Effects of elevated [CO₂] on stem and root lodging among rice cultivars

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Received June 10, 2012; accepted September 24, 2012; published online January 23, 2013

Studies showed that elevated [CO₂] would improve photosynthetic rates and enhance yields of rice; however, few studies have focused on the response of rice lodging, which is a major cause of cereal yield loss and quality reduction, under elevated [CO₂]. In this study, we examined the effects of elevated [CO₂] on stem and root lodging using 4 rice cultivars (86Y8, *japonica* hybrid; LYP9, 2-line *indica* hybrid; variety 9311, type of *indica* inbred rice, and SY63, 3-line *indica* hybrid) grown under two [CO₂] levels: 400 and 680 μmol mol⁻¹. Our results indicated that under elevated [CO₂], the stem-lodging risk (SLR) of 9311 decreased, while in SY63 the SLR increased, 86Y8 and LYP9 were not significantly affected; the risk of root lodging was reduced for all cultivars, because root biomass (instead of root number) and bending strength were increased significantly, and then the increase of anti-lodging ability is far higher than that of self-weight mass moment for all cultivars. These findings suggested that higher [CO₂] can enhance the risk of stem-lodging for cultivars with strong-[CO₂]-responses, but may not aggravate the root lodging for all rice cultivars.

climate change, cultivars, lodging, rice

Citation: Zhu C W, Cheng W G, Sakai H, et al. Effects of elevated [CO₂] on stem and root lodging among rice cultivars. *Chin Sci Bull*, 2013, 58: 1787–1794, doi: 10.1007/s11434-012-5640-y

The enrichment in atmospheric CO₂ concentrations together with other factors which cause climate change may greatly affect the worldwide agricultural production in the future [1]. Because the current atmospheric [CO₂] is less than optimal for photosynthesis, globally rising elevated [CO₂] promotes growth and enhances yield of C₃ crop [2–4]. Rice is one of the most important staple foods for human nutrition [5], and taking advantage of elevated [CO₂] for increasing yield is essential to ensure food security. Lodging, a frequent field occurrence, is a major cause of cereal yield loss and quality reduction [6], because it directly decreases canopy photosynthesis and disturbs the translocation of C and N within shoot and root [7,8]. Setter et al. [9] demon-

strated that in rice, yield losses can be as much as 1% for every 2% of stem that has lodged. Hence, if lodging risk is increased in rice under elevated [CO₂], the potential for increases in yield would be limited [9].

A better understanding of the mechanisms for lodging response will be helpful to reduce the incidence of lodging under elevated [CO₂] by enabling plant breeders to choose those characteristics in rice which are expected to increase lodging resistance, and increase food security. Lodging is accelerated by heavier panicles and longer culms, which increases the plant's mass moment (mass multiplied by distance from the point of attachment). Elevated [CO₂] has been shown to increase the rate of grain filling and the final weight of the panicles as a result of increased panicle size [3,4]. During the grain-filling period, panicle weight under

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elevated $[\text{CO}_2]$ is consistently heavier than that under ambient $[\text{CO}_2]$. Therefore, the plant's mass moment around the base, which represents the force applied to the stem and thus the likelihood of lodging may increase if the culm length does not decrease to compensate under elevated $[\text{CO}_2]$. Elevated $[\text{CO}_2]$ tends to reduce stem lodging in rice due to the shorter and thicker basal internodes using a single cultivar [8]. There are markedly different growth responses to elevated $[\text{CO}_2]$ among cultivars [10]; in particular, recent studies have found that some cultivars (e.g., indica hybrids) show far higher increase yield, because of avoiding the photosynthetic down-regulation which is a major limitation to $[\text{CO}_2]$ fertilization effect [11–13]. These results suggested that shoot weight, plant height, and stem diameter would have different responses to elevated $[\text{CO}_2]$ among cultivars. These traits can impact the risk of stem lodging, and may cause different responses in lodging risk under elevated $[\text{CO}_2]$; hence, the effect of elevated $[\text{CO}_2]$ on lodging risk is uncertain. In addition, while the stiff stems of modern cereal resist buckling, reducing incidence of stem lodging, they can transmit the forces generated by wind action into the ground—forces which can cause root lodging in which the root system rotates in the soil [14]. Studies confirmed that during rice growth, after stem lodging, root lodging is the next greatest lodging risk, and also proved that the larger roots system and thicker crown roots in subsoil were the very important characteristics for anti-lodging for root [15, 16]. Although most studies approved that elevated $[\text{CO}_2]$ promoted root growth, and increased the root volume, root biomass of rice [17,18], no study has examined the risk of root lodging under elevated $[\text{CO}_2]$.

