



Uniconazole application strategies to improve lignin biosynthesis, lodging resistance and production of maize in semiarid regions

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ABSTRACT

Lodging stress significantly reduces the grain yield and quality. Uniconazole is a plant growth regulator and it can potentially reduce lodging stress by enhancing lignin metabolism and lodging resistance. We conducted a field study in the semiarid regions of China to determine suitable uniconazole application strategies based on the culm morphological characteristics, rind penetration strength, lignin metabolism, lodging stress, and grain yield from summer maize during 2015 and 2016. Seeds were soaked in uniconazole at concentrations of 0 (SCK₀), 25 (SU₂₅), 50 (SU₅₀) and 75 (SU₇₅) mg kg⁻¹. In another experiment, uniconazole was applied to the foliage at concentrations of 0 (FCK₀), 25 (FU₂₅), 50 (FU₅₀) and 75 (FU₇₅) mg L⁻¹ at the eight-leaf stage. Our results suggested that uniconazole significantly alleviated lodging stress by enhancing lignin metabolism and optimizing the culm morphological characteristics. Uniconazole significantly increased the lignin content and activities of lignin-related enzymes such as phenylalanine ammonia-lyase, cinnamyl alcohol dehydrogenase, tyrosine ammonia-lyase, and peroxidase, where their maximum values were obtained with SU₂₅ and FU₂₅ treatments. The grain yield and ear characteristics increased but then decreased as the uniconazole concentration increased, where treatments SU₂₅ and FU₂₅ obtained the highest grain yield and ear characteristics. Seed soaking significantly enhanced lignin accumulation and alleviated lodging stress compared with foliar application. Our results suggest that the lignin content is closely related to lodging resistance in maize and higher lignin accumulation in the third basal internode can improve lodging resistance. Uniconazole application significantly reduced the risk of lodging stress and improved the grain yield of maize, where the most effective treatments were soaking seeds at 25 mg kg⁻¹ and foliar application of 25 mg L⁻¹ at the eight-leaf stage.

1. Introduction

Lodging in plants refers to the stem breaking from an upright position, which reduces the crop yield and quality (Peng et al., 2014; Wang et al., 2015; Wu and Ma, 2018; Zhang et al., 2017a). Lodging stress is a complex phenomenon that is influenced by many factors, including high plant populations, excessive use of nitrogenous fertilizers, heavy rains, strong winds, storm or hail, topography, soil type, tissue damage by insects, and diseases (Xu et al., 2017; Zhang et al., 2014a; Berry and Spink, 2009; Ye et al., 2016; Spink and Berry, 2005; Piñera-Chavez et al., 2016; Xue et al., 2016; Yu et al., 2017). Kuai et al. (2016) reported that excessive nitrogenous fertilizer application decrease in expression of phenylalanine ammonia-lyase (PAL) and thus

reduced lignin content and lodging resistance. Lodging stress occurs due to stem lodging when the stem is broken at or below an ear-bearing node, or root lodging when plants lean more than a certain degree (30° or 45°) from a vertical position (Ye et al., 2016; Novacek et al., 2013; Sterling et al., 2003). Lodging damages the vascular bundles, cause problems with mechanical harvesting and results in yield losses (Wang et al., 2006; Liu et al., 2018). Yield losses due to lodging stress are 5–20% in maize (Sui-Kwong et al., 2011; Flint-Garcia et al., 2003), 12–80% in wheat (Acreche and Slafer, 2011; Stapper and Fischer, 1990; Vera et al., 2012), and 22% in soybean (Noor and Caviness, 1980). Xue et al. (2016) reported that lodging stress results in approximately 30% of annual grain yield losses in maize. Lodging stress reduces photosynthesis in the canopy and negatively affects crop production (Setter

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et al., 1997; Berry and Spink, 2012). Previous studies have shown that lodging resistance can be improved by reducing the plant height, but excessively reducing the height can also decrease the grain yield (Guoping et al., 2001; Peng et al., 2014). In maize basal internodes play a key role in lodging resistance (Xu et al., 2017; Zhang et al., 2014a). Thus, improving the physical strength of the culm, including rind penetration strength, internode plumpness and diameter of basal internodes is a new target for lodging stress reduction in crops (Zheng et al., 2017; Wang et al., 2015; Flint-Garcia et al., 2003; Xu et al., 2017).

Lignin is a major component of the secondary cell wall and it provides mechanical strength to reduce lodging stress in plants (Wang et al., 2014; Peng et al., 2014; Chen et al., 2011). Greater accumulation of lignin in the basal internodes of wheat promotes lodging resistance (Peng et al., 2014; Chen et al., 2011). In rice a significant positive correlation was found between lignin accumulation and physical strength of culm (Zhang et al., 2014b). Wang et al. (2014, 2015) showed that the lignin content is positively correlated with lodging resistance in common buckwheat. Zhang et al. (2016) reported that structural carbohydrate plays a crucial role in lodging resistance. Higher physical strength and cellulose content of the basal internodes can result in reducing the lodging rate (Liu et al., 2016). Boudet et al. (2003) concluded that the activities of lignin-related enzymes such as phenylalanine ammonia-lyase, cinnamyl alcohol dehydrogenase (CAD), 4-coumarate: coenzyme A ligase (4CL), and peroxidase (POD) have crucial roles in the lignin biosynthesis pathway. The activities of tyrosine ammonia-lyase (TAL), CAD and PAL enzymes have crucial roles in the greater lignin accumulation in wheat (Chen et al., 2011). Peng et al. (2014) reported that the enzyme activities of TAL, PAL, and POD are positively correlated with lignin biosynthesis in wheat. In addition Wang et al. (2015) showed that the activities of CAD, 4CL, PAL, and POD enzymes are positively correlated with the lignin content in common buckwheat.

