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Highlight

The fructose transporter *At*SWEET17 supports Arabidopsis shoot branching by increasing mobilization of carbohydrates from vacuoles to supply the newly forming inflorescence branch, thereby maintaining efficient reproduction under drought stress.

Abstract

Sugars Will Eventually be Exported Transporters (SWEETs) are the most recently discovered family of plant sugar transporters. By acting as uniporters, SWEETs facilitate the diffusion of sugars across cell membranes and play an important role in various physiological processes such as abiotic stress adaptation. *At*SWEET17, a vacuolar fructose facilitator, was shown to be involved in the modulation of the root system during drought. In addition, previous studies have shown that overexpression of an apple homolog leads to increased drought tolerance in tomato plants. Therefore, SWEET17 might be a molecular element involved in the plant´s drought response. However, the role and function of SWEET17 in aboveground tissues of Arabidopsis under drought stress remains elusive. By combining gene expression analysis and stem architecture with the sugar profiles of different aboveground tissues, we uncovered a putative role of SWEET17 in carbohydrate supply and thus cauline branch elongation, especially during periods of carbon limitation, as occurs under drought stress. Thus, SWEET17 seems to be involved in maintaining efficient plant reproduction under drought-stress conditions.

Keywords

abiotic stress, branching, drought, fructose, inflorescence, SWEET17, transporter, vacuole

Abbreviations

field capacity	FC
fresh weight	FW
dry weight	DW

Introduction

As sessile organisms' vascular plants are constantly exposed to changing environmental conditions that can alter either rapidly, or gradually. Therefore, plants must constantly precept, react and adapt to changing abiotic stimuli (Kleine et al., 2021; Schwenkert et al., 2022).

As plant metabolism adapts, environmental conditions can affect important factors such as plant size and phenotype, biomass accumulation, and overall yield. One abiotic factor that markedly impairs plant growth and development is drought. Drought stress occurs for a variety of reasons, including low rainfall, high and low (below freezing) temperatures, high soil salinity, or high light intensity. From an agricultural and physiological perspective, drought stress sets in when water availability decreases due to low soil moisture or when the rate of transpiration from leaves exceeds the water uptake by the roots (Salehi-Lisar and Bakhshayeshan-Agdam, 2016). Due to the projected global warming and climate change, the frequency and intensity of drought stress will increase worldwide (Dai, 2013; Basu et al., 2016; Bashir et al., 2021). Therefore, the probability of yield loss due to exceptional drought events will increase by about 20% in the future and already exceeds 70% for several crops, such as soybean and corn (Leng and Hall, 2019). Plants react with a number of processes after onset, covering morphological, physiological, and biochemical adaptations. This systemic reprogramming aim to maintain homeostasis by decreasing water depletion and/or increasing cellular water uptake. Such adaptations may include increased root formation, onset of stomata closure, the relative decrease of shoot growth, and stimulation of sugar accumulation (Basu et al., 2016; Ahluwalia et al., 2021; Bashir et al., 2021; Seleiman et al., 2021).

The accumulation of sugars has been well documented in a variety of metabolic and transcriptomic analyses under drought stress (Rizhsky et al., 2004; Cramer et al., 2007; Urano et al., 2009). It is known that sugars act as compatible solutes and decrease the water potential of the cell to maintain water retention and a high cell turgor (Krasensky and Jonak, 2012; Takahashi et al., 2020). In addition, sugars stabilize proteins and membranes (Hoekstra et al., 2001) and act as radical scavengers to maintain cellular redox balance under conditions of increasing accumulation of reactive oxygen species (ROS) promoted by drought stress (Miller et al., 2010; Kaur and Asthir, 2017). Accordingly, to fulfill their function as protein/membrane stabilizers and ROS quenchers, sugars need to be distributed throughout the whole plant system and in different subcellular compartments under abiotic stress (Pommerrenig et al., 2018; Keller et al., 2021a). Accodingly, abiotic stresses, such as drought, lead to altered expression and activity of intra- and intercellular sugar transporters (Xu et al., 2018; Kaur et al., 2021).

Overall, the plant genome harbors a wide number of genes encoding carbohydrate-transport proteins that can be grouped into three major transporter families: the monosaccharide transporter-like (MST) family, the sucrose transporters (SUT/SUC), and the sugars will eventually be exported transporter (SWEET) proteins (Doidy et al., 2012; Pommerrenig et al., 2018; Wen et al., 2022). Of these three families, SWEETs are the most recently described transporter group (Chen et al., 2010) and to date, common features of all characterized SWEETs are their ability to mediate both influx and efflux of mono- and/or disaccharides at low sugar affinities (Chen et al., 2015). SWEET transporters generally exhibit seven transmembrane domains and most SWEETs are located at the plasma membrane (Ji et al., 2022). However, three of them, namely SWEET2, SWEET16, and SWEET17 have previously been shown to localize to the tonoplast (Chardon et al., 2013; Klemens et al., 2013; H.Y. Chen et al., 2015). Since the vacuole is the largest cellular organelle and because one of its main functions is the regulation of dynamic sugar storage and distribution, it does not surprise that especially vacuolar SWEET transporters show differential expression under abiotic stress conditions (Chardon et al., 2013; Klemens et al.,2013; Guo et al., 2014; H.Y. Chen et al., 2015; Ji et al., 2022).

Recently, SWEET17, a vacuolar transporter with high specificity for fructose (Chardon et al. 2013; Guo et al., 2014), was shown to be involved in fructose-stimulated modulation of the root system under drought and is therefore directly involved in the plant's drought response (Valifard et al., 2021). As *SWEET17* expression is not only confined to the root region and high expression levels could also be found in above-ground tissue, like the inflorescence stem (Guo et al., 2014), where its expression is explicitly confined to the vasculature (Chardon et al., 2013; Aubry et al., 2022), we focused on the role of this transporter in aboveground tissues under drought stress. To this end, we combined gene expression analysis, studies of the plant architecture and metabolite measurements of dissected Arabidopsis shoot tissues to reveal a possible involvement of SWEET17 in inflorescence branching under drought stress.

