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Elevated CO_2 improves lodging resistance of rice by changing physicochemical properties of the basal internodes

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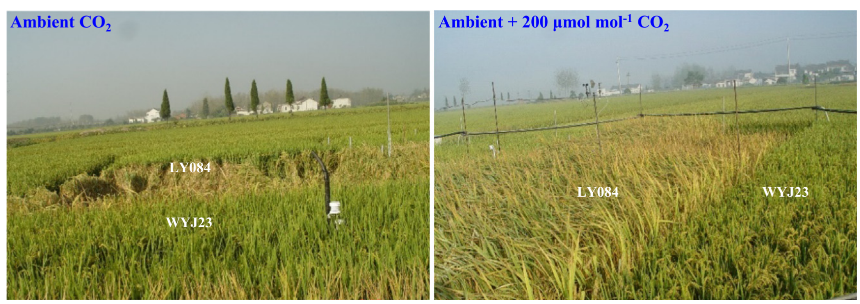
HIGHLIGHTS

- Lodging resistance of rice cultivars was investigated under fully open-air field.
- Elevated CO_2 decreased lodging incidence of the lodging-susceptible cultivar.
- Increases in culm density and starch content led to stronger breaking-resistance.
- Improved lodging resistance contributed to the yield gain from elevated CO_2.

GRAPHICAL ABSTRACT



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ABSTRACT

Elevated atmospheric CO_2 concentration has been shown to increase rice yield but its effect on plant lodging resistance is still under debate. In this study, we examined lodging incidence in the field and lodging-related traits of two rice cultivars with contrasting lodging susceptibility under ambient and elevated CO_2 (ca. 200 μmol mol^{-1} above ambient) concentrations by using a free-air CO_2 enrichment (FACE) system. Elevated CO_2 (E-CO_2) increased lodging resistance as shown by reduced visual lodging incidence in the field at the late grain filling stage in E-CO_2 plots. This coincided with enhanced in situ pushing resistance of intact plants one week before lodging occurred. The positive CO_2 effect was more pronounced in the lodging-susceptible cultivar LY084. In contrast, the cultivar WYJ23 displayed greater pushing resistance in the field, and no lodging occurred at either ambient or elevated CO_2 conditions throughout the cropping season. The field observations were consistent with the physicochemical characterization of basal internodes of rice plants at the grain filling stage. Greater lodging-resistance of WYJ23 was mainly attributed to its shorter plant height and thicker culm wall of basal internodes. The improvement of lodging resistance by E-CO_2 for the lodging-susceptible cultivar LY084 was mainly related to enhanced culm density, which was explained by elevated starch deposition in the stem. Less lodging incidence under elevated CO_2 contributed to an increase in grain yield by 36% for LY084. In conclusion, rice production could benefit from elevated CO_2 in a changing climate because of an increase in lodging resistance as a result of CO_2-induced improvements in mechanical strength of basal internodes.

1. Introduction

Lodging is one of the major constraints for achieving high yield of small grain cereals including rice (Setter et al., 1997). Lodging in rice

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can be classified into stem lodging and root lodging, the former (also referred to as bending or buckling of the basal internodes) being the predominant form in transplanted rice (Islam et al., 2007). Lodging-induced self-shading reduces light interception of the plant canopy and thereby decreases photosynthesis, disturbs assimilation, water and nutrient transport into grains, and results in lower yields (Setter et al., 1997; Kashiwagi et al., 2010; Wu et al., 2012). In addition, lodged plant populations are exposed to high humidity and are therefore susceptible to diseases and pests, resulting in poor grain quality (Wu et al., 2012; Salassi et al., 2013). Also, lodging reduces mechanical harvesting efficiency and thereby reduces rice growers' profits (Kono, 1995; Salassi et al., 2013).

Lodging is difficult to control because it is a complex process determined by many factors including varieties, weather, soil type, crop management, and disease episodes. The introduction of semi-dwarf varieties in rice production substantially reduced lodging risk and increased the yield in the early 1960s (Chandler Jr, 1969). However, in recent years, the potential risk of rice lodging has been increasing because of the release of high-yielding varieties with large panicles, the increase of nitrogen fertilizer application, and shifts from labor-intensive transplanting to simplified planting techniques such as direct-seeding or seedling broadcasting (Duy et al., 2004; Lang et al., 2012; W.J. Zhang et al., 2014). In addition, extreme weather conditions such as typhoons accompanied by heavy rain at the late growth stage are other major reasons for lodging, which is predicted to occur more frequently due to global climate change (Ishimaru et al., 2008; Phelan, 2010). The occurrence of typhoons will increase by 2–11% in temperate regions at the end of this century because of global warming (Knutson et al., 2010; Masutomi et al., 2012). Since wind is the most significant dynamic factor that results in lodging (Berry et al., 2004; Gardiner et al., 2016), an increase in crop lodging will have increased negative impacts to crop production and food security.

The rise in atmospheric CO_2 concentration has been well recognized as the major global climate change factor (IPCC, 2013). Previous studies on rice responses to high CO_2 concentration were mainly focused on yield and grain quality, with less attention to lodging (Ainsworth, 2008; Yang and Peng, 2011; Wang et al., 2011). The majority of CO_2 fumigation experiments were conducted in closed or open-top gas chambers with limited space, which are not suitable for studying lodging, a phenomenon usually occurring under field conditions, with strong influence from the natural environment factors. Compared with chambers, the free-air CO_2 enrichment (FACE) system provides larger space for growing rice populations (Long et al., 2006). The plants grown in FACE are subjected to natural wind and rain, two environmental factors that favor lodging occurrence in the field.

