Short Paper

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Tropospheric ozone reduces resistance of Japonica rice (*Oryza sativa* L., cv. Koshihikari) to lodging

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Abstract

To clarify the effects of ozone (O_3) on the resistance of Japonica rice (*Oryza sativa* L.) to root lodging, the Japanese major rice cultivar Koshihikari was exposed to four levels of O_3 in open-top chambers (mean O_3 concentration: 17.3, 32.4, 51.1, and 66.3 nl l^{-1}). We evaluated the resistance to root lodging by measuring pushing resistance at 15 days after heading (DAH) and the dry masses of plant organs such as roots at harvest (35 DAH). Exposure to O_3 significantly reduced pushing resistance per panicle, suggesting that the O_3 reduced resistance to root lodging. Because the degree of O_3-induced reduction in pushing resistance per panicle correlated with that of O_3-induced reduction in root dry mass per panicle, the O_3-induced reduction in the resistance to root lodging could be caused by O_3-induced reduction in root development. There was a significant negative correlation between relative value of pushing resistance per panicle and O_3 concentration or dose, indicating that resistance to root lodging decreases with increasing O_3 concentration. In East Asia, because the O_3 concentration is projected to increase in the near future, lodging issues in the rice cultivation could become serious.

Key words: Photochemical oxidant, Pushing resistance, Root development, Root lodging

1. Introduction

The concentration of tropospheric ozone (O_3), the main component of photochemical oxidants, has been increasing globally, especially in Europe, North America, and East Asia (Cooper *et al*., 2014). Since 1950s, it has been recognized that O_3 has negative impacts on vegetation such as visible foliar injury, inhibition of net photosynthesis, and reductions in growth and yield (Heggestad and Middleton, 1959; Ainsworth *et al*., 2012; Emberson *et al*., 2013). Because of its phytotoxicity, the current levels of O_3 are sufficiently high to reduce the yield of major staple crops (Fuhrer, 2009). Van Dingenen *et al*. (2009) estimated that present-day global O_3-induced crop yield losses were more than 10% for O_3-sensitive crops, such as wheat (*Triticum aestivum* L.) and soybean (*Glycine max*). Although rice (*Oryza sativa* L.) is classified as being moderately resistant to O_3 and global O_3-induced yield losses of rice were less than those of wheat and soybean (Van Dingenen *et al*., 2009), the current levels of O_3 in Japan and China are high enough to significantly reduce the rice yield (Yamaguchi *et al*., 2014; Feng *et al*., 2015). Additionally, Sawada *et al*. (2016) reported O_3-induced deterioration of the grain quality of Japonica rice without a significant reduction in the yield after exposure to O_3. To estimate the risk of O_3 on crop production, it is necessary to clarify the effects of O_3 on parameters related to food productivity besides the yield.

Lodging, the bending of plant stems from their vertical position, reduces canopy photosynthesis, crop yield, and mechanical harvesting efficiency in many cereals such as rice, wheat, and barley (Setter *et al*., 1997; Berry *et al*., 2004). There are two types of lodging: stem lodging, which results from the bending or breaking of culm internodes, and root lodging, which results from root anchorage failure (Berry *et al*., 2004). Terashima *et al*. (1994) suggested that rice cultivars tolerant to root lodging develop more roots than those susceptible to lodging, suggesting that the dry matter partitioning to roots could be an important factor for increasing the resistance to root lodging. On the contrary, it is well known that exposure to O_3 reduces the allocation of carbohydrates to roots, resulting in reduced dry matter partitioning to roots (Grantz *et al*., 2006). These results suggest that the exposure to O_3 reduces the resistance to root lodging through reduction in the dry matter partitioning to roots.

Rice is a primary agricultural crop in Japan. However, the current levels of O_3 are high enough to reduce the yield of rice (Yamaguchi *et al*., 2014). Furthermore, the concentration of O_3 has been increasing due to transboundary air pollution and reduced NO titration in Japan (Akimoto *et al*., 2015), and the concentration of O_3 in East Asia is expected to increase due to an increase in the emission of its precursors (Wild *et al*., 2012). Kobayashi *et al.* (1995) reported the O_3-induced reduction in dry matter partitioning to leaf sheath and culm of Japonica rice (cv. Koshihikari) and O_3-induced severe lodging, which might be stem lodging. Because they also observed O_3-induced reduction in the dry matter partitioning to roots, it is possible that the exposure to O_3 reduces resistance of rice to root lodging. To evaluate the adverse effects of O_3 on rice productivity, it is necessary to clarify the effects of O_3 on the resistance of Japonica rice to root lodging, in addition to its effects on yield and grain quality. In the present study, we hypothesized that exposure to O_3 reduced dry matter partitioning to roots and consequently reduced

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resistance of Japonica rice to root lodging. To test the hypothesis, we conducted an experimental study on the effects of O_3 on the resistance of Japonica rice cv. Koshihikari to root lodging.

