage, and at the lower part of the panicle. Given that silica is transported along with the transpiration stream (Takahashi and Hino, 1978), the reduction of silica deposition on the husk might be related to the decreased transpiration from the panicle under elevated [CO2]. In a previous study, we measured the transpiration rate of the panicle at the late flowering stage under the same experimental conditions as in the present study (silica concentration in the culture solution; 100 mg L−1), and demonstrated that panicle transpiration in the elevated [CO2] condition was suppressed by approximately 12% compared with that in ambient [CO2] (Takahashi and Kurata, 2007). This suppressed transpiration rate could cause poor silica deposition on the husk epidermis and it might affect the silica role in maintaining the water content of the panicle. The mechanism associated with the suppression of transpiration from the panicle by elevated [CO2] observed during flowering is still unknown and needs to be investigated further.

Decreasing transpiration rates from panicle under elevated [CO2] could increase temperature on the panicle, resulting in increased sterility (Matsui et al., 1997). In addition, Sumida and Ohyama (1990) found that silica uptake by rice plants increased with the increased temperature. Further study on the effects of elevated [CO2] on the silica deposition in relation to temperature is necessary.

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* In Japanese with English abstract.
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*** In Japanese.