In this study, we tested the hypothesis that if a rice line shows a strong response to CO_2 , it is more likely to be more susceptible to lodging in shoot and root. We chose 4 rice cultivars (*Oryza sativa* L.): 86 You 8 Hao (86Y8, a japonica hybrid), Liang You Pei Jiu (LYP9, a two-line indica hybrid), variety 9311 (a type of indica inbred rice), and Shanyou 63 (SY63, a three-line indica hybrid), which was based on prior testing for response to elevated $[\text{CO}_2]$: SY63 appeared to have a strong growth response [3], LYP9 appeared to have moderate growth response [4], cultivars 9311 and 86Y8 have never been tested.

1 Materials and methods

1.1 Experimental design

The study was conducted using naturally sunlit, controlled-environment growth chambers (Climatrons, Shimadzu, Kyoto, Japan) at National Institute for Agro-Environmental Sciences, Tsukuba, Japan (36°01'N, 140°07'E). The two chambers were used to impose two CO_2 levels: 680 $\mu\text{mol mol}^{-1}$ CO_2 (elevated) and 400 $\mu\text{mol mol}^{-1}$ CO_2 (ambient) during day and night. The chambers have been used for elevated $[\text{CO}_2]$ experiments of rice since 1996 [17]. Each

chamber, measuring 4 m × 2 m × 2 m (L × W × H), has two stainless-steel containers (1.5 m × 1.5 m × 0.3 m, L × W × H) filled with water to hold the pots. We rotated the treatments among the two chambers every 3 weeks: to minimize variation due to the controlling system, the pots from each chamber were transferred to the other and environmental settings were changed such that each of the pots received the same conditions for the entire duration of treatment [19]. Temperature inside the chambers was maintained at a constant 32°C from 08:00 to 16:00 h (Japan Standard time), reduced by 2.5°C h⁻¹ beginning at 20:00, maintained at 22°C from 22:00 to 04:00, and again increased by 2.5°C h⁻¹ beginning at 08:00 [19]. The average day temperature was (31.8±0.2) and (32.1±0.6)°C, and night temperature was (21.5±0.1) and (21.5±0.1)°C; day $[\text{CO}_2]$ was 434.8±47.8 and 695.0±9.2 $\mu\text{mol mol}^{-1}$, night $[\text{CO}_2]$ was 561.1±64.7 and 718.4±50.4 $\mu\text{mol mol}^{-1}$; day relative humidity: 69.7±6.4 and 59.8±12.3, night relative humidity 79.8±2.7 and 79.3±2.9 for ambient and elevated $[\text{CO}_2]$ chamber [19].

1.2 Growth of rice plants

Pre-germinated seeds were sown on 13 July 2009 in seedling trays at 3 seeds per cell. Two weeks after sowing, seedlings were transplanted into plastic pots (19.5-cm inside diameter, 27.0-cm height, 0.2-cm thickness) filled with 7.4 kg of alluvial soil in grown chambers. The alluvial soil was collected from the plow layer (top 20 cm) of a rice field in Yawara, Ibaraki Prefecture, Japan. Three seedlings were transplanted into each pot. Every cultivar was replicated ($n = 4$ pots, each with 3 seedlings). The soil had an average pH 5.8 and contained 19.7 g kg⁻¹ organic carbon and 2.0 g kg⁻¹ total nitrogen. The soil in each pot was mixed with 1.44 g $(\text{NH}_4)_2\text{SO}_4$, 0.72 g urea, 1.91 g KCl, and 5.72 g P_2O_5 as basal fertilizer. An additional 1.92 g $(\text{NH}_4)_2\text{SO}_4$ per pot was top-dressed around the panicle initiation stage.