Materials and Methods

Plant cultivation and harvest

Wild types (Col-*0*) and two *sweet17* loss of function mutants (*sweet17-1* (SALK_012485.27.15.x) and *sweet17-2* (SAIL_535_H02); Chardon et al., 2013) were grown under different growth conditions based on the experimental design and purpose. For soil experiments, seeds were sown on standard soil (ED-73; Einheitserde Patzer; Sinntal-Altengronau, Germany) and plants were grown under short day conditions (10h light, 14h dark) with a light intensity of 125 µmol quanta m^{-2} s^{-1} at 21°C. To stimulate plants for initiation of reproductive growth, four-week-old

plants were transferred from short day to long day conditions (16h light, 8h dark) with the same light intensity and temperature as present at short days.

For growth in hydroponic culture, seeds were germinated on germination medium, which was filled in detached lids from Eppendorf reaction tubes containing little holes, as described by Conn et al., (2013). The agar-filled lids were placed floating on plastic boxes containing liquid germination medium in a way, that developing roots can grow through the agar and extend directly to the liquid medium. After one week of growth, liquid germination medium was gradually exchanged with basal nutrient solution in the same composition as described in Conn et al., (2013). The basal nutrient solution was replaced weekly to ensure constant nutrient levels and pH of the medium. Plant material was harvested at the time points noted in the corresponding figure legends and if applicable was separated in the different aboveground-tissues leaf, stem, branch, flower and silique using a scalpel. Branch samples thereby represent primary cauline branches (CI). Plant material was directly frozen in liquid nitrogen after harvest and stored at -80°C until usage.

Application of drought and osmotic stress

To analyze the effects of drought stress on plant performance, drought was applied to the soil and hydroponic cultures based on different methods. For soil experiments, plants were exposed to drought conditions based on soil field capacity as explained in Valifard et al., (2021). Therefore, plants were kept at a determined water content in the soil, adjusted to a field capacity of either 100% (control) or 50%. The water content in the soil was checked and adjusted at 48-hour intervals until harvest.

To apply and analyze the short-term effects of drought, artificial drought stress was applied to plants grown in hydroponic systems using polyethylene glycol 8000 (PEG 8000). Therefore, four-week-old plants grown in hydroponics were exposed to -0.5 MPa osmotic potential by an exchange of the basal nutrient solution with basal nutrient solution containing 0.2 g of PEG 8000 per g of solution, according to equations by Michel, (1983). Thereby, the exchange of the medium to the PEG solution marked timepoint zero of the analysis.

Carbohydrate extraction and quantification

Frozen plant material was ground using a mortar and pestle. Carbohydrates were extracted as described in (Keller et al., 2021b). Briefly, 50 mg of pulverized plant material was extracted in 80% ethanol at 80°C for 30 minutes. After centrifugation (5min, 14000rpm), the supernatant was transferred into a new reaction tube and evaporated using a vacufuge concentrator (Eppendorf, Hamburg, Germany). The pellet remaining after evaporation was resolved in $_{dd}H_2O$. Sediments

remaining from the carbohydrate extraction were washed with 80% ethanol and $_{dd}H_2O$ twice and used for starch digestion. For that, 200 µl $_{dd}H_2O$ were added to the washed pellet and samples were autoclaved for 40 minutes at 121°C. For hydrolytic cleavage of the starch, 200 µl of an enzyme mixture (5 U α-Amylase; 5 U Amyloglucosidase; 200 mM Sodium-Acetate; pH 4.8) was added to the autoclaved pellet and the mixture was incubated at 37°C for at least four hours followed by heat inactivation of enzymes at 95°C for ten minutes. Quantification of the extracted sugars (glucose, fructose, sucrose) and the hydrolyzed starch was performed using a coupled enzymic test (spectrophotometric analysis) as described in Stitt et al., (1989).

Histological localization of *SWEET17*

The tissue localization of *SWEET17* was monitored by histochemical analysis of transgenic plants, expressing the GUS (b-GLUCURONIDASE) reporter gene under control of the *SWEET17* promotor region (Valifard et al., 2021). Therefore, transgenic *ProSWEET17:GUS* plants were grown under short day conditions for four weeks and were transferred to long day conditions, followed by an application of drought stress at 50% FC for additional four weeks. Tissues of eight-week-old plants were stained by 5-bromo-4-chloro-3-indolyl-β-glucuronic acid (X-Gluc) solution according to Chardon et al., (2013) and the tissue localization of the *ProSWEET17:GUS* was documented using a Nikon SMZ1111 stereomicroscope combined with a ProgResC3 camera and the ProgResCapturePro 2.8 software (Jenoptik, Jena, Germany). To create thin sections of tissues, stained samples were dehydrated and embedded in Technovit 7100 resin (Kulzer, Hanau, Germany) as previously described by De Smet et al., (2004). Cross sections of four to 5.5 µm were prepared using a Reichert-Jung Biocut 2030 Microtome (Leica biosystems, Nußloch, Germany) and sections were observed as described above.

Determination of reproductive growth parameters and yield

For determination of reproductive growth parameters and yield, total inflorescence height, as well as the length and number of all primary cauline branches (CI) with a minimum length of 1 cm, were measured on eight-week-old plants. For determination of the seed weight per plant, inflorescences of single plants were covered with paper bags as soon as all flowers turned to siliques. After ripening, seeds of single plants were harvested separately and the seed weight per plant was determined for ten individual plants of each line. From those ten individual plants, seeds of five plants were used to count and weight 500 seeds to determine the 500 seed weight.

