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CADMIUM INDUCED MODIFICATION OF SUGAR ACCUMULATION AND TRANSLOCATION ALONG SWEET SORGHUM STEM

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ABSTRACT

Sweet sorghum is an important bioenergy crop with a high heavy metal resistance, great biomass and sugar enrichment in stem. However, the influence of heavy metals on sugar accumulation in sweet sorghum is still unknown. In this study, Cd induced modification of sugar storage and translocation in stem was monitored using two sweet sorghum cultivars Keller (KE) and E-tian (ET). Brix degree, which represents sugar content in stem juice, displayed significant reduction in response to exogenous Cd treatment in both lines. The sugar enrichment was more obviously repressed in the lower internodes while it was hardly affected in the top internodes. Excessive Cd results in drastically enhanced Cd accumulation, preferentially in the lower internodes. More interestingly, negative correlation between Cd and sugar content was detected along internodes, indicating antagonistic translocation between Cd and sugar along stem of sweet sorghum. The preferential compartmentation of Cd and sugar in different regions of stem provides novel insights into understanding and application of sweet sorghum for combining biofuel production with phytoremediation of heavy metal in soil.

Keywords: sweet sorghum, cadmium, brix, sugar, stem.

1. INTRODUCTION

Heavy metal contamination in soil has become a public concern due to industrial development and human activities, such as mining and smelting of metalliferous ores, electroplating, fertilizer and pesticide application, and fuel production [1]. Excessive heavy metals, for example, lead (Pb), chromium (Cr), zinc (Zn), cadmium (Cd), copper (Cu), and nickel (Ni), in agricultural areas seriously threaten food safety and public health. Elimination or remediation of heavy metal contamination in soil is urgently in request to prevent human and animals from toxicity. Phytoremediation is a cost-effective and eco-friendly technique to clean up heavy metal pollution in soil. Hyperaccumulators include >400 plants that not only tolerate high-level heavy metals, but also translocate them upward to aerial tissues [2]. Consequently heavy metals would be gradually removed from soil through harvesting their aboveground parts. But the usage of hyperaccumulators is limited due to small biomass and habitat requirement [2]. Instead plants with high biomass have greater phytoremediation potential than hyperaccumulators despite relatively lower resistance to heavy metals [3]. Hyperaccumulators and high-biomass plants are considered for phytoremediation in practice.

Sorghum (Sorghum bicolor L.) is a pro-poor multipurpose crop providing food, feed, fiber and fuel across a range of agro-ecosystems [4]. Sweet sorghum consists of natural variant cultivars of sorghum with abundant sucrose storage in culm and great biomass, and is thereby considered an ideal feedstock for biofuel production. It possesses stronger drought tolerance than other biofuel crops such as sugarcane and maize, and is more able to thrive on marginal land; hence it requires less input for similar output. Sweet sorghum will be a competitive candidate species for soil remediation due to its great biomass and strong resistance to adverse environmental conditions.

To preliminarily evaluate its potential for phytoremediation, a number of morphological and physiological characteristics of sorghum were investigated under heavy metal stresses (Cd, Pb, Zn, Cu) in previous studies [5 – 7]. Sorghum could not only tolerate high concentrations of heavy metals, but also capture and translocate metal ions to aerial parts [5 – 7]. Therefore, despite potential usability of crop plants including sorghum in soil cleanup, the possible risk of introducing heavy metals accumulated in edible parts into food chains must be avoided [8]. Due to non-food usage, sweet sorghum will attract more attention for phytoremediation in heavy-metal contaminated areas. Nevertheless, physiological behaviors and genetic control of sweet sorghum cultivars in response to heavy metal exposures are still poorly understood.

Sugar content determines the potential of sweet sorghum for biofuel production. In this study, Cd induced modification of sugar storage and translocation in stem was explored in two sweet sorghum cultivars. Interestingly, negative correlation between sugar and Cd distribution along internodes was detected in response to Cd exposure. These results provide novel insights into the coupling of bioenergy production with heavy metal phytoremediation for sweet sorghum.

2. MATERIALS AND METHODS

2.1. Plant material and experimental design

The elite lines of sweet sorghum Keller (KE) and E-Tian (ET) were used for experiments. KE (GRIN access code PI 653617) initially developed in the U.S. has excellent performance globally across a series of environmental conditions while ET introduced in China in 1970s possesses rich sugar storage in stem.