Uniconazole is a plant growth regulator and its application can reduce the height of plants and protect them from various stresses (Schlutenhofer et al., 2011; Wang et al., 2015; Hussein et al., 2014; Song et al., 2008; Zhang et al., 2012). Uniconazole belongs to the triazole group (Fletcher and Hofstra, 1990). The exogenous application of uniconazole significantly reduces plant height and enhances the internode diameter (Sellmer et al., 2001). The application of uniconazole in maize decreases the endogenous gibberellin content and reduces the plant height (Schlutenhofer et al., 2011). Dressing seeds with uniconazole at 200 mg kg⁻¹ and foliar application with 75 mg L⁻¹ significantly increased lignin biosynthesis, internode plumpness, and the internode diameter by improving lodging resistance and the stem strength in common buckwheat according to Wang et al. (2015). Zhang et al. (2017b) reported that the application of plant growth regulator significantly reduced lodging stress by reducing plant and ear heights and improve grain yield in maize. Plant and ear heights, center of gravity was reduced while rind penetration strength, internode plumpness and lodging resistance in maize was improved significantly with plant growth regulator application (Ye et al., 2016; Xu et al., 2017). Sinniah et al. (2012) also reported that the foliar application of triazole resulted in reduction in culm and internode length while improve internode diameter and bending resistance. Previous studies have suggested that the application of plant growth regulators can reduce lodging stress and increase the grain yield (Ye et al., 2016; Tripathi et al., 2003; Xu et al., 2017). Uniconazole has the ability to reduce the plant height and increase the yield but higher concentrations of uniconazole have negative effects on the ear length and cob weight in maize (Schlutenhofer et al., 2011). Han and Yang (2009) concluded that applying uniconazole can increase the grain yield and quality in wheat with high plant populations.

Previous studies have shown that the exogenous application of uniconazole can reduce lodging stress in various crops (Wang et al., 2015; Dong et al., 2008; Han et al., 2011). However, the effect of uniconazole application on the culm mechanical strength in maize has

not been investigated, especially with respect to lignin biosynthesis. Thus, in the present study, we aimed to determine the effects of uniconazole treatment by seed soaking or foliar application at the eight-leaf stage on lignin metabolism, the culm morphological characteristics, and its relationship with lodging resistance in maize. The results of this experimental study provide important information regarding the culm strength and the avoidance of lodging stress in order to increase maize production in semiarid regions.

2. Materials and methods

2.1. Experimental location

Field experiments were conducted at the Institute of Water Saving Agriculture in Arid Areas of China (34°20'N, 108°04'E; elevation, 466.7 m), Northwest A&F University, Yangling, Shaanxi province, China, during the summer in 2015 and 2016. The area where the experimental site was located is classified as semiarid with a mean annual temperature of 12.9 °C (maximum = 42 °C, minimum = -17.4 °C) and annual mean precipitation of 580 mm per year. The climatic data for 2015 and 2016 when the experimental studies were conducted are shown in Fig. 1. The soil at the experimental site was classified as light silt loam. Mean of soil analyses in 2015 and 2016 showed that the organic carbon, total nitrogen, available phosphorus, and available potassium contents in the 0–20 cm top soil layer were 15.23 g kg⁻¹, 1.21 g kg⁻¹, 12.10 mg kg⁻¹, and 160.12 mg kg⁻¹, respectively.

2.2. Field experiment, materials, and design

The plant growth regulator uniconazole was provided by United Chemicals Factory of Lanyue, Chengdu, Sichuan province, China. Maize genotype Zhengdan 958, which is commonly cultivated in the semiarid regions of China, was sown in this experiment. In the first experiment, maize seeds were sterilized with 0.3% sodium hypochlorite solution for 10 min and then washed three times with distilled water. The maize seeds were then soaked in uniconazole solution at 0 (SCK₀), 25 (SU₂₅), 50 (SU₅₀), and 75 (SU₇₅) mg kg⁻¹ of seeds at room temperature for 12 h in an incubator. After 12 h the seeds were rinsed with distilled water and air dried for 24 h before sowing. In the second experiment, uniconazole solution was applied to the foliage at concentration of 0 (FCK₀), 25 (FU₂₅), 50 (FU₅₀), and 75 (FU₇₅) mg L⁻¹ at the eight-leaf stage for two consecutive days after sunset at the rate of 284 mL m⁻².

Randomized complete block design with three repeats was used for both experiments. The overall plot size was 35 m², with a width of 7 m and length of 5 m. The inter-row spacing was 60 cm and the inter-plant spacing was 20 cm. Seeds were sown on June 14 and 15, and harvesting at October 5 and 7 in 2015 and 2016, respectively. Nitrogen in the form of urea was applied at the rate of 235 kg ha⁻¹, phosphorus in the form of single superphosphate was applied at the rate of 150 kg ha⁻¹, and potassium in the form of potassium sulfate was applied at the rate of 150 kg ha⁻¹. All of the phosphorus and potassium, and 60% of nitrogen were applied at sowing, and the remaining 40% of the nitrogen was applied at the seven-leaf stage. All other agronomic practices were uniformly applied to all treatments.

2.3. Sampling and measurement

2.3.1. Internode diameter (mm) and internode plumpness (g cm⁻¹)

The internode diameter was measured for the second basal internode at the jointing, tasseling and grain filling stages, and for the third basal internode at the tasseling and grain filling stages for five tagged plants in four central rows using a digital vernier caliper. The internode plumpness was measured for the third basal internode at the grain filling stage for three randomly selected plants in four central rows by dividing the internode dry weight by the length of the internode, as described previously by Peng et al. (2014).

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