Determination of branch elongation with sugar supply

For analysis of branch elongation on supply of different sugars, wild types and *sweet17* lines were grown under short-day conditions for four weeks and transferred to long-day conditions afterwards. Approximately seven days after transfer to long-day conditions, primary cauline branches started to emerge from the inflorescence stem. 13 to 15 newly emerging primary cauline branches (CI) from first and second nodes of approximately 5 mm length were excised from each line and placed on agar plates containing half-strength MS containing either no sugar or supplied with 30mM glucose, 30mM fructose or 30 mM sucrose. Thereby, branches were excised containing approximately 5 mm of the main inflorescence stem below and above the branch, similar to the analysis of branch emergence performed by Fichtner et al., 2017. Any cauline leaves were removed from the sections. To inhibit growth of bacteria or fungi, the plates also contained 200 µg/ml Carbenicillin and 50 µg/ml Nystatin. The agar plates were placed in an upright position with branches facing up. Each agar plate was imaged using an EPSON Perfection V330 Photo scanner (Epson, Suwa, Japan) in daily intervals until six days after excision and branch length was determined using ImageJ (Schneider et al., 2012). From initial branch lengths at day zero of observation, length increase in percent was calculated.

RNA extraction

Total mRNA was isolated from cauline branches and full rosettes of plants grown on soil and in hydroponic culture. Therefore, approximately 50 mg of ground tissue were extracted using the NucleoSpin RNA Plant Kit (Macherey-Nagel, Düren, Germany) following the user guidelines. Quality and quantity of the extracted RNA were photometrically checked using the NanoPhotometer N50 (Implen, München, Germany) and 1 µg of total mRNA was translated to cDNA using the iScript cDNA Synthesis Kit (Bio-Rad, Hercules, CA, USA) according to the instructions.

Expression analysis via RT-qPCR

Analysis of gene expression was performed by quantitative real time PCR and was carried out in a CF X96™ real time cycler (Bio-Rad, Feldkirchen, Germany) using a standard two-step protocol with an annealing/elongation step at 58°C for 45 seconds. For quantification, the fluorescent dye iQ SYBR® Green (Bio-Rad Laboratories, Feldkirchen, Germany) was used according to the manufacturer's guidelines. The calculation of relative gene expression was performed using a modified $2^{-\Delta\Delta CT}$ method (Livak and Schmittgen 2001). For transcript normalization the protein phosphatase 2A (PP2AA3; *AT1G13320*) and the SAND family protein (*AT2G28390*) were used

as reference genes (Czechowski et al., 2005). Primers including their primer efficiencies used for expression calculation are documented as Supplementary Table S1.

Results

SWEET17 is transiently expressed in shoot tissue during drought stress

It is well known that plants accumulate sugars after drought exposure to mitigate the destructive effects of osmotic stress (Fulda et al., 2011; Sami et al., 2016). Therefore, especially tonoplast sugar transporters are stimulated under drought and osmotic stress, leading to an increased sugar distribution via an accumulation of sugars in the vacuole (Kaur et al., 2021; Keller et al., 2021a). One of those vacuolar transporters is SWEET17, whose expression was shown to be upregulated in specific root cells and involved in the initiation of lateral root development under drought stress (Valifard et al., 2021). While the role and function of SWEET17 under drought stress was recently described in the root tissue (Valifard et al., 2021), little is known about the function of the transporter in aboveground tissues under similar stress conditions.

We therefore aimed to elucidate the role of SWEET17 in the response of aboveground tissues to drought stress by conducting gene expression analysis under those stress conditions. To this end, wild types were grown in hydroponic culture for three weeks and treated with PEG 8000 to induce a controlled stress at an osmotic potential of -0.5 MPa, and full rosettes were harvested at different time points during the treatment. It turned out that *SWEET17* transcript levels increased significantly in the shoot as early as one hour after the onset of osmotic stress (Figure 1A), reached about three to four-fold abundance until twelve hours of stress, before returning to pre-stress levels after one day of treatment (Figure 1A). Thus, *SWEET17* gene expression resembles the expression patterns of the known drought-induced vacuolar transporters *TST2* and *TST1* (Wormit et al., 2006) (Supplementary Figure S1).

sweet17 mutants exhibit substantial accumulation of fructose during drought stress

Because SWEET17 activity is linked to fructose transport and sugar accumulation in roots under drought stress, we were interested in studying corresponding effects in shoots. To investigate the effects of SWEET17 deficiency on the sugar content of aboveground tissues under drought, full rosettes of the well-characterized *sweet17-1* knock out line (Chardon et al., 2013; Valifard et al., 2021) and wild-type plants, grown in hydroponics under PEG 8000 induced osmotic stress, were analyzed (Figure 1B).

Three-week-old rosette tissue of both, wild types and *sweet17* mutants, exhibited accumulation of glucose starting twelve hours after the addition of PEG. Glucose contents peaked at 36 and 72 hours after the onset of stress, followed by a decrease of glucose levels at 96 and 120 hours under drought in wild types and *sweet17-1* mutants, respectively (Figure 1B). Although glucose content decreased after 96 hours of osmotic stress, it was still significantly higher than before the onset of the stress treatment in both lines (Figure 1B). Nevertheless, the accumulation of glucose in rosettes of wild types and *sweet17-1* mutants under osmotic stress was comparable (Figure 1B). Unlike glucose, fructose accumulation could only be observed in rosettes of *sweet17-1* mutants under stress treatment. At each analyzed time point after the onset of osmotic stress, the fructose content was significantly higher in *sweet17-1* rosettes than in corresponding wild-type samples (Figure 1B). Starting from 0.76 µmol g^{-1} DW in wild types, fructose increased to a maximum of 1.87 µmol g^{-1} DW and 2.08 µmol g^{-1} DW after 36 and 96 hours under PEG-induced drought, respectively. In contrast, endogenous fructose content in the *sweet17-1* mutant was 0.63 µmol g^{-1} DW and increased to remarkable 16.55 µmol g^{-1} DW within the first 36 hours after the application of PEG, a value nearly nine times the wild-type level (Figure 1B). The levels of sucrose and starch showed comparable changes after exposure to a reduced water potential as observed for glucose contents in wild types and the *sweet17-1* mutant. For both metabolites, a significant increase was observed in wild types and *sweet17-1* no later than 36 hours after the onset of stress and remained high throughout the treatment (Figure 1B and Supplementary Figure S2). Similar to glucose, sucrose and starch contents tended to be higher in wild types than in *sweet17-1* plants (Figure 1B, Supplementary Figure S2). Nevertheless, differences in glucose, sucrose and starch contents between wild types and *sweet17-1* are minor compared to differences in the fructose content after PEG-induced drought stress (Figure 1B).