2. Materials and methods

2.1. Plant material

The Japonica rice cultivar "Koshihikari" was used as the plant material because it is the most widely cultivated variety in Japan. Two- to three-leaf seedlings of Koshihikari were planted in 1/2000a Wagner's pots (ø256 mm × 297 mm in height, approximately 14 L) filled with flooded andisols (12 L) at three hills per pot and one seedling per hill on 1 May 2015. The seedlings were grown on the roof floor of the Nagasaki University (Nagasaki, Japan) until 16 May in order to ensure the rooting and were subsequently grown in 16 open-top chambers (OTCs: 60 cm in width, 120 cm in height, 82.5 cm in depth) placed on the roof floor without any covers. Three pots were assigned to each chamber, for a total of 48 pots. To acclimatize the plants to the chamber, the ambient air was directly introduced into each OTC from 16 to 20 May. NPK (15:15:15) fertilizer was applied at 2.25 g per pot, which corresponds to 6.75 g N m^{-2}, before planting.

2.2. O_3 exposure

The rice plants in the OTCs were exposed daily to O_3 removal-filtered air (FA), non-filtered air (NF), NF supplemented with approximately 20 nl l^{-1} O_3 (NF+) or 35 nl l^{-1} O_3 (NF++). The chambers assigned to the FA treatment were equipped with an O_3 removal filter, a honeycomb-structured filter coated with a catalyst for O_3 decomposition reaction (HONEYCLE-ZV, No. 8803ZV, NICHIAS Corporation, Tokyo, Japan), and the chambers assigned to NF, NF+, and NF++ treatments were equipped with a non-coated filter (No. 8801, NICHIAS Corporation). The ambient air firstly passed the filter, was drawn by the FAN, and was blown into the chambers. Supplementary O_3 was generated by an electrical discharge generator (SO-03UN, Hamanetsu Co., Shizuoka, Japan). The generated O_3 was passed through a water trap to remove nitrogen by-products before being injected into the NF+ and NF++ chambers. The O_3 concentrations in the chambers assigned to the NF+ and NF++ treatments were controlled by a flow rate of O_3 injection using handy valve. Supplementation of O_3 was constant and lasted throughout the exposure period (i.e., 24 h/day). Four chamber replications were included for each gas treatment, for a total of 16 OTCs. Pots were rotated within and among the chambers at 7- to 10-day intervals to minimize variation among the chambers. The gas treatments lasted for 109 days, from 21 May to 7 September 2015, except during the rotations and when a typhoon struck Japan on 24 and 26–27 July.

2.3. Monitoring of climatic parameters and O_3 concentration

The air temperature and relative air humidity inside each chamber were continuously measured using a TR-72wf Thermo Recorder (T&D Corporation, Nagano, Japan). The photosynthetic photon flux density (PPFD) outside the chamber was continuously measured using a LI-190 Quantum Sensor (LI-COR, Lincoln, NE, USA). The O_3 concentration inside the chambers was monitored using a UV absorption O_3 monitor (Model 202 Ozone Monitor, 2B Technologies, Colorado, United States) and recorded at 30-sec intervals using a voltage recorder (VR-71, T&D Corporation). To measure the O_3 concentration inside the 12 chambers (four chambers assigned to FA and NF treatments and eight chambers assigned to NF+ and NF++ treatments), the air inside the chambers was sampled sequentially using an electric valve system for a period of 5 min, and was introduced into the O_3 monitor. The average concentration during the 5-min sampling period was used as the 1-h average concentration for each chamber. The 1-h average concentration was used to calculate the average concentration, the concentration accumulated over a threshold O_3 concentration of 40 nl l^{-1} during daylight hours (daylight AOT40), and the sum of all hourly average concentrations above 60 nl l^{-1} (SUM06) (Table 1). The accumulation period for daylight AOT40 and SUM06 was from 21 May to 18 August or 7 September.

Table 1. The concentration, SUM06, and daylight AOT40 of O_3 in each gas treatment during the O_3-exposure period.

