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Accumulation of water-soluble carbohydrates and gene expression in wheat stems correlates with drought resistance

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ABSTRACT

In order to understand the effects of sugar metabolism on drought resistance in wheat, two wheat cultivars with different levels of drought resistance were used in this study. We investigated the accumulation pattern of water-soluble carbohydrates (WSC) and expression profiles of twelve fructan metabolism-related genes in peduncle (PED), penultimate (PEN), and lower internode (LOW) stem tissues under drought stress. LH7, a higher drought-resistance cultivar, contained a higher stem dry weight and higher content of WSC in PED, PEN, and LOW tissues, while XN979, a lower drought-resistance cultivar, contained lower values. The tissues from LOW internodes had the highest WSC content, while PED had the lowest. The mRNA levels of genes encoding fructan synthesis-related enzymes, sucrose: sucrose 1-fructosyltransferase (1-SST), sucrose: fructan 6-fructosyltransferase (6-SFT), and fructan: fructan 1- fructosyltransferase (1-FFT) showed higher expression levels at early time points following stress, whilst the genes encoding degradation-related enzymes, fructan exohydrolases (1-FEH), and invertase (INV), showed higher expression at a later time point. Compared with XN979, LH7 showed higher expression levels of genes encoding fructan synthesis-related enzymes at all growth stages, whilst the expression of *1-FEH-W3*, *6-FEH*, and *INV3* were higher at a later stage; these expression levels would benefit fructan accumulation and remobilization at early and later stages, respectively. Drought stress induced most of fructan metabolism related genes expression level decreasing in LH7 PED, but enhancing in LH7 LOW part at early time points following stress. The results confirm that there are complex, coordinated expression patterns of fructan synthesis- and degradation-related genes in stems under drought stress. In summary, *1–SST-A2*, *6-SFT, 1-FFT-A*, *1-FEH-W3*, *6-FEH*, and *INV3* play important roles in fructan accumulation. In addition, higher expression of genes related to fructan synthesis and degradation occurs during early and later stages of drought stress, respectively, enhancing the drought resistance of wheat cultivar LH7.

1. Introduction

Wheat (*Triticum aestivum* L.) is a staple food for about one third of the world's population. However, wheat plants are often subjected to various environmental stresses during their life cycle, with drought considered to be a key factor determining crop distribution and productivity (Sylvester-Bradley et al., 1990). Drought stress is known to cause yield losses by limiting photosynthesis, reducing stem elongation, and altering activities of carbon-metabolizing enzymes (Ma et al., 2016; Engelbrecht et al., 2007; Jiang et al., 2012). Drought stress can also have a negative impact on grain weight and yield; however, pre-anthesis drought priming has the potential to alter source-sink relationships, for both drought-sensitive and drought-tolerant wheat cultivars, to improve grain filling in response to post anthesis drought stress (Abid et al., 2017). Li et al. (2017) found that the drought-resistant cultivar 'Changhan58' sustained a higher photosynthetic rate in wheat ears and enhanced overall drought resistance by decreasing transpiration rate. Furthermore, greater fructan content in the stem internodes and higher exo-hydrolase activity of fructan correlated with higher grain yield under drought stress (Chen et al., 2015).

Grain growth in wheat depends on photosynthetic assimilates being transferred directly to the grain and redistributed from reserve pools in

Abbreviation: DAS, days after stress; 1-FEH, fructan exohydrolases; 1-FFT, fructan: fructan 1- fructosyltransferase; INV, invertase; LOW, lower internode; PED, peduncle; PEN, penultimate; WSC, water-soluble carbohydrates; 6-SFT, sucrose: fructan 6-fructosyltransferase; 1-SST, sucrose: sucrose 1-fructosyltransferase

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vegetative tissues (Ehdaie et al., 2008). Water-soluble carbohydrates (WSC), mainly glucose, fructose, sucrose, and fructans, accumulated in the stem and sheath of wheat during the period from stem elongation to the early phase of grain filling, which could be remobilized during the later stage of grain filling (Wardlaw and Willenbrink, 2000). A reserve of WSC is an important carbon source for grain yield in wheat and barley (Bonnett and Incoll, 1992; Schnyder, 1993) and is positively associated with grain yield under both irrigation and drought (Foulkes et al., 2007). Redistribution of WSC during grain filling can potentially contribute to about 20% of the final grain weight under favorable conditions (Wardlaw and Willenbrink, 2000), while stem WSC could potentially contribute to about 50% of grain yield when wheat crops undergo drought stress during the grain filling period (Aggarwal and Sinha, 1984). Research has shown that concentrations of WSC were higher in drought-tolerant genotypes than in sensitive ones (Goggin and Setter, 2004; Yang et al., 2007). It was also suggested that the ability to store and remobilize large amounts of WSC to grains was used as a selection criterion for wheat breeding (Ruuska et al., 2006). The accumulation and remobilization efficiency of stem WSC differed between internodes, and each internode responded differently to drought (Ehdaie et al., 2006). Li et al. (2015) found that stem WSC in lower internodes significantly correlated to 1,000-grain weight, especially at the mid-grain filling stage under drought stress. Ma et al. (2014) also reported that when plants were under severe stress, the remobilization efficiency of dry matter increased by 137% in the lower internodes, compared with 35% in the upper internodes. Xue et al. (2008) suggested that differential carbon partitioning in wheat stems was one mechanism that contributed to genotypic variations in the accumulation of WSC influencing grain weight and yield under a water-limiting environment. Manipulating stem non-structural carbohydrates provides an avenue to stabilize and increase productivity of wheat in the face of rapidly changing demands in the next century (Slewinski, 2012).

Fructans (polyfructosylsucrose) are water-soluble and nonstructural polysaccharides, consisting of linear or branched fructose chains attached to a sucrose moiety (Goggin and Setter, 2004; Joudi et al., 2012). Fructans are the main storage forms of WSC in wheat stems and are not only sources of carbon and energy (Livingston et al., 2009; Xue et al., 2011) but are also involved in stress responses, perhaps even acting as signals (Van den Ende, 2013; Peshev and Van den Ende, 2014). Fructan metabolism is mediated by a complex set of biosynthetic and hydrolytic enzymes, and is synthesized starting from sucrose (Fig. 1) (Van den Ende et al., 2006; Gao et al., 2010; Xue et al., 2013). Three types of fructan-synthesizing enzymes have been characterized in the vegetative tissues of wheat: sucrose: sucrose 1-fructosyltransferase (1-SST), fructan: fructan 1- fructosyltransferase (1-FFT), and sucrose: fructan 6-fructosyltransferase (6-SFT) (Gao et al., 2010). Two sucrose molecules produce 1-kestose and glucose through the action of 1-SST, and this process is irreversible (Van den Ende et al., 2006). The enzyme 6-SFT also transfers fructose from a sucrose donor but prefers either 1-kestotriose as acceptor forming 1 & 6-kestotetraose, or another fructan introducing a β (2–6) linkage (Gao et al., 2010). Subsequently, 1-FFT can polymerize trisaccharides or oligosaccharides to produce longer polysaccharides in this irreversible reaction process (Kawakami and Yoshida, 2005). Fructan degradation is catalyzed by three types of fructan exohydrolases (FEH), 1-FEH, 6-FEH, and 6&1-FEH (Van den Ende et al., 2005; Van Riet et al., 2008). When the demand for grain filling is high and sucrose becomes limiting, fructans are degraded by 1-FEHs to release more sucrose and fructose (Zhang et al., 2009). The complete degradation of fructan also requires the participation of invertase (INV). Sucrose is hydrolyzed to produce fructose and glucose through the action of INV (Sturm, 1999).

Analysis of affymetrix expression array data revealed that the expression of the majority of the genes involved in fructan and starch synthetic pathways positively correlated with sucrose levels in the leaves of some recombinant inbred lines (RIL) (Xue et al., 2013). Li et al. (2015) also found that pyramiding WSC-favorable alleles was not only effective for obtaining accessions with higher content of WSC, but also for enhancing 1,000-grain weight under different water regimes. Khoshro et al. (2014) reported that higher fructan content, mobilization efficiency, and expression levels of *1-SST*, *6-SFT*, *1-FEHw3*, and *6-FEH* genes might improve the drought resistance of the cultivar (Zagros). Zhang et al. (2015) suggested that the dynamics of fructan metabolism and FEH activities could be used as indicators of remobilization efficiency in the lower parts of stems. Although it is well documented that accumulation of WSC has a positive relationship with grain yield and can improve the resistance or tolerance of plants to environmental stress, the underlying molecular mechanism of WSC metabolism in wheat stems is still poorly understood. In this study, two wheat genotypes with different levels of drought resistance were used to investigate the accumulation pattern of WSC and expression profiles of twelve corresponding metabolism-related genes in different stem segments under drought stress. The results will provide useful information for wheat production under adverse conditions.

2. Materials and methods

2.1. Experimental design

The experiment was conducted in 2015–2017 at Henan Agricultural University Experimental Station, Henan province, China. Two common wheat (*Triticum aestivum* L.) cultivars were used: Luohan7 (LH7), a higher drought resistant cultivar with a drought resistance index (DRI)

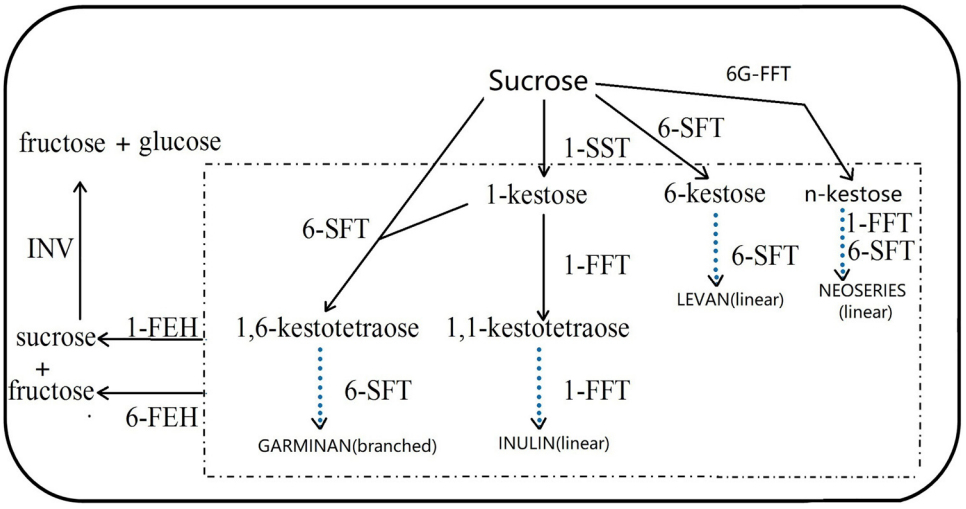

Fig. 1. Overview of fructan metabolic pathways and its correlated enzyme.
Fructans are synthesized starting from sucrose and are mediated by several fructosyltransferase (Xue et al., 2013). Fructans are linear or branched polysaccharides, and are classified into four structurally distinct major categories in higher plants: inulin, levan, garminan, and neoseries (Ritsema and Smeekens, 2003; Cimini et al., 2015). 1-FEH, fructan 1-exhohydrolase; 1-SST, sucrose: sucrose 1-fructosyltransferase; 6-SFT, sucrose: fructan 6-fructosyltransferase; 1-FFT, fructosyltransferase. Broken arrows indicate the formation of fructan with different degree of polymerization.

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