Loss of *SWEET17* results in altered sugar profiles in the inflorescence and branches

Since *SWEET17* expression was shown to be upregulated in aboveground tissues under PEG-induced drought stress (Figure 1A) and since loss of *SWEET17* severely affects drought-related sugar profiles (Figure 1B), we wanted to investigate which of the aboveground tissues are most affected by *SWEET17* deficiency under natural drought stress by water limitation. This analysis was of special importance since *SWEET17* expression is highest in the inflorescence stem (Guo et al., 2014). To this end, *sweet17-1*, *sweet17-2* and wild types were grown on soil under short day conditions for four weeks and subsequently transferred to long day conditions to initiate reproductive growth. With the shift in growth conditions, plants were subjected to water limitation to 50% field capacity (FC) or 100% FC, respectively for four weeks afterwards. Eight-week-old

plants then were subsequently dissected into the tissues: leaves, stems, primary cauline branches (CI), flowers and siliques prior to the extraction of sugars and starch (Figure 2). Our analysis revealed that overall glucose and sucrose concentrations were highest in the siliques of wild types, while glucose concentrations were lowest in the leaves and sucrose concentrations were lowest in branches (Figure 2A and 2C).

As observed earlier, glucose contents were increasing in leaf tissues upon drought treatment in wild types as well as in *sweet17* mutants, and overall glucose levels were comparable between all lines (Figure 2A). In stems, primary cauline branches, flowers and siliques no increase of glucose could be observed in any of the plant lines after growth at 50% FC. In addition, *sweet17* mutants exhibited lower glucose contents than wild types in those tissues (Figure 2A). Regarding fructose, the highest contents could always be observed in *sweet17* mutants, especially upon drought stress at 50% FC (Figure 2B), while wild types did not show any accumulation of fructose under drought in any of the analyzed tissues (Figure 1B, Figure 2B). The biggest differences in fructose contents between wild type and *sweet17* plants could be observed in stems and cauline branches under control, as well as under drought conditions. Thereby, the concentration of fructose was already five- to 5.5-fold higher in *sweet17-1* stems and cauline branches than in corresponding wild type tissues under unstressed conditions and increased to approximately seven times the concentration of wild types under drought stress, indicating an important role of the transporter in these tissues particularly under drought (Figure 2B).

Unlike fructose, sucrose contents were lower in stems, cauline branches, flowers and siliques of *sweet17* mutants when compared to corresponding wild type tissues under unstressed conditions (Figure 2C). In leaves, sucrose contents were comparable between the different plant lines (Figure 2C). Drought stress led to an increase in sucrose contents in leaves and flowers of all tested lines, while in stems, cauline branches and flowers sucrose concentrations increased solely in *sweet17* mutants, resulting in levels comparable to those of the wild types at 50% FC (Figure 2C). In contrast to that, in siliques, a significant increase in starch could be observed in all lines when exposed to drought, while starch contents decreased in the leaves of the wild type (Figure 2D). Overall starch levels were comparable between wild types and mutant plants except for the leaf tissue since mutant plants showed at least twice as high starch contents as present in wild types under each condition (Figure 2D).

SWEET17 is expressed in the inflorescence stem during drought stress and branch formation

To investigate the tissue distribution of *SWEET17* in Arabidopsis, especially in stems and cauline branches of the inflorescence where differences in fructose contents between wild types and *sweet17* mutants are most pronounced (Figure 2B), transgenic lines carrying the promotor region of the *SWEET17* gene fused to the β-glucuronidase reporter gene (*ProSWEET17:GUS*) were used (Valifard et al., 2021).

Histochemical localization of *ProSWEET17:GUS* in eight-week-old flowering plants demonstrated *SWEET17* promotor activity throughout the upper inflorescence under unstressed conditions and when plants were exposed to drought stress (50% FC; Figure 3A and 3B). Although the blue signal appeared throughout the whole upper inflorescence, *SWEET17* tissue localization analysis performed on cross sections of inflorescence stems revealed *SWEET17* promotor activity mostly in the xylary system along with faint signals in the cortex and the pith parenchyma (Figure 3C). However, this distribution pattern was more pronounced in plants exposed to drought stress, with a strong blue signal observed in the pith region (Figure 3D). Interestingly, when the cross-sections represented areas where primary cauline branches connect to the main inflorescence stem, the blue GUS-signal could strongly be observed in the cortex in connecting areas of the outgrowing branch (Figure 3E, as indicated by arrows). Latter staining pattern was also visible in plants exposed to drought stress (Figure 3F), suggesting a role of SWEET17 in the formation of cauline branches, especially where cortex parenchyma is re-differentiated to initiate meristematic cells required for branch development.

sweet17 mutants exhibit reduced elongation of cauline branches and lower seed yield per plant

Our analyses so far showed that *SWEET17* expression is drought induced and is present at sites of branch outgrowth (Figure 3). Interestingly, when comparing wild types and *sweet17* mutants under unstressed and especially drought stress conditions, cauline branches also showed most marked differences in their sugar composition (glucose and fructose) (Figure 2). Next, we analyzed effects of lacking SWEET17 activity on inflorescence morphology under control (100% FC) and drought conditions (50% FC).

We observed that mutant plants exhibited an overall shorter inflorescence under both, well-watered and drought stress conditions, when compared to corresponding wild type plants (Figure 4A-C). However, under drought stress, wild type and mutant plants showed reduced inflorescence

heights when compared to control conditions, with *sweet17* inflorescences being significantly shorter than that of wild types (Figure 4C). Unlike inflorescence height, the number of primary cauline branches with a minimum length of 1 cm did not differ between wild type and mutants under control conditions (Figure 4D). When exposed to drought stress, the number of cauline branches >1 cm was significantly reduced in all lines (Figure 4D). However, this decrease was more pronounced in *sweet17* mutants (Figure 4D). Similar behavior was observed for the mean length of primary cauline branches (Figure 4E). While only *sweet17-2* mutants showed significantly shorter primary cauline branches than wild types at 100% FC, at 50% FC branch length was reduced in all lines. There, both *sweet17* mutant lines showed significantly reduced primary cauline branch lengths when compared to the wild type (Figure 4E).

To clarify, whether the reduced number of CI branches, as observed in Figure 4D is due to a reduced number of cauline nodes or empty axils, we extended our analysis and quantified the total number of cauline nodes in wild types and *sweet17* mutants grown at 100% FC and 50% FC, respectively (Supplementary Figure S3). In this analysis, we were able to reproduce the result of a lower inflorescence height in *sweet17* mutants in comparison to the wild type under 100% FC and 50% FC conditions (Supplementary Figure S3A-B and S3D), as well as a reduced number of primary cauline branches (> 1 cm), and a lower CI branch length in *sweet17* mutants under drought stress (Supplementary Figure S3E and S3F). However, the number of cauline nodes did not differ significantly between wild types and *sweet17* mutants under any of the analyzed conditions (Supplementary Figure S3G). Therefore, differences in the number of primary cauline branches (> 1 cm) between wild types and *sweet17* plants rather derive from reduced branch length of CI branches, as some of those appear to be shorter than 1 cm in *sweet17* mutants (Supplementary Figure S3C), than a reduced number of cauline nodes. A lack of functional SWEET17 protein therefore influences branch elongation rather than branch number, especially under drought stress.

Overall, already under control conditions, in *sweet17* mutants a lower inflorescence height and the observed reduced branch length resulted in a decreased seed yield per plant (Figure 4F), while showing similar 500 seed weight (Figure 4G) as wild types. A decrease of seed yield could also be observed in wild types under drought conditions (Figure 4F). This negative effect was more severe in *sweet17* mutants (Figure 4F).

Expression of key regulators of branching and branch elongation are altered in *sweet17* mutants

The observation that *sweet17* mutants exhibit shorter primary cauline branches, especially under drought stress (Figure 4), prompted us to investigate the expression of key transcription factors regulating branch initiation and branch elongation (Figure 5). The process of branching is regulated by many different factors, including light phases, developmental stages, sugar availability and hormones like cytokinins and strigolactone (Rameau et al., 2015; Barbier et al., 2019). Accordingly, the complex regulation required for this process comprises different transcription factors.

One of these transcription factors is *BRANCHED1* (*BRC1*), an inhibitor of bud outgrowth that maintains bud dormancy (Aguilar-Martinez et al., 2019). Interestingly, *BRC1* expression was higher in *sweet17-2* mutants compared with wild types under unstressed conditions and drought stress led to an induction of *BRC1* expression especially in the *sweet17* mutants (Figure 5A).

In Arabidopsis, a series of bHLH (basic helix-loop-helix) transcription factors including ACTIVATOR FOR CELL ELONGATION1-3 (ACE1-3), PACLOBUTRAZOL-RESISTANT1 (PRE1) and INCREASED LEAF INCLINATION1 BINDING bHLH1 (IBH1) have been identified as regulators of cell elongation in response to environmental factors and developmental stages (Ikeda et al., 2012; Zhiponova et al., 2014; Wang et al., 2018). The expression of *ACE1* and *PRE1*, both being inducers of cell elongation, were already significantly reduced in *sweet17-2* mutants under control conditions (Figure 5B and 5C). Under drought, *ACE1* expression did not change in any of the analyzed lines, therefore *sweet17-2* still showed significantly reduced expression values when compared to the corresponding wild type (Figure 5B). Like *ACE1* expression, also *PRE1* expression was significantly reduced in *sweet17-2* plants in comparison to wild types under control conditions (Figure 5C). Under drought stress, overall *PRE1* levels were slightly but non-significantly reduced in all analyzed lines, with both *sweet17* lines showing the lowest *PRE1* expression levels (Figure 5D). Expression profiles of *IBH1* did not differ between *sweet17* mutants and wild types under unstressed conditions (Figure 5D). However, under drought stress *IBH1* expression was significantly induced in both *sweet17* mutants leading to significantly higher expression values than in wild types (Figure 5D).

Fructose supply can rescue deficits in branch elongation in *sweet17* mutants

Given that *sweet17* mutants exhibit altered expression of branch regulators (Figure 5), we wanted to clarify whether altered branch development in *sweet17* mutants is solely due to a lack of fructose availability. Therefore, we excised newly emerging primary cauline branches of the first and second node from wild types and *sweet17* lines and analyzed branch elongation on agar plates containing no sugars or 30 mM of glucose, fructose, or sucrose (Figure 6). Especially when grown on agar plates lacking any additional sugar, *sweet17* mutant lines showed clear deficits in branch elongation three to six days after excision (Figure 6A). Supply of sugars to the medium in general had growth stimulatory effects in all lines (Figure 6B-D). Anyhow, only fructose supply was able to rescue the growth deficit of *sweet17* branches in comparison to the wild type (Figure 6B). Glucose and sucrose supply, on the other hand, stimulated branch elongation also of *sweet17* lines but mutants showed significantly reduced branch elongation at five and six days after excision in comparison to the wild type (Figure 6C and 6D).

Discussion

The functions of sugars in plant metabolism are manifold. Sugars not only represent the main source of cellular energy and precursors of several important and abundant metabolites, but they also represent the major transport form of nutrients and energy, are involved in post-translational modification of proteins and lipids, play important roles in signal transduction, act as compatible solutes and represent efficient quenchers for reactive oxygen species (ROS). Latter abilities make sugars important components of the complex plant stress resistance program (Ruan et al., 2014; Keller et al., 2021a; Ji et al., 2022). Therefore, the ability to store and transport sugars intra- and intercellular is essential for the plant's adaptation to its environment and has an impact on the plant's developmental processes (Wingenter et al., 2010; Klemens et al., 2013, Klemens et al., 2014; Patzke et al., 2019; Rodrigues et al., 2020; Guo et al., 2023).