Period	Treatment	Concentration (nl l^{-1})			SUM06[c]	AOT40[d]
		24-h	12-h[a]	8-h[b]	(μl l^{-1} h)	(μl l^{-1} h)
21 May-18 Aug	FA	17.3 (1.0)	17.6 (0.9)	17.9 (0.9)	0.0 (0.0)	0.0 (0.0)
	NF	32.4 (0.1)	35.8 (0.4)	37.8 (0.3)	7.8 (0.1)	5.4 (0.1)
	NF+	51.1 (1.1)	54.7 (0.8)	57.3 (0.6)	49.4 (5.2)	17.1 (0.4)
	NF++	66.3 (2.9)	67.1 (2.5)	68.2 (2.1)	103.3 (8.5)	24.9 (1.7)
21 May-7 Sep	FA	18.3 (0.9)	18.8 (0.8)	19.1 (0.8)	0.0 (0.0)	0.0 (0.0)
	NF	32.5 (0.1)	36.1 (0.4)	38.2 (0.3)	8.5 (0.2)	6.6 (0.2)
	NF+	51.9 (1.6)	55.6 (1.3)	58.5 (1.1)	64.4 (8.2)	21.8 (1.1)
	NF++	66.8 (1.7)	68.1 (1.7)	69.3 (1.5)	131.0 (7.5)	31.3 (1.5)

FA: O_3 removal-filtered air; NF: Non-filtered air; NF+: NF plus additional O_3 at approximately 20 nl l^{-1}; NF++: NF plus additional O_3 at approximately 35 nl l^{-1}. Each value is the mean of two (for FA and NF) or four (for NF+ and NF++) chamber replicates, and the standard deviation is shown in parentheses. [a]12-h: 6:00–18:00. [b]8-h: 9:00–17:00. [c]SUM06: Sum of all hourly average concentrations above 60 nl l^{-1}. [d]Daylight AOT40: Concentration accumulated over a threshold O_3 concentration of 40 nl l^{-1} during daylight hours (photosynthetic photon flux density of >230 μmol m^{-2} s^{-1}). The accumulation period for daylight AOT40 and SUM06 was from 21 May to 18 August or 7 September.

2.4. Measurement of pushing resistance

On 19 August, the 15 days after heading, the pushing resistances of all rice plants were measured. The heading date, which was defined as the 50% of the plants emerged the panicle, was 4 August. A digital force gauge (FG-5000A, FUSO Co. Ltd, Tokyo, Japan) was set perpendicularly at 10 cm from the bottom of the plant. Pushing resistance was measured when the plant was pushed to an angle of 45° from the vertical position, which reflects the resistance to root lodging (Terashima *et al*., 1992).

2.5. Measurement of whole-plant growth and root-to-shoot ratio

On 8 and 9 September (35 days after heading), all the rice plants were harvested to determine the whole-plant growth and dry mass ratio of roots to shoots (root-to-shoot ratio). The harvested plants were divided into panicle, leaf blade, leaf sheath, and root parts. The separated plant organs were dried in an oven at 80°C for 5 days and then weighed. Whole-plant dry mass was calculated as the sum of the dry masses of all plant organs. The root-to-shoot ratio was calculated as the ratio of root dry mass to the sum of the dry masses of the panicle, leaf blade, and leaf sheath.

2.6. Statistical analysis

The mean values of three pots in each chamber were used for the statistical analysis ($n = 4$ for each treatment). All statistical analyses were performed with IBM SPSS Advanced Statistics 19. Analysis of variance (ANOVA) was used to test the significance of O_3 effects on the growth and pushing resistance at $p < 0.05$. Because there were no significant interactions between O_3 and chamber replication, the chamber replication was classified into error term. When a significant effect of O_3 was observed, Tukey's HSD test was used to clarify the significant difference among the four treatments ($p < 0.05$). The association of pushing resistance per panicle to root dry mass per panicle was analyzed by Pearson's correlation test, and that to O_3 indices was analyzed by linear regression.

3. Results and discussion

During the exposure period from 21 May to 7 September 2015, average daily mean, daily maximum, and daily minimum air temperature inside the OTCs were 25.5°C, 30.2°C, and 22.2°C, respectively. Average daily mean and daily minimum relative air humidity during the exposure period inside the chambers were 77.2% and 56.8%, respectively. Average daily mean and daily maximum PPFD and highest 1-h value of PPFD outside the chambers during the period were 347, 1236, and 2024 μmol m^{-2} s^{-1}.