Following immersion overnight in distilled water, the seeds were germinated for 3 days in darkness at 28 ^{o}C. The seedlings were subsequently transplanted into plastic pots (diameter: 30 cm; height 25 cm) with peat soil (2 kg soil for 2 seedlings per pot; Cd concentration in soil: 0.05 ppm) and cultivated under glasshouse conditions (28 – 32 ^{o}C with 14 - 16 hours light / 22 – 26 ^{o}C with 8 - 10 hours dark). For Cd treatment, $CdCl_2$ in solution was mixed with soil to increase Cd concentration to 100 ppm at the eight-leaf stage. The plants without Cd exposure were used as the control. The samples were harvested 75 days after Cd exposure for the measurement of Cd content and sugar accumulation. There are 12 biological replicates for Cd treatment and control.

2.2. Brix assessment

Each internode of sweet sorghum plants was sampled separately and grinded for juice collection. The extracted juice was loaded onto a refractometer PAL-BX/RI (ATAGO, Bellevue, WA, USA) for determining Brix degrees. The internodes were numbered according to the proximity to panicles.

2.3. Cd concentration assay

The samples were dried in a ventilated oven at 105 ^oC for 30 mins and 70 ^oC for 48 hours and subsequently grinded into powders. 0.1 g of the grinded sample was transferred to a mixture of HNO_3 and $HClO_4$ (3:1; v/v) for digestion overnight. Cd concentration was determined using a flame atomic absorption spectrometry HITACHI Z5000 (Tokyo, Japan).

2.4. Data analysis

The data were calculated using Statistix (version 10.0). Significant differences were determined by least significant differences (LSD) at 5 % level of probability.

3. RESULTS

3.1. Cd induced reduction of sugar content in stem juice

The soluble sugar accumulated in sweet sorghum is mainly stored in the internodes of stem. Brix degree is the indication of sugar content in an aqueous solution. One Brix degree is 1 g of sucrose in 100 g of solution and represents the strength of the solution as percentage by mass. Brix degree in the stem of ET was higher than that of KE at normal condition, indicating that more sugar was accumulated in ET (Figure 1). Nevertheless, both lines displayed significant decrease of Brix degree in response to Cd stress, up to 12.2 % in KE and 30.3 % in ET (Figure 1). Therefore, sugar accumulation was repressed by Cd treatment in stem juice of sweet sorghum lines.

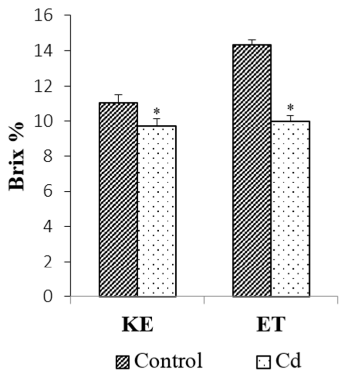

Figure 1. Quantification of sugar content in stem juice of sweet sorghum lines KE and ET subject to exogenous Cd treatment. The asterisk above bars represents significant difference at 0.05 level of probability.

3.2. Cd modified translocation of sugar content along stem

The sugar content of each internode was determined to detail the influence of Cd exposure on sugar distribution along stem. Both KE and ET lines displayed variant sugar concentrations in internodes (Figure 2a and b). Without Cd exposure, sugar content in KE displayed negative correlation with internodes that are numbered according to the proximity to panicles (Pearson correlation coefficient $R^2 = 0.87$, $p < 0.01$, Figure 2a) while sugar is preferentially enriched in the middle internodes of ET (Internode No. 4 - 6; Figure 2b). In line with the results indicated by Figure 1, most of the internodes in both KE and ET lines display inhibited sugar accumulation in response to Cd treatment (Figure 2a and b). Notably, Cd treatment leaded to more drastic reduction of sugar content in lower internodes than upper ones of both lines (Figure 2a and b). More interestingly, Cd treatment results in negatively correlated patterns of sugar distribution along internodes from topmost to lowermost in both KE and ET lines (The correlation coefficient R = 0.8717 for KE and 0.9342 for ET, $p < 0.01$, Figure 2a and b).