1.3 Gas exchange

Photosynthetic rates were measured on the most recently fully expanded leaves at the panicle initiation stage and heading stage using two open gas-exchange systems (LI-6400, Li-Cor Inc., USA) with LED light sources at the same time. After net photosynthesis at saturated light (A_{sat}) was measured under the $[\text{CO}_2]$ used for plant growth, $[\text{CO}_2]$ within the chamber was changed to a different concentration (400 or 680 ppm, 1 ppm=10⁶ $\mu\text{g g}^{-1}$) to measure the short-term response of A_{sat} to variation in $[\text{CO}_2]$. $[\text{CO}_2]$ response curves for A_{sat} were measured at $[\text{CO}_2]$ of 50, 100, 150, 250, 380, 580, 700, 800, 1000, and 1200 $\mu\text{mol mol}^{-1}$ and determined at 28°C leaf temperature at 1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD). The relationship between A_{sat} and C_i was determined based on the model of Farquhar [20] using maximum likelihood regression to predict V_{cmax} and J_{max} described. That is, the maximum carbox-

ylation rate (V_{cmax}) was determined from points below the inflection of the A_{sat}/C_i plot and the maximum electron transport rate (J_{max}) was determined from values above the inflection [21]. The measurement was conducted from 08:30 to 15:00 local time. Due to time limitation, we included only 86Y8, 9311 and SY63 in the gas-exchange measurement.

1.4 Sampling and plant measurements

Sampling was done on 4 November 2009 for 86Y8, 9 November 2009 for LYP 9, 11 November 2009 for 9311, and 13 November 2009 for SY63. Three main tillers were selected from each of 4 pots, for a total of 12 tillers from each variety. The stem length and fresh weight of tillers were measured. Internodes were numbered from I–V starting from the panicle neck down to the base of the shoot, and the internode lengths were measured. It is well known that stem breakage in crops typically occurs at the lower internodes. Hoshikawa and Wang demonstrated that in rice, breaking occurred mainly at internodes IV and V [7]. Based on this information, we measured the lodging risk at internodes IV and V of rice grown under two CO_2 concentrations. The cross-sectional areas of internodes IV and V were determined by measuring the largest and smallest diameters at the middle of each internode and calculating the area based on the assumption that the stem cross-section was elliptical [8].

The breaking resistance (F_{max}) of internodes IV and V was measured using a digital gauge (7000 series, Akion Engineering Corp., Japan). The bending strength of the stem (S_s), expressed in kg cm, was calculated as follows: $S_s = F_{\text{max}} \times L/4$, where F_{max} is the maximum force that the stem will withstand before it breaks and L is the distance (60 mm) between the supporting points (the bending force was applied perpendicular to the middle of the two supporting points). The index of lodging risk (ILR) was calculated by the formula $\text{ILR} = M/S_s$, where M (g cm) is the self-weight mass moment generated by a single tiller and is the product of height (H) and fresh weight (FW) from the potential breaking point to the top of the tiller. The FW was measured using a keen knife cut off breaking point after observed F_{max} and entire fresh weight as soon as possible [6].