Although FACE technology has been applied in rice since 1998 (Okada et al., 2001), only two reports about rice lodging in response to elevated CO_2 in FACE can be found, and the two experiments were conducted in Japan with relatively low N application (<15 g m^{-2}). Shimono et al. (2007) found that lodging risk of *japonica* rice increased with the increase of N application from 8 g m^{-2} to 15 g m^{-2}, but elevated CO_2 alleviated lodging risk at high N (15 g m^{-2}). Contrary to this, Zhu et al. (2013) found that elevated CO_2 had no significant effect on lodging risk of the Japanese cultivar Koshihikari and even increased lodging risk of the Chinese hybrid Sanyou63. However, the mechanisms underlying lodging responses to CO_2 and the influence of management and environmental factors remains poorly understood. On the other hand, the effects of elevated CO_2 on rice yields are more conclusive in short-term experiments: elevated CO_2 increases rice yield in general due to increases in tiller number and grain filling capacity (Ainsworth, 2008; Wang et al., 2015). Theoretically, a higher number of tillers per unit land area increases population density, and heavier panicles impose more pressure on culms. Both factors would increase lodging risk (Duy et al., 2004; Wu et al., 2012; Hirano et al., 2017). On the other hand, elevated CO_2 alters assimilate distribution within plant organs with a higher proportion of non-structural carbohydrates being stored in culms (Yang et al., 2006), which may increase the culm strength and reduce lodging susceptibility (Kashiwagi and Ishimaru, 2004; Ishimaru et al., 2008; Kashiwagi et al., 2006, 2008, 2010). Lodging resistance also depends on cell wall composition. Higher proportions of structural carbohydrates (lignin or/and cellulose) enhanced stem stability in rice (J. Zhang et al., 2014) and wheat (Nguyen et al., 2016), but some studies reported no clear relationship between lodging resistance and cellulose or/and lignin levels (Ishimaru et al., 2008; Kashiwagi et al., 2008; Frei, 2013; Gomez et al., 2018).

Two rice producing countries, Japan and China, have very different nitrogen fertilizer strategies in rice cultivation. The amount of N fertilizer applied per unit land area in Japan is relatively low with a maximum of 15 g m^{-2} (Shimono et al., 2007). In China, 25 g m^{-2} is the standard N level practiced by farmers, with some areas even reaching 35 g m^{-2} (Yang et al., 2006; Liu et al., 2008). Biomass responses to elevated CO_2 were greater when N supply levels were high (Ainsworth, 2008; Reich and Hobbie, 2013; Wang et al., 2015; Reich et al., 2018). However, high N application increased lodging risk in rice (Wu et al., 2012; W.J. Zhang et al., 2014). Therefore, it is important to understand how elevated CO_2 affects lodging in rice production area characterized by high N input. Hence, we conducted a FACE experiment in a rice field with two Chinese rice cultivars, WYJ23 (conventional *japonica*) and LY084 (hybrid *indica*) grown at ambient or elevated CO_2 (200 μmol mol^{-1} above ambient). The field lodging status was recorded and its association with lodging risk of whole plants and basal internodes was investigated. In addition, different lodging-related physicochemical traits of the basal internodes were determined during the grain filling stage. The hypotheses are: (1) Elevated CO_2 changes stem properties and panicle size. These alterations induce changes in the overall mechanical properties of plants, and consequently affect lodging resistance of rice. (2) The CO_2-induced alteration in lodging resistance of rice contributes to its yield gain from elevated CO_2.

2. Materials and methods

2.1. Experimental site and treatments

Two rice cultivars representing two different rice types, the hybrid *indica* LY084 and the inbred *japonica* WYJ23, were grown in a paddy field located at the town of Xiaoji, Yangzhou, Jiangsu Province, China (119°42′E, 32°35′N), where a free-air CO_2 enrichment (FACE) experimental system was established. A full description of this set-up is provided by Liu et al. (2002). In brief, the FACE system consists of six octagonal plots having either elevated CO_2 levels (hereafter called E-CO_2 plots) or ambient CO_2 concentrations (hereafter called A-CO_2 plots). Each plot had a size of ca. 80 m^2. To minimize CO_2 contamination, each plot was at least 90 m away from the nearest other plot. In the E-CO_2 plot, pure CO_2 was emitted from the periphery towards the center through emission tubes located about 50–60 cm above the plant canopy. The rice canopy CO_2 concentrations were monitored and controlled by a real-time computer network. The CO_2 concentration in each E-CO_2 plot was constantly controlled at a level of 200 μmol mol^{-1} above the ambient plots through coordination by a CO_2 monitor, a wind sensor, a humidity sensor and a computer feedback unit that controlled CO_2 release. In the A-CO_2 plots, plants were grown under ambient CO_2 conditions without ring structures. The CO_2 fumigation began after seedling transplanting and continued until plant maturity. The treatment time in each day was from sunrise to sunset. The actual average daytime increase of CO_2 concentration during the fumigation period was 198.0 μmol mol^{-1}. Detailed descriptions of the soil properties for the site can be found in the previous publication (Jing et al., 2016).

2.2. Crop cultivation

Rice seeds were sown into a nursing bed on 20 May 2013, and then grown under ambient air for 30 days. Uniform seedlings were manually