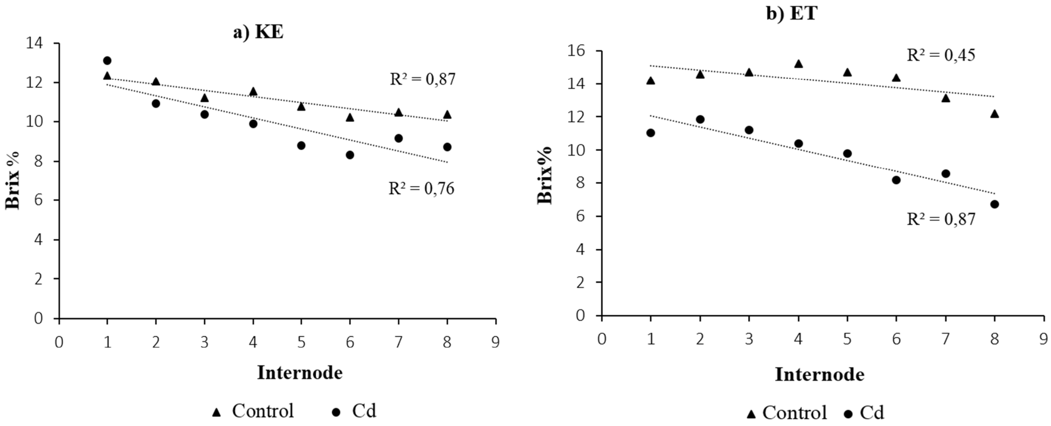

Figure 2. Cd modified Brix degrees along internodes in sweet sorghum lines KE and ET. The internodes were numbered according to the proximity to panicles. R indicates Pearson correlation coefficient.

3.3. Cd enrichment in stem

Compared to the control, more Cd was significantly enriched in stem of both sweet sorghum lines under excessive Cd condition (Figure 3). KE and ET lines were able to accumulate Cd up to 7.7 and 4.8 μg/g DW (Figure 3).

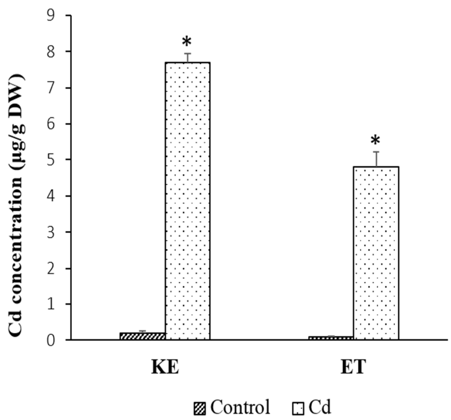

Figure 3. Cd concentration in stem of sweet sorghum lines KE and ET under Cd stress. The asterisk above bars represents significant difference at 0.05 level of probability. DW means dry weight.

3.4. Cd distribution along internodes

Under Cd exposure, the enriched Cd inhibited differential distribution within the stem of both KE and ET lines, which positively correlates with the position of internodes numbered according to the proximity to panicles (The correlation coefficient R = 0.8944 for KE and ET, $p < 0.01$, Figure 4a and b). Cd preferentially accumulated in the top internodes while less in the lower ones (Figure 4a and b).

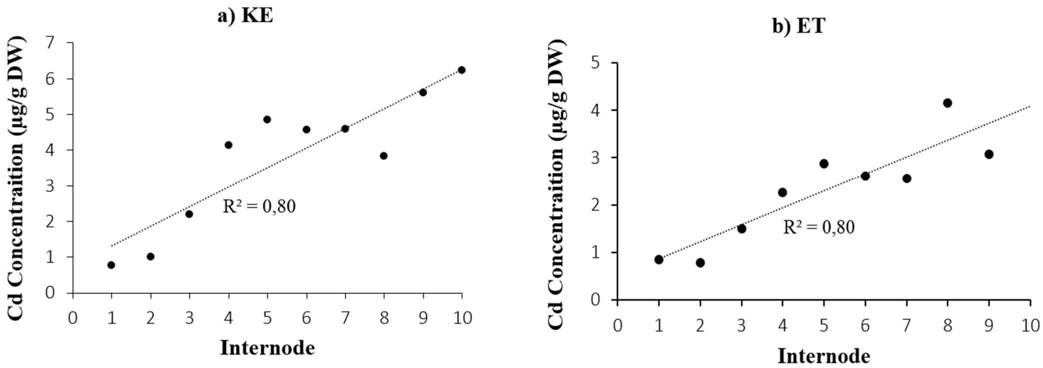

Figure 4. Positive correlation between Cd concentration and internode position along the stem. The internodes were numbered according to the proximity to panicles. R indicates Pearson correlation coefficient.

3.5. Negative correlation between Cd and sugar accumulation along internodes

Under Cd stress, sugar was preferentially in the top and middle internodes (Figure 2) while Cd was more accumulated in the lower internodes (Figure 4). Hence Cd and sugar may be accumulated antagonistically along internodes. Correlation analysis demonstrated that sugar content displayed highly negative correlation with Cd concentration along internodes from the top to the bottom in both KE and ET (The correlation coefficient R = -0.9055 for KE and -0.9110 for ET, $p < 0.01$, Figure 5a and b).