The mean 24-h O_3 concentrations from the beginning of the exposure to 15 days after heading (when the pushing resistance was measured) in the FA, NF, NF+, and NF++ treatments were 17.3, 32.4, 51.1, and 66.3 nl l^{-1}, respectively (Table 1). Although the mean O_3 exclusion efficiency in the FA treatment was not so high (≈45%), the AOT40 and SUM06 during the experimental period in the FA treatment was 0.0 μL l^{-1} h, suggesting that the air provided to the plants was clean. The difference in the concentration between daytime (8-h) and daily (24-h) average was nonsignificant (Table 1). In general, however, the O_3 concentration is high during daytime and peaks in the afternoon, resulting in the much higher daytime average concentration of O_3 than the daily average concentration of O_3 (e.g., Akimoto *et al*., 2015). In Nagasaki, unlike the situation around the metropolis, the concentration of O_3 is strongly influenced by Asian continental outflow air masses and relatively high O_3 concentration is observed in the spring and autumn during both daytime and nighttime (e.g., Kanaya *et al*., 2016). As a result, the difference between daytime and daily average concentrations of O_3 in the present study site was less than that observed around the metropolis.

Table 2 shows the effects of O_3 on whole-plant dry mass, root-to-shoot ratio, panicle number per plant, and pushing resistance per plant. There were no significant effects of O_3 on the whole-plant dry mass, root-to-shoot ratio, and panicle number per plant. The pushing resistance per plant in the NF+ and NF++ treatments was significantly lower than that in the FA and NF treatments. Although the effect of O_3 on panicle number per plant was not statistically significant, the panicle number obviously affected the pushing resistance per plant and caused considerable variation in the resistance. Because of this, we evaluated the resistance to root lodging by pushing resistance per panicle. The pushing resistance per panicle in the NF++ treatment was significantly lower than that in the FA and NF treatments (Fig. 1). This result indicates that relatively high concentration of O_3 reduces the resistance of Japonica rice to root lodging. It is well

Table 2. Effects of O_3 on whole-plant dry mass and root-to-shoot dry mass ratio at harvest (35 days after heading, DAH) and panicle number per plant and pushing resistance per plant at 15 DAH in rice (*Oryza sativa* L. cv. Koshihikari).

Treatment	Whole-plant dry mass (g)	Root/shoot ratio (g g^{-1})	Panicle no. per plant ($plant^{-1}$)	Pushing resistance (N $plant^{-1}$)
FA	27.9 (0.5)	0.172 (0.012)	5.8 (0.1)	9.59 (0.21) a
NF	28.0 (0.3)	0.164 (0.010)	6.0 (0.1)	9.60 (0.10) a
NF+	26.6 (0.6)	0.152 (0.005)	6.0 (0.1)	8.41 (0.24) b
NF++	26.5 (0.5)	0.143 (0.006)	6.0 (0.1)	7.53 (0.30) b
ANOVA	n.s.	n.s.	n.s.	***

FA: O_3 removal-filtered air; NF: Non-filtered air; NF+: NF plus additional O_3 at approximately 20 nl l^{-1}; NF++: NF plus additional O_3 at approximately 35 nl l^{-1}. Each value shows the mean of four chamber replications, and the standard error is shown in parentheses. ANOVA: ***$p < 0.001$, n.s. = not significant. Values with different letter indicate significant difference among the four treatments (Tukey's HSD test, $p < 0.05$).

known that the O_3 accelerates plant senescence (e.g., Ainsworth *et al*., 2012). In the present study, the exposure to O_3 tended to accelerate heading and the heading date was one day earlier in the NF+ and NF++ treatments than in the FA and NF treatments (data not shown). Terashima *et al*. (1992) reported that the pushing resistance remained constant for about 20 days after heading, suggesting that the O_3-induced early senescence did not cause the O_3-induced reduction in the resistance to root lodging. On the contrary, the root dry mass per panicle in the NF++ treatment was significantly lower than that in the FA treatment (Fig. 1). Because the root lodging resistance of rice is related to root development (Terashima *et al*., 1994), the pushing resistance per panicle was plotted against the root dry mass per panicle (Fig. 1). As a result, the degree of O_3-induced reduction in pushing resistance per panicle correlated with that of O_3-induced reduction in root dry mass per panicle. These results indicate that the O_3-induced reduction in resistance to root lodging might have been caused by the reduction in root development from exposure to O_3.

The relative value of pushing resistance per panicle had significant negative linear relationships to the 24-h O_3 concentration and daylight AOT40 (Fig. 2). This result suggests that resistance to root lodging decreases with increasing O_3 concentration. Kobayashi *et al*. (1995) reported that the exposure to O_3 induced severe lodging of rice in the year when the conditions for the rice cultivation were conducive to lodging (e.g., low light intensity). Although there was no significant difference in the pushing resistance per panicle between the FA and NF treatments (Fig. 1), the negative linear relationship suggests that the exposure to ambient levels of O_3 could induce severe lodging when the condition for rice cultivation is conducive to lodging. In East Asia, furthermore, because the O_3 concentration is projected to increase in the near future (Wild *et al*. 2012), lodging issues in rice cultivation could become serious.