The coronal root system of each plant was removed from the pot and carefully washed to clean away the soil prior to testing. The thick coronal roots were cut from the plant base. Rigid roots with a diameter of ≥ 0.5 mm and a length of ≥ 25 cm [7] were then subjected to 3-point tests for bending strength using a digital gauge (7000 series, Akion Engineering Corp., Japan). In this test, the two supporting points were 50 mm apart. At least 15 roots were measured per pot. The roots were taken out of the water about 5 min before testing. During washing, many roots were broken, and it was very difficult to accurately count the roots. For this reason, we used the root weight instead of root number. The bending strength of the root (S_r) was calculated as $S_r =$

$(F_{\text{max}} \times L/4) \times (RW/TN)$, where RW is root dry weight and TN is tiller number. ILR was calculated as described above, using the height (H) and fresh weight (FW) of the entire tiller [16].

1.5 Statistical analysis

To test for significant differences, analysis of variance (Two-way ANOVA) was used with $[\text{CO}_2]$ as the main treatment and rice variety as sub-treatment (SPSS Inc., Chicagao, IL, USA). Every value is mean $\pm$ SD; $n = 4$. ns, not significant ($P > 0.05$); $*0.01 \leq P \leq 0.05$; $**P < 0.01$. All figures were constructed using Sigmaplot 11.0 (Systat Software Inc., San Jose, CA, USA).

2 Results

2.1 Gas exchange

At panicle initiation stage, A_{sat} was not different between ambient and elevated $[\text{CO}_2]$ at the same measured $[\text{CO}_2]$ for all cultivars, which meant no photosynthetic down-regulation. However, at heading stage, A_{sat} of the 9311 grown at elevated $[\text{CO}_2]$ decreased significantly and the hybrid rice cultivars were not affected. This indicated that under elevated $[\text{CO}_2]$, at heading stage, the inbred rice already showed the down-regulation, but not in the *indica* hybrid rice (Table 1). The values of V_{cmax} and J_{max} were consistent with these results (Table 1). Compared with A_{sat} of plants grown under ambient and elevated $[\text{CO}_2]$ with the growth $[\text{CO}_2]$, elevated $[\text{CO}_2]$ significantly increased A_{sat} of the hybrid rice (34.2% for 86Y8 and 35.2% for SY63), whereas A_{sat} of 9311 increased by 20% at heading stage (Table 1).

2.2 Bending strength of stems and roots

The bending strength of internodes IV and V and of the roots are shown in Figure 1. Elevated $[\text{CO}_2]$ enhanced the anti-breaking strength in all cultivars; however, varietal differences in the magnitude of responses to elevated $[\text{CO}_2]$ were observed. The increase in bending strength caused by elevated $[\text{CO}_2]$ ranged from 12.5% to 34.6% for internode IV, from 19.9% to 28.9% for internode V, and from 20.4% to 45.0% for the roots.

2.3 Plant height, weight and self-weight mass moment

Tiller height, fresh weight and self-weight mass moment are shown in Figure 2. None of the cultivars showed a significant response to $[\text{CO}_2]$ enrichment except for SY63, whose main tiller height increased significantly under elevated $[\text{CO}_2]$. Varietal differences in fresh weight response under elevated $[\text{CO}_2]$ were ranked as follows: SY63 (35.3%) > LYP9 (20.0%) > 86Y8 (19.8%) > 9311 (7.8%, not significant). The average increase of fresh weight was significantly

Table 1 Effects of elevated [CO₂] on gas exchange of flag leaf at heading stage for 86 You 8 Hao (86Y8), 9311, and Shanyou 63 (SY63)^{a)}