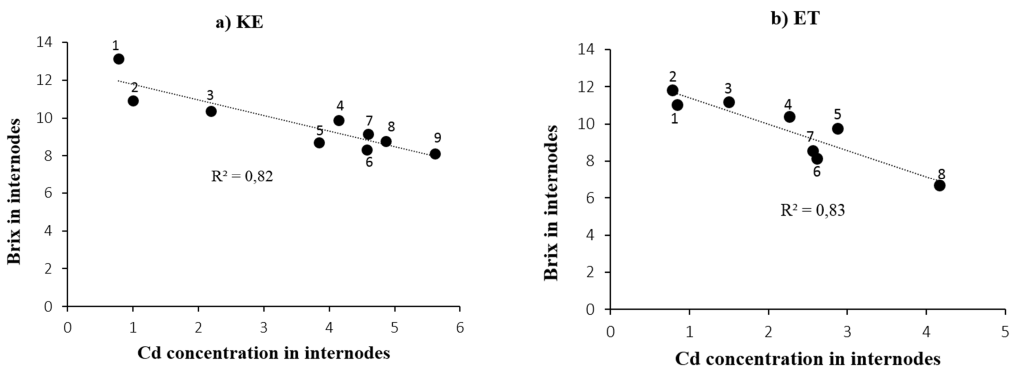

Figure 5. Negative correlation between sugar content and Cd concentration along internodes. The numbers indicate internode position according to the proximity to panicles. R indicates Pearson correlation coefficient.

4. DISCUSSION

4.1. Inhibitory action of Cd excess on sugar enrichment in stem of sweet sorghum

Because of great biomass and high tolerance to heavy metals including Cd, sweet sorghum is considered as a potential species for heavy metal phytoremediation. Sugar enrichment is the most important property of sweet sorghum for bioenergy production [9]. Hence the influence of excessive Cd on sugar enrichment in stem must be demonstrated for dual application of sweet sorghum for biofuel production and phytoremediation. Our results indicate that exogenous Cd treatment impairs sugar accumulation in stem of sweet sorghum, especially in the lower internodes (Figure 1 and 2). This inhibitory effect may result from the reduced photosynthate production in leaves or / and restricted sugar transport to lower internodes along stem. More importantly, the KE line displays obviously less reduction in sugar enrichment than ET under Cd exposure (Figure 2), suggesting its larger capability of sugar accumulation in stem. These results highlight genetic diversity of sweet sorghum in sugar maintaining against Cd toxicity and also suggest the possibility of breeding for Cd resistant cultivars with less reduction of sugar enrichment.

4.2. Antagonistic translocation between Cd and sugar along internodes of sweet sorghum

Sweet sorghum is able to accumulate a large quantity of heavy metals including Cd, Cu, Pb, and Zn due to its great biomass [5, 10], the majority of which is fixed in root and stem tissues [11]. Furthermore, Cd is accumulated preferentially in the lower internodes while scarcely in the upper internodes of both sweet sorghum lines KE and ET (Figure 4). These results suggested that excessive Cd accumulation is avoided in leaves, florescence, and seeds essential for photosynthate fixation and reproduction. Our results indicated that photosynthesis rate and seed production are sensitive to Cd toxicity and easily repressed by Cd exposure (Dinh et al., unpublished data). Therefore, Cd accumulation in lower internodes benefits the resistance of sweet sorghum to Cd toxicity.

Although overall repression of sugar content in stem by Cd excess, the internodes display variant ability for maintaining sugar enrichment in sweet sorghum lines (Figure 2). The restriction of sugar storage represents Cd toxicity to sweet sorghum stem. The negative correlation of sugar and Cd concentration in internodes suggests antagonistic translocation between Cd and sugar along stem in sweet sorghum. It makes sense due to opposite directions of sugar and Cd transport through vascular system in stem. Sugar is transported downward through phloem while Cd is usually delivered upward in xylem [12]. However, the molecular mechanism of how Cd damages sugar trafficking and storage in stem is still poorly understood. Because of the antagonistic distribution of sugar and Cd in stem, different internodes or regions of sweet sorghum stem can be collected separately for biofuel fermentation and Cd recycling. Hence, the preferential accumulation of sugar and Cd in different regions of stem may facilitate the combination of biofuel production and phytoremediation using sweet sorghum.

5. CONCLUSION

In this study, Cd induced modification of sugar storage and translocation in stem was explored in two sweet sorghum cultivars. Sugar accumulation was repressed by Cd treatment in stem juice of sweet sorghum, both cultivars displayed significant decrease of Brix degree in response to Cd stress. Cd treatment leaded to more drastic reduction of sugar content in lower internodes than in upper ones of both cultivars. There was negative correlation between sugar content and Cd concentration along internodes.

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