Yamaguchi *et al*. (2014) reported that O_3-induced yield losses of Japonica rice could be explained by exposure to O_3 during heading. Additionally, in the study of Sawada *et al*. (2016), the O_3-induced deterioration of Japonica rice grain quality occurred during the grain filling period. These results suggest that the O_3 concentration during the reproductive period is an important factor determining the yield loss and deterioration of grain quality. Conversely, because roots develop during the vegetative period, exposure to O_3 during the vegetative period could be related to the O_3-induced reduction in lodging resistance. In many cereals such as rice, lodging reduces canopy photosynthesis, crop yield, and mechanical harvesting efficiency (Setter *et al*., 1997; Berry *et al*., 2004). Therefore, O_3 levels during both the reproductive and vegetative periods should be considered when estimating the adverse effects of O_3 on rice productivity, including yield, grain quality, and lodging.

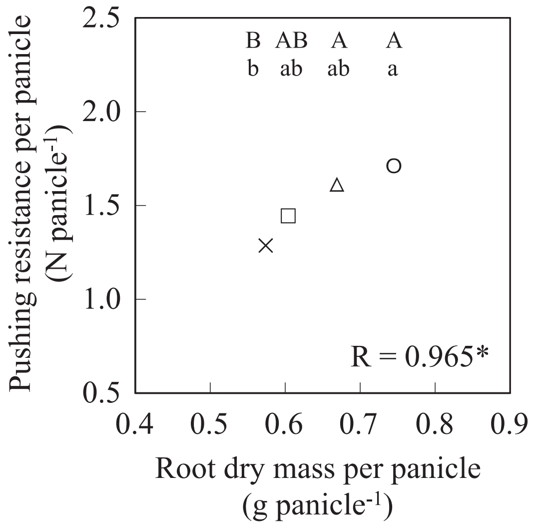

Fig. 1. Relationship between pushing resistance per panicle and root dry mass per panicle. Circle: FA, Triangle: NF, Square: NF+, Cross: NF++. *$p < 0.05$. Different capital and lower-case letter above the plot indicates the significant difference among the four values in the pushing resistance per panicle and root dry mass per panicle, respectively (Tukey's HSD test, $p < 0.05$).

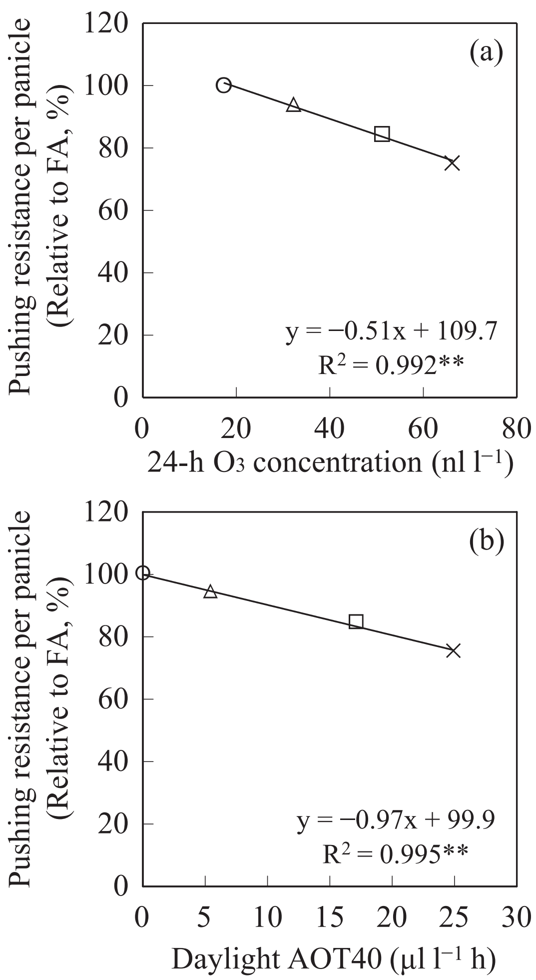

Fig. 2. Relationships between the relative value of pushing resistance per panicle and (a) 24-h average O_3 concentration and (b) daylight AOT40. The period for calculation of the O_3 indices was from the beginning of treatment to immediately before the measurement of pushing resistance (21 May–18 Aug 2015). Circle: FA, Triangle: NF, Square: NF+, Cross: NF++. **$p < 0.01$.

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