Plant sugar sensing is a well-described process and leads to the adjustment of the expression of a wide number of genes (Rolland et al., 2002; 2006). The best characterized plant sugar sensing system is represented by the sensor protein HEXOKINASE1 (Xiao et al., 2000; Moore et al., 2003), which connects changes in the cytosolic glucose concentration to altered transcription efficiency of nuclear-located genes (Cho et al., 2006). Thus, it is not surprising that especially the subcellular composition of sugars affects the development of both, soil-located and aboveground plant organs (see e.g., Tjaden et al., 1998, Patzke et al., 2019, Valifard et al., 2021; Guo et al.,

2023). Detailed analyses of various mutants revealed that especially the activity of vacuolar sugar transporters is important for the control of cytosolic sugar levels (Wormit et al., 2006; Wingenter et al., 2010; Poschet et al., 2011; Klemens et al., 2013).

In line with these facts is the observation that the vacuolar fructose facilitator SWEET17 (Chardon et al., 2013; Guo et al., 2014) is critical for the initiation of lateral root formation, especially under drought stress (Valifard et al., 2021). SWEET17 was shown to be one of the 17 members of the SWEET family in Arabidopsis and, like SWEET2 and SWEET16, SWEET17 is located at the vacuolar membrane (Chardon et al., 2013; Klemens et al., 2013; Chen et al., 2015; Eom et al., 2015). Homologous genes of *AtSWEET17* were shown to be upregulated in other species in response to a range of environmental stress stimuli, including salt, osmotic and drought stress (Zhou et al., 2018; Lu et al., 2019). Therefore, it is not surprising that also *AtSWEET17* gene expression exhibits strong induction upon drought stress, regardless of the tissue analyzed (Figure 1A; Valifard et al., 2021).

Since SWEET17 was shown to act as a fructose facilitator, loss-of-function of this transporter, which preferentially acts as a vacuolar exporter under unfavorable conditions (Guo et al., 2014; Chandran 2015), results in accumulation of fructose in the vacuole and thus a higher total cellular fructose content (Figure 1B, Figure 2B; Chardon et al., 2013). The opposite reaction was observed in SWEET17-overexpressor plants, which showed significantly lower fructose contents in comparison to the wild type, especially when grown in a challenging environment (Guo et al., 2014).

Similar to other stress stimuli, osmotic stress leads to homeostatic imbalances in plant cells quickly after its onset (Kollist et al., 2019). Consequently, plants must adapt to these challenging conditions, which occurs at various levels comprising alterations in morphology, metabolism and gene expression. To counteract the deleterious effects of severe drought stress, plants accumulate high levels of osmoprotective compounds, such as proline and various sugars to restore their osmotic balance (Gurrieri et al., 2020; Keller et al., 2021a). This general response nicely fits with the observation that drought stressed Arabidopsis plants accumulate glucose and sucrose (Figure 1B, Figure 2).

Interestingly, only *sweet17* mutants were able to accumulate fructose under drought stress conditions (Figure 1B, Figure 2). As fructose accumulating in vacuoles mainly originates from sucrose cleavage via vacuolar invertases, those findings indicate an essential function of the vacuolar invertase during adaptation to drought. Latter conclusion is fully in line with the generally

important function of vacuolar invertase for sucrose hydrolysis in Arabidopsis under various conditions (Vu et al., 2020). Moreover, as shown in mono- and dicot species, drought induces vacuolar invertase gene expression and the resulting enzyme activity is a critical element of the response to drought stress (Kakumanu et al., 2012; Chen et al., 2021). Vacuolar sucrose, the substrate of invertases, originates from an increased activity of vacuolar sugar transporters like TST1 and TST2, which's expression is known to be upregulated under drought stress (Supplementary Figure S1; Wormit et al., 2006). In wild types invertase cleavage products glucose and fructose can sufficiently be exported from the vacuole via sugar porters like SWEET17 (Chardon et al., 2013; Valifard et al., 2021) and ESL1 (Yamada et al., 2010; Slawinski et al., 2021), while in the vacuole of *sweet17* plants fructose remains to be trapped to a higher extend, leading to the observed fructose levels (Figure 1B, Figure 2B).

Drought induced differences in fructose accumulation between wild types and *sweet17* plants as well as *SWEET17* expression is most pronounced in cauline branches (Figure 2B, Figure 3A and 3B). These changes are in line with our and previous observations revealing high expression of *SWEET17* in the xylem parenchyma of the inflorescence stem (Figure 3C; Guo et al., 2014). In those cells, SWEET17 is involved in the maintenance of fructose homeostasis to sustain the formation of xylem secondary cell wall (Aubry et al., 2022).

Both *SWEET17* transcript and SWEET17 protein were also detected in the cortex (Figure 3C; Guo et al., 2014; Aubry et al., 2022; Hoffmann et al., 2022) and the pith (Figure 3D; Hoffmann et al., 2022) of the stem, whereby expression of *SWEET17* in the pith is promoted under drought stress. Key characteristics of pith cells are their large size, large vacuoles and the fact that pith cells are surrounded by vasculature (Lev-Yadun, 1994; Zhong et al., 2000; Keller et al., 2021b), making them an ideal storage tissue. In addition, a variety of sugar transporters, as e.g. carbohydrate transporters of the EARLY RESPONSE TO DEHYDRATION SIX-LIKE (ERDL) and SUCROSE TRANSPORTER (STP) families, which are known to be expressed in the inflorescence stem, show high expression levels in the pith of this organ (Shi et al., 2021; Dinant and Le Hir, 2022). Therefore, the pith and in particular its subcellular sugar distribution may play an important role in plant developmental processes, such as the development of the vascular system, a process that is clearly influenced by sugar signaling and thus by sugar availability and distribution (Dinant and Le Hir, 2022). In accordance with suggestions by Dinant and Le Hir (2022), increased *SWEET17* expression in the pith allows fructose to be mobilized from vacuoles and serve as a carbohydrate source for local sinks such as the xylem tissue (Spicer 2014; Aubry et al., 2022). However, not only vascular tissue but also buds of cauline branches represent local

sinks. Thus, increased expression of *SWEET17* could support bud outgrowth and branch development. This hypothesis gains support by strong *SWEET17* expression in the cortex, especially where cauline branches are connected to the main stem (Figure 3E and 3F). This expression pattern resembles *SWEET17* expression in the outgrowing region of lateral roots where fructose specifically mobilized from vacuoles via SWEET17 is involved in the controlled initiation of lateral root formation (Valifard et al., 2021).

Shoot branching, like root development (Takahashi et al., 2003), is stimulated by the availability of sugars (Rabot et al., 2012; Mason et al., 2014; Barbier et al., 2015; Fichtner et al., 2017; Barbier et al., 2019). Sugar availability, as well as auxin-, strigolactone- and cytokinin levels exert influence on the process of branching (Thimann and Skoog 1933; Dun et al., 2012; Rameau et al., 2015; Balla et al., 2016; Dierck et al., 2016; Barbier et al., 2019). All these factors trigger changes in *BRANCHED1* (*BRC1*) expression, a central regulator of shoot branching, because it inhibits bud outgrowth and maintains bud dormancy (Aguilar-Martinez et al., 2019). *BRC1* expression under both, control and drought conditions was found to be higher in *sweet17* mutants when compared to corresponding wild types (Figure 5A). This went along with a lower number of primary cauline branches (> 1 cm) in mutant plants under drought (Figure 4B and 4D) and because *BRC1* expression was shown to be downregulated by external sucrose (Mason et al., 2014), it is reasonable to expect additional regulation by the supply of fructose and glucose. However, in our analysis we showed that differences in the number of primary cauline branches (> 1cm) are rather due to differences in branch elongation. As bud emergence was not analyzed in greater detail, we cannot exclude that also differences in bud outgrowth might contribute to the observed delay in the growth and development of primary cauline branches (Figure 4E and Supplementary Figure S3E). Anyhow, such differences are likely, especially as we were able to observe a positive correlation in the branch elongation pattern between wild types and *sweet17* mutants with *BRC1* expression when grown at 100% FC or under drought stress at 50% FC (Figure 4E and 5A). *Sweet17-2* plants that showed significantly increased *BRC1* expression under 100% FC showed significantly shorter primary cauline branches under the same conditions, while significantly higher *BRC1* transcript levels in *sweet17* mutants at 50% FC likely contributed to the decreased CI branch length of the same plants (Figure 4E and 5A). Thus, increased fructose mobilization by high expression of *SWEET17*, as occurring under drought, likely leads to a suppression of *BRC1* which stimulates branching.

Elongation and growth of plant cells is regulated by a tri-antagonistic series of helix-loop-helix (bHLH) transcription factors including ACTIVATOR FOR CELL ELONGATION1-3 (ACE1-3),

PACLOBUTRAZOL-RESISTANT1 (PRE1) and INCREASED LEAF INCLINATION1 BINDING bHLH1 (IBH1) (Bai et al., 2012; Ikeda et al., 2012; Zhiponova et al., 2014; Wang et al., 2018). Expression of these factors differed significantly between wild types and *sweet17* mutants, especially under drought treatment (Figure 5B-D). Thereby, reduced expression of the positive regulators *ACE1* and *PRE1* as well as an increased expression of the cell elongation inhibitor *IBH1* resulted in a decreased branch length in *sweet17* mutants, especially under drought stress (Figure 5B-D). As the expression of the tri-antagonistic signaling cascade can be influenced by various environmental factors (Bai et al., 2012), it is reasonable to expect regulation of these genes by sugar availability. Differences in the expression of such cell growth regulators between wild types and *sweet17* plants reinforce the idea of a possible involvement of SWEET17 not only in shoot branching but also in branch elongation.

With the help of plate experiments we were able to get valuable insights whether defects in branch development in *sweet17* mutants are likely due to impaired cell-to-cell carbon distribution before phloem loading or cell-to-cell distribution of carbohydrates in meristem-related regions post phloem transport. Thereby, supply of glucose, fructose and sucrose stimulated the overall branch growth. Anyhow, *sweet17* mutants, as already observed in vivo (Figure 4E), showed significantly reduced branch elongation when grown on agar without any sugars, but also under glucose and sucrose supply (Figure 6A, 6C and 6D). Only fructose supply was able to rescue growth deficits of *sweet17* branches, underlining the importance of fructose in the developmental process of branch elongation (Figure 6B), similar as observed for lateral root growth (Valifard et al., 2021). Based on the observed growth defects in excised branches it appears likely that defects in branch elongation are rather due to defects in the cell-to-cell distribution of carbohydrates post phloem transport, given an even distribution of carbohydrates to branches in wild types and *sweet17* mutants due to excision and placement on agar (Figure 6). Therefore, it is highly likely that SWEET17 is involved in the export of sucrose degradation products from the vacuoles of developing branch tissue, providing sugar as a building block for development. In potato it was shown that sucrose supply stimulates the outgrowth of lateral buds (Salam et al., 2021) and that such stimulation went along with an increase in vacuolar invertase activity. Similar to *sweet17* mutants, potatoes defective in vacuolar invertases show a decreased number of lateral branches and reduced branch elongation (Salam et al., 2021), underlining the importance of sucrose degradation products such as fructose for local stimulation of development.

During drought, *sweet17* mutants showed impaired biomass accumulation because of a limited water uptake ability caused by lower root biomass (Valifard et al., 2021). Low water availability

usually results in metabolic impairments such as decreased photosynthesis (Pinheiro and Chaves, 2011) and altered long-distance solute transport (Keller et al., 2021a). Together these factors result in inhibition of growth and therefore accumulation of sugars in leaf blades (Chaves and Oliveira, 2004) as observed in drought affected *sweet17* mutants (Figure 2). While sugars are synthesized and accumulate in source tissues, sink tissues like roots or siliques rely on carbohydrate distribution via the phloem, which is impaired under drought stress. In accordance, *sweet17* mutants accumulated higher carbohydrate contents in the leaves, while siliques showed lower contents of glucose and sucrose than the corresponding wild types under drought (Figure 2), highlighting a possible involvement of *sweet17* in carbohydrate distribution to branches and reproductive organs. Due to impaired carbohydrate allocation from source tissues, especially the elongation of cauline branches is affected in *sweet17* mutants under drought stress (Figure 4D). As *sweet17* mutants overall tend to be more sensitive towards drought due to a reduced number of lateral roots (Valifard et al., 2021), it can not be ruled out that this effect is resulting from overall growth defects of *sweet17* lines under drought stress. Anyhow, branch elongation differed already between wild type and *sweet17* mutants when grown under control conditions, as seen in vivo (Figure 4E) as well as in plate assay of excised branches (Figure 6). Differences in branch elongation between wild types and *sweet17* mutants became more drastic during drought treatment (Figure 4E), indicating that this phenotype is rather not attributed to general growth deficits during drought, but to an important role of SWEET17 in cell-to-cell allocation of carbohydrates to meristematic active cells to fuel growth and development.

Conclusion

Overall, our results reveal high expression of *SWEET17* in the pith and cortex in areas of branch emergence of the inflorescence stem (Figure 1A and Figure 3). Further, we observed marked differences in the sugar profiles of the main inflorescence stem and cauline branches, between wild types and *sweet17* mutants (Figure 2), and differential expression of branching and branch elongation regulators (Figure 5). In summary, these results suggest a supportive role of SWEET17 in shoot branching. Reduced inflorescence height and a limited branch length in *sweet17* mutants resulted in lower seed yield per plant, indicating an important function of SWEET17 for plant reproduction. We believe that in wild types, when grown under drought conditions - in which sugar availability in sink tissues is limited by impaired photosynthesis and reduced functionality of the carbohydrate transport circuit (Li et al., 2017; Liang et al., 2020; Keller et al., 2021a) - SWEET17 might lead to increased mobilization of sugars from the vacuoles of the pith to maintain sufficient carbohydrate supply to lateral bud formation (Figure 7). Further,

SWEET17 is essential for post-phloem cell-to-cell distribution of sucrose cleavage products to meristematic active tissues (Figure 7) to provide energy and building blocks for proper inflorescence development, as indicated by an impaired branch elongation of *sweet17* mutants under control- (Figure 4E and Figure 6) and even under pronounced under drought conditions (Figure 4E). Therefore, our findings support the general assumption that SWEET proteins increase sugar mobilization to sink tissues during abiotic stress and therefore maintaining crop productivity (Anjali et al., 2021).

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Author Contributions

M.V., I.K., A.K. and J.B.: Investigation; H.E.N and M.V.: Conceptualization; M.V. and I.K.: Validation, Visualization; I.K.: Writing- original draft preparation; M.V., R.L.H., B.P. and H.E.N.: Writing- Review & Editing; H.E.N.: Supervision

Conflicts of interest

The authors declare no conflict of interest.

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Data Availability

All data supporting the findings of this study are available within the paper and within its supplementary materials published online.

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Figure legends

Figure 1: Drought-induced expression of SWEET17 and response of *sweet17-1* mutant plants to short-term drought stress. Plants were grown in hydroponic system for three weeks and seedlings were exposed to artificial drought stress produced by PEG8000 (Ψs = −0.5 MPa). Full rosette tissue was harvested at different time points after onset of drought treatment and used for determination of gene expression and sugar quantification. A) Expression profile of *SWEET17* in wild type plants under short term drought stress. *SWEET17* expression was quantified in relation to *PP2AA3* and *SAND* expression and normalized on its expression in an unstressed control. Bars represent the mean from n =3 biological replicates ± SE. Different letters indicate significant differences between timepoints according to one-way ANOVA with post-hoc Tukey testing ($p < 0.05$). B) Shoot sugar content of wild type and *sweet17-1* mutant plants grown under artificial drought stress. Bars represent the mean from n =3 biological replicates ± SE. Different letters indicate significant differences between the different lines and timepoints according to two-way ANOVA with post-hoc Tukey testing ($p < 0.05$).

Figure 2: Sugar and starch content in aboveground tissues of Arabidopsis wild type and *sweet17* mutants in response to drought stress. Seeds were sown on soil and grown under short day conditions for four weeks and then were transferred to long day conditions followed by application of drought stress at 50% FC. After eight weeks of growth plants were dissected in leaf, stem, branch, flower and siliques and contents of glucose (A), fructose (B), sucrose (C) and starch (D) were measured. Starch contents were determined as hydrolyzed glucose. Branch samples thereby refer to primary cauline branches (CI). Bars represent the mean from n = 3 biological replicates ± SE. Different letters indicate significant differences between the different lines and conditions according to two-way ANOVA with post-hoc Tukey testing ($p < 0.05$).

Figure 3: Expression pattern of *SWEET17* in Arabidopsis stem tissues. Histochemical localization of ProSWEET17:b-GLUCURONIDASE (GUS) activity in eight-week-old inflorescence stem of Arabidopsis plants grown at 100% FC (A, C, E) and under drought stress at 50% FC (B, D, F). Seeds were sown on soil and grown under short day conditions for four weeks and transferred to long day conditions followed by application of drought stress at 50% FC. GUS signal was detected in the pith, xylem parenchyma and cortex (C, D) especially in places of cauline branch development (E, F) in eight-week-old plants. Pictures show representative staining from three individual plants grown at 100% and 50% FC, respectively. Inflorescence stems were embedded in resin (Kulzer Technovit 7100) and cross sections of 4 µm (C, D, E) and 5.5 µm (F) thickness were analyzed. Scale bars represent 250 µm (A, B), 30 µm (C, D), 100 µm (E, F).

