



# Sucrose signaling pathways leading to fructan and anthocyanin accumulation: A dual function in abiotic and biotic stress responses?



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## ABSTRACT

In a changing world, plants are exposed to ever changing environmental conditions. Since plants cannot escape from their environment, they require extra flexibility to adapt themselves to stressful conditions, such as drought and salt stresses. One of these adaptations includes the vacuolar accumulation of fructans (fructose-based oligo- and polysaccharides) and anthocyanins (a type of glucosylated flavonoids), both involved in biotic and abiotic stress responses. As part of the recently emerging concept of “sweet immunity” leading to improved tolerance to both abiotic and biotic stresses, possible synergisms between these two types of biomolecules are discussed. Moreover, sucrose-specific signaling pathways stimulate both the production of fructans and anthocyanins, with a central role for MYB-type of transcription factors and a strict dependence on Ca<sup>2+</sup>. This review summarizes recent insights in these signal transduction pathways and their cross-talks with hormonal signaling pathways, with focus on the stress hormone abscisic acid. Although most of the current research is dedicated on the model plant *Arabidopsis thaliana*, we also focus on wheat as an example of an economically important crop that is able to accumulate both fructans and anthocyanins under various stresses.

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## 1. Introduction

In large parts of the world plant production and crop yields are limited due to abiotic stresses including drought, heat, cold, freezing and soil salinity. Abiotic stresses can also make crops more vulnerable to biotic stresses (Shahbaz and Ashraf, 2013). Together, all these stresses seriously compromise food and biomass production. In our changing world, it is important to expand our agricultural systems to drier and saline lands to meet increased food demands, especially in developing countries (Shinozaki and Yamaguchi-Shinozaki, 1999; Huang et al., 2012; Koyoro et al., 2012; Krasensky and Jonak, 2012).

Among all these stresses, salt stress is certainly one of the most prominent ones causing osmotic and ionic stresses at the cellular level. In general, few crop species are adapted to the presence of high salt levels (Igartua, 1995; Hollington, 1998; Sankar et al., 2011; Radić et al., 2013). In general, plant responses to high salinity are rather complicated, including multiple processes and mechanisms. Extreme salt levels lead to so-called hyperosmotic stress associated with ionic imbalances caused by the increase of toxic ions such as

Na<sup>+</sup> and Cl<sup>-</sup>. Moreover, salt stress has an unfavorable effect on mineral homeostasis, especially Ca<sup>2+</sup> and K<sup>+</sup> homeostasis (Isayenkov, 2012; Krasensky and Jonak, 2012). Typically, salt stress enhances abscisic acid (ABA) levels, stimulating stomatal closure which is also associated with increased levels of reactive oxygen species (ROS) and nitrogen oxide (NO) (Allen et al., 1999; Du et al., 2013; Iqbal and Ashraf, 2013). Some of these reactive species trigger signaling pathways that may lead to differential gene expression and (partial) stress adaptation (Ding et al., 2010).

Wheat is one of the most abundant food crops, which is attacked by numerous viral, bacterial and fungal pathogens and also by insects and nematode pests. An important challenge in current molecular biology of wheat and other crops is to decipher how thousands of genes are differentially expressed under biotic and abiotic stresses, aiming to overcome the detrimental effects of these stresses (Park et al., 2001; Zhu, 2001; Nakashima et al., 2007; Rahaie et al., 2013). Transcription factors (TFs) regulate the expression of target genes by specifically binding to the *cis-acting* elements of (an array of) genes. TFs are classified into different families based on differences in the DNA-binding domains and overall 3D structure (Agarwal et al., 2012; Zhang et al., 2012). Well-known stress-related TF families include the MYB, DREB, NAC, and WRKY types (Singh et al., 2002; Huang et al., 2012). Several studies identified tolerance genes and investigated the TFs involved in wheat salt tolerance (Lee et al., 2007; Ding et al., 2009; Mondini et al., 2012; Zhang et al.,

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2012). More in particular, plant-specific NACs (NAM, ATAF1, ATAF2 and CUC2) constitute a major TF family with well-known roles in plant developmental programs (Singh et al., 2002; Guo et al., 2004; Huang et al., 2012) and stress responses (Nakashima et al., 2012; Puranik et al., 2012).