Variety	Growth [CO ₂] ^{b)}	Panicle initiation stage				Heading stage			
		<i>A</i> _{sat} (at 400 μmol mol ⁻¹) ^{c)}	<i>A</i> _{sat} (at 680 μmol mol ⁻¹) ^{c)}	<i>V</i> _{cmax} ^{d)}	<i>J</i> _{max} ^{e)}	<i>A</i> _{sat} (at 400 μmol mol ⁻¹) ^{c)}	<i>A</i> _{sat} (at 680 μmol mol ⁻¹) ^{c)}	<i>V</i> _{cmax} ^{d)}	<i>J</i> _{max} ^{e)}
		(μmol m ⁻² s ⁻¹)	(μmol m ⁻² s ⁻¹)	(μmol m ⁻² s ⁻¹)	(μmol m ⁻² s ⁻¹)	(μmol m ⁻² s ⁻¹)	(μmol m ⁻² s ⁻¹)	(μmol m ⁻² s ⁻¹)	(μmol m ⁻² s ⁻¹)
86Y8	Ambient	22.2±0.6	33.5±1.7	101.7±7.9	191.5±20.7	18.4±0.9	25.2±1.2	80.2±6.4	130.2±6.7
	Elevated	21.2±1.0	32.0±0.6	104.2±7.9	189.7±4.9	17.4±1.1	24.7±1.0	81.4±5.7	131.8±7.6
	% change by [CO ₂]	-4.5	-4.5	2.5	-0.9	-5.4	-2	1.5	1.4
9311	Ambient	22.0±2.1	31.4±2.2	109.4±7.4	173.7±8.0	25.1±0.5	34.7±0.6	122.7±5.7	178.6±2.3
	Elevated	23.3±3.7	32.7±3.7	104.3±5.5	185.1±7.9	20.7±1.7	30.1±1.9	100.8±5.0	160.6±8.4
	% change by [CO ₂]	5.9	4.1	4.7	6.6	-17.6	-13.3	-17.9	-10.10
SY63	Ambient	21.3±2.4	29.8±2.4	103.8±11.3	178.4±15.9	26.4±0.7	35.3±1.3	128.8±5.1	198.0±6.0
	Elevated	21.4±1.6	30.8±2.3	111.6±17.3	182.9±31.8	25.3±1.2	35.7±1.4	120.7±5.7	204.9±7.9
	% change by [CO ₂]	-0.5	3.4	7.5	2.5	-4.2	1.1	-6.3	3.5
ANOVA results									
[CO ₂]		ns	ns	ns	ns	*	ns	ns	ns
Variety		ns	ns	ns	ns	**	**	**	**
[CO ₂]×Variety		ns	ns	ns	ns	ns	ns	ns	ns

a) Values are means ± SD; *n* = 4. ANOVA results are shown in inset: ns, not significant (*P* > 0.05); *0.01 ≤ *P* ≤ 0.05; ***P* < 0.01. b) Ambient, growth at 400 μmol mol⁻¹; elevated, growth at 680 μmol mol⁻¹. c) *A*_{sat}, net photosynthesis at saturated light intensity. d) *V*_{cmax}, maximum carboxylation efficiency. e) *J*_{max}, maximum rate of electron transport.

20.8% by elevated [CO₂], as indicated by a significant interaction between [CO₂] and variety. Self-weight mass moment had the different responses: SY63 (47.8%) > LYP9 (22.0%) > 86Y8 (21.9%) > 9311 (9.2%, not significant).

2.4 Root biomass per tiller

Elevated [CO₂] markedly promoted root growth across cultivars (Figure 3). The increase of root biomass per tiller caused by elevated [CO₂] was 17.2% for 86Y8, 38.0% for LYP9, 12.0% for 9311, and 30.1% for SY63. The average increase of fresh weight was significantly 24.3% due to elevated [CO₂], a no-significant interaction between [CO₂] and variety indicated that varietal similarity in the root biomass responses to [CO₂]. The increase in root biomass per tiller is expected to enhance the resistance to root lodging under elevated [CO₂].

2.5 Lodging risk index

As shown in Figure 4, differences in lodging risk were calculated among the four cultivars. Under ambient [CO₂], 86Y8 showed the highest stem and root lodging risk, SY63 had the lowest stem lodging risk, and LYP9 has the lowest root lodging risk. Under elevated [CO₂], internodes IV and V showed the same trend of change across cultivars. Elevated [CO₂] significantly reduced the lodging risk of internodes IV and V of the 9311 cultivar. However, the lodging index of SY63 was enhanced by elevated [CO₂] whereas those of 86Y8 and LYP9 showed no significant change. The root lodging declined significantly across all 4 cultivars with [CO₂] enrichment. These results showed differential

responses between shoots and roots.

2.6 Cross-sectional area and length of internodes

The cross-sectional areas of internode IV and V increased significantly under elevated [CO₂] (Table 2, Figure 2). The lengths of internode IV and V decreased across cultivars (Table 2); however, the lengths of panicle, internodes I and II increased to some extent for all cultivars. For internode III, both increases and decreases were seen. The responses of the low internodes (IV and V) were associated with the responses of bending strength: increased cross-sectional area and decreased internode length were accompanied by increased bending strength.

3 Discussion

Our results proved the hypothesis that if a rice line shows a strong response to CO₂ (grows more), it is more likely to be more susceptible to lodging. The hypothesis is accepted for stem lodging, and rejected for root lodging. This study showed that, although elevated [CO₂] enhanced the bending strength of stem across cultivars, the stem lodging risk showed different responses: the lodging risk of 9311 decreased, that of SY63 increased, and those of 86Y8 and LYP9 did not change significantly. In contrast, [CO₂] enrichment reduced the risk of root lodging for all rice cultivars.

In this study, we measured self-weight mass moment and bending strength, which are the two major crop traits that determine lodging resistance [16]. Elevated [CO₂] enhanced

Figure 1 Effect of CO₂ enrichment on resistance to breaking (kg cm⁻¹) of internodes and roots for 86 You 8 Hao (86Y8), Liang You Pei Jiu (LYP9), 9311, and Shanyou 63 (SY63). Values are means $\pm$ SD; $n = 4$. ANOVA results are shown in inset: ns, not significant ($P > 0.05$); *, $0.01 \leq P \leq 0.05$; **, $P < 0.01$.

the anti-lodging bending strength of the stem due to the shortening and thickening of the lowest internodes for all cultivars (Table 2). A significant negative correlation between the length of these internodes and the bending strength of rice has been reported [8]. The physiological mechanism for the shorter and thicker internodes under elevated [CO₂] is still unclear. This response may be associated with the decrease of the hormones that promote internode elongation [8,22]. In addition, an improved carbohydrate supply to growing internodes may also enhance bending strength because the structural carbohydrate (cellulose and lignin) concentrations increased at the lowest internodes under elevated [CO₂] [23]. Theoretically, elevated [CO₂] might be expected to promote growth (biomass weight and

Figure 2 Effects of elevated CO₂ on tiller height, fresh weight and self-weight mass moment for 86 You 8 Hao (86Y8), Liang You Pei Jiu (LYP9), 9311, and Shanyou 63 (SY63). Values are means $\pm$ SD; $n = 4$. ANOVA results are shown in inset: ns, not significant ($P > 0.05$); *, $0.01 \leq P \leq 0.05$; **, $P < 0.01$.

height), which increased the plant's mass moment, and thus increases the lodging risk if the increase of bending strength is not enough (an increased ratio of self-weight mass moment to bending strength) [3–5]. Elevated [CO₂] was found to decrease the lodging index of variety *Akitakomachi* [8] and of 9311 (Figure 4). This may be due to photosynthetic acclimation in these conventional (i.e., non-hybrid) cultivars after long-term exposure to high [CO₂] [11]; thus, their biomass were far lower than what was expected under elevated [CO₂] without considering down-regulation effects [24]. In addition, the increase of biomass was mostly due to tiller number, and the increased rate of biomass and height per tiller was very low [25]. Under elevated [CO₂], the increase in self-weight mass moment was proportionately lower than that of bending strength, thus lodging risk

Figure 3 Effect of elevated $[\text{CO}_2]$ on the dry weight of roots per tiller for 86 You 8 Hao (86Y8), Liang You Pei Jiu (LYP9), 9311, and Shanyou 63 (SY63). Values are means $\pm$ SD; $n = 4$. ANOVA results are shown in inset: ns, not significant ($P > 0.05$); *, $0.01 \leq P \leq 0.05$; **, $P < 0.01$.

declined. On the other hand, under elevated $[\text{CO}_2]$, photosynthetic down-regulation did not occur in the hybrid rice (Table 1). The hybrid rice had stronger growth-responses than the inbred 9311; this is especially true for SY63, whose weight per tiller sharply increased (Figure 2). These results were consistent with previous findings that increases in biomass and yield of hybrid rice under increased $[\text{CO}_2]$ were greater than that of conventional rice [3,4]. Here, the increase in self-weight mass moment of SY63 was proportionately greater than the increase in bending strength, thus, its lodging risk increased. In contrast, 86Y8 and LYP9 had similar magnitudes of increase in self-weight mass moment and bending strength, so their lodging risks did not change significantly under elevated $[\text{CO}_2]$.

Usually, $[\text{CO}_2]$ enrichment increased the root-to-shoot ratio and the root number per tiller in rice [26], and markedly enhanced root bending strength $[\text{CO}_2]$ (Figure 1), so the increase in anti-lodging strength of the roots was much higher than that of the self-weight moment. As expected, $[\text{CO}_2]$ enrichment decreased the risk of root lodging in all 4 rice cultivars. In this study, we did not obtain an accurate count of the roots due to the huge roots number. Yang demonstrated that under elevated $[\text{CO}_2]$, the increase of the number of adventitious roots, and the root volume and root dry weight per plant were similar (about 30%) at 80 days after transplanting [17]. The findings suggested that under elevated $[\text{CO}_2]$, the increase in root biomass was mainly attributable to an increase in root number. It has been reported that root length and diameter of rice increased slightly under elevated $[\text{CO}_2]$ [18]. The slight increase in root diameter was an important factor for the enhancement of root resistance to lodging (Figure 1). We acknowledge that using root biomass instead of root number to calculate lodging index may slightly overestimate the reduction of lodging risk indexes under elevated $[\text{CO}_2]$. However, it is important to explore the trend in lodging indexes of roots as global $[\text{CO}_2]$ increases, we would be able to develop

Figure 4 Effect of elevated $[\text{CO}_2]$ on the lodging index of stem and root for four cultivars: 86 You 8 Hao (86Y8), Liang You Pei Jiu (LYP9), 9311, and Shanyou 63 (SY63). Values are means $\pm$ SD; $n = 4$. ANOVA results are shown in inset: ns, not significant ($P > 0.05$); *, $0.01 \leq P \leq 0.05$; **, $P < 0.01$.

appropriate crop management strategies to adapt and adjust for the effects on rice yield caused by root lodging.

To increase rice yield under elevated $[\text{CO}_2]$, the farmer might tend to choose cultivars with higher increases in biomass and yield [5]. However, the use of such cultivars should be carefully considered because if there is a strong response to elevated $[\text{CO}_2]$, the enhanced height and tiller weight may cause a sharp increase in the self-weight moment. As such, the risk of stem lodging will likely increase, and may cause yield reductions. Hence, in future breeding for rice to be grown under elevated $[\text{CO}_2]$, studies should focused on the stem lodging resistance as well as enhance rice yield by rice genetic improvement. To date, these data is the first to compare and contrast the lodging responses for

Table 2 Effects of growth under elevated [CO₂] on internode length and cross-sectional area for 86 You 8 Hao (86Y8), Liang You Pei Jiu (LYP9), 9311, and Shanyou 63 (SY63)^{a)}

Variety	Growth [CO ₂] ^{b)}	Panicle length (cm)	Internode length (cm)					Cross-section area (mm ²)	
			I	II	III	IV	V	IV	V
86Y8	Ambient	19.6±2.1	28.7±1.7	16.1±1.1	14.5±1.9	11.0±2.2	5.8±1.1	31.0±2.8	40.7±7.6
	Elevated	20.4±1.2	29.9±1.1	19.6±0.7	13.7±1.4	8.7±1.5	5.5±0.3	47.1±5.6	51.7±10.6
	% change by [CO ₂]	4.08	4.18	21.74	-5.52	-20.91	-5.17	51.94	27.03
LYP9	Ambient	21.7±1.5	27.8±2.0	14.5±3.7	17.4±2.2	8.5±0.9	6.0±0.6	44.8±2.4	53.3±8.2
	Elevated	23.2±1.3	30.6±1.4	16.1±1.1	15.6±0.4	6.7±0.3	5.5±0.3	50.8±4.3	69.6±7.5
	% change by [CO ₂]	6.9	10.07	11.03	-10.34	-21.18	-8.33	13.39	30.58
9311	Ambient	20.7±5.4	26.4±1.4	12.7±1.3	17.4±0.5	7.9±0.9	7.0±0.7	37.8±7.9	51.7±5.0
	Elevated	22.0±0.3	27.1±0.9	15.2±0.5	17.0±0.7	7.4±0.6	6.1±0.4	46.8±1.8	61.9±4.4
	% change by [CO ₂]	6.28	2.65	19.69	-2.30	-6.33	-12.86	23.81	19.73
SY63	Ambient	21.1±1.9	26.5±0.8	14.1±0.8	14.1±1.5	6.7±0.4	5.8±1.0	36.3±6.2	46.5±12.0
	Elevated	25.3±3.7	29.8±1.4	15.6±1.1	14.8±0.8	6.4±0.8	5.7±0.6	45.5±4.3	61.8±2.8
	% change by [CO ₂]	20.0	12.45	10.64	4.96	-4.48	-1.72	25.34	32.90
ANOVA results									
[CO ₂]		*	*	**	ns	*	ns	**	**
Variety		ns	*	**	**	**	**	**	**
[CO ₂] × Variety		ns	ns	ns	ns	ns	ns	ns	ns

a) Internodes were numbered from the neck of panicle to the shoot base, from I to V. Values are means ± SD; *n* = 4. ANOVA results are shown in inset: ns, not significant (*P* > 0.05); *, 0.01 ≤ *P* ≤ 0.05; **, *P* < 0.01. b) Ambient, growth at 400 μmol mol⁻¹; elevated, growth at 680 μmol mol⁻¹.

different cultivars of rice under elevated [CO₂]. Although preliminary, the information does not examine all aspects for the mechanisms of different responses (i.e. genetic, molecular, morphological, etc.), the results should serve as a basis for additional clarification regarding optimization of rice growth and yield as atmospheric [CO₂] continues to increase. Such optimization could, potentially, serve as a selection factor for improving yields of rice in the future world of higher [CO₂].

It is important to note that our results were based on a growth-chamber experiment, so the analysis of safety factors only took into account the self-weight of the stems, and ignored the potential effects of strong wind or heavy rain and the dynamic forces caused by stem sway. Future quantitative research to study the effect of cultivar and management on rice lodging should use more sophisticated analyses of lodging based on the dynamics and aerodynamics of crops in the field under future global climate change scenarios [16].

4 Conclusions

In the future, elevated [CO₂] would increase photosynthetic rates and enhance yields of rice. Due to different growth response to [CO₂], elevated [CO₂] reduced the lodging risk of weak-[CO₂]-responses variety, did not change the lodging risk of moderate-[CO₂]-responses variety and increased the lodging risk; however, lodging risk of root for all cultivars was reduced significantly due to higher root/shoot un-

der elevated [CO₂]. It indicated that elevated [CO₂] may not aggravate the root lodging in all cultivars, but we should focus on the increased risk of stem lodging for cultivars with high increase of yield under elevated [CO₂] in future.

This work was supported by the Ministry of Agriculture, Forestry and Fisheries of Japan project, "Development of technology for mitigation and adaptation to climate change in Agriculture, Forestry and Fisheries" and a Grant-in-Aid for Scientific Research (P09515) from the Japan Society for the Promotion of Science.

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