Plants as photo-autotrophic organisms depend on photosynthesis, i.e. the fixation of carbon from carbon dioxide into simple sugar molecules, with the help of sunlight. Next to their role as a carbon and energy source, sugars have acquired important regulatory functions in different organisms early in evolution (Rook and Bevan, 2003). Generally, in higher plants, high sugar levels stimulate expression of genes involved in sink function, such as growth, storage of proteins and biosynthesis of starch (polymers of glucose: Glc) and fructans (polymers of fructose: Fru) (Gupta and Kaur, 2005). In contrast, low sugar levels promote photosynthesis and mobilization of energy reserves, such as breakdown of storage starch or lipids. Next to the total amounts of the small water-soluble carbohydrates Glc, Fru and sucrose (Suc), it seems that the relative proportions of these sugars are important; Glc, Fru and Suc-specific signaling pathways have now been described in plants (Bolouri Moghaddam and Van den Ende, 2013a). Invertases and other Suc-splitting enzymes (e.g. sucrose synthase or SuSy) can have a drastic impact on these different sugar signaling pathways.

Sugar signaling events include sugar sensing, signal transduction and target gene expression (Goddijn and Smeekens, 1998; Gupta and Kaur, 2005; Rosenquist, 2007). So far, hexokinase (HXK) remains the only well-established sugar sensor in plants, specifically sensing Glc (Moore et al., 2003). However, a Suc-specific signaling pathway seems to be used in many processes including sugar-mediated feedback repression of photosynthesis genes and induction of fructan and starch biosynthetic genes (Vijn and Smeekens, 1999; Rolland et al., 2002). Trehalose 6-phosphate (T6P), synthesized from G6P and UDP-glucose (UDPGlc) by T6P synthase (TPS), is emerging as a central regulator in this Suc-specific pathway (Zhang et al., 2009a). T6P is a direct precursor of the trehalose disaccharide, a well-known stress protectant (Bolouri-Moghaddam et al., 2010).

Increased proline levels, a widely distributed multifunctional osmoprotectant (Szabados and Savouré, 2010) are often associated with increased Suc levels, demonstrating that proline synthesis also depends on Suc-specific signaling events (Hanson et al., 2008). Accordingly, proline, Suc and fructan levels increased together in salt-stressed wheat, reaching higher levels in salt-tolerant cultivars as compared to a salt-sensitive ones (Kafi et al., 2003). Free proline levels dramatically increased with high salt treatments in *Thellungiella* (Ghars et al., 2012; Wang et al., 2013). In *Arabidopsis*, soluble sugars, anthocyanins (see below) and proline increase together under drought stress (Sperdouli and Moustakas, 2012).

Plants use a wide array of natural products that often accumulate within vacuoles. Many of those play an essential role in defense responses against herbivores and pathogens. Flavonoids are well-known secondary metabolites, harboring the anthocyanins as typical water-soluble vacuolar compounds (Neilson et al., 2013). Another class of water-soluble vacuolar compounds with anti-stress properties are fructans, occurring in about 15% of flowering plants (Hendry, 1993). Different types of linear and branched fructans can be discerned (Di Bartolomeo et al., 2013). Because of their economic importance, wheat, barley and *Lolium* sp. are among the best-studied fructan accumulators. Wheat plants accumulate branched graminan- ( $\beta$ 2,6 and  $\beta$ 2,1 linkages) and linear levan-type ( $\beta$ 2,6 linkages) fructans, especially under stress conditions (Yoshida et al., 2007). Suc stimulates fructan synthesis as a substrate and as an inducer of fructan biosynthetic genes (Müller et al., 2000). Increased Suc and anthocyanin levels occur when wheat leaves are subjected to UV-B (Pradhan et al., 2008; Lv et al., 2013).

Some wheat accessions (blue and purple wheat) also accumulate anthocyanins in their grains, which is interesting for food applications (Kniewel et al., 2009). Both fructans and anthocyanins were proposed to play a role in vacuolar antioxidant mechanisms, contributing to cellular ROS homeostasis (Van den Ende and Valluru, 2009; Bolouri-Moghaddam et al., 2010). While the strong antioxidant capacities of anthocyanins are known since long (Shinozaki and Yamaguchi-Shinozaki, 1999; Gould et al., 2002; Nagata et al., 2003), the ROS scavenging properties of fructans and other soluble plant sugars were only recently recognized (Stoyanova et al., 2011; Hernandez-Marin and Martínez, 2012; Keunen et al., 2013; Peshev et al., 2013).

This review summarizes recent insights on how vacuolar fructans and anthocyanins might contribute to abiotic and biotic stress responses, how sugar signaling and stress hormone pathways might be involved, and how stress-related TFs could influence (or fit into) such signaling pathways. Focus will be on wheat as an example of an economically important crop that is able to accumulate both fructans and anthocyanins under stress. Drought and salt stresses are major problems during wheat grain production (Joudi et al., 2012; Munns et al., 2012).

## 2. Fructan metabolism in wheat under stress

Fructans are the major storage carbohydrates in temperate grasses and cereals, while starch is often only present at low levels (Chalmers et al., 2005). Fructans play a role in freezing (Yoshida et al., 1998; Kawakami and Yoshida, 2002), drought (Pilon-Smits et al., 1995; Vijn and Smeekens, 1999; Hinch et al., 2000, 2002; Joudi et al., 2012) and salt tolerance (Kerepesi et al., 2002). Plants accumulate fructans for several reasons including their high solubility in water, their resistance to crystallization at subzero temperatures and the fact that the fructan biosynthetic machinery still functions normally under cold stress (Livingston et al., 2009; Krasensky and Jonak, 2012). Furthermore, fructans can stabilize membranes (Vereyken et al., 2001; Hinch et al., 2002; Valluru and Van den Ende, 2008) by inserting at least part of the polysaccharide into the lipid head group region of the membrane (Livingston et al., 2009). However, also Suc and trehalose (Tre) have such membrane stabilizing properties, but probably higher concentrations are needed to reach the same effects (Van den Ende and Valluru, 2009).

Fructans temporarily accumulate in stems and young kernels of wheat (Van den Ende et al., 2003, 2011) and in reproductive organs (Ji et al., 2010). When Suc, the major transport compound in most plants, arrives in such tissues, it can be degraded by Suc splitting enzymes (invertase, SuSy) to sustain growth and/or it can be polymerized into fructans. Suc is the essential substrate for fructan synthesis in wheat by the sequential action of 3 fructosyltransferases (FTs), including 1-SST (sucrose: sucrose 1-fructosyltransferase), 1-FFT (fructan: fructan 1-fructosyltransferase) and 6-SFT (sucrose: fructan 6-fructosyltransferase). Fructan hydrolysis occurs by different types of FEHs (fructan exohydrolases) including 1-FEHs (preferentially degrading  $\beta$ 2,1 linkages) and 6-FEHs (preferentially degrading  $\beta$ 2,6 linkages) (Van den Ende et al., 2003; Kawakami and Yoshida, 2005). 1-SST and 6-SFT are involved in fructan synthesis during cold hardening (Kawakami and Yoshida, 2002), while 6-SFT and 1-FFT play a role in further elongating branched graminans. FTs evolved from vacuolar invertases, while FEHs evolved from cell wall invertases within the family 32 of Glycoside Hydrolases (GH32) (Lasseur et al., 2009; Le Roy et al., 2013). They typically contain highly conserved consensus amino acid motifs including the  $\beta$ -fructosidase motif (DPN) and the RDP and EC motifs harboring the three crucial acidic amino acids in the active site (Van den Ende et al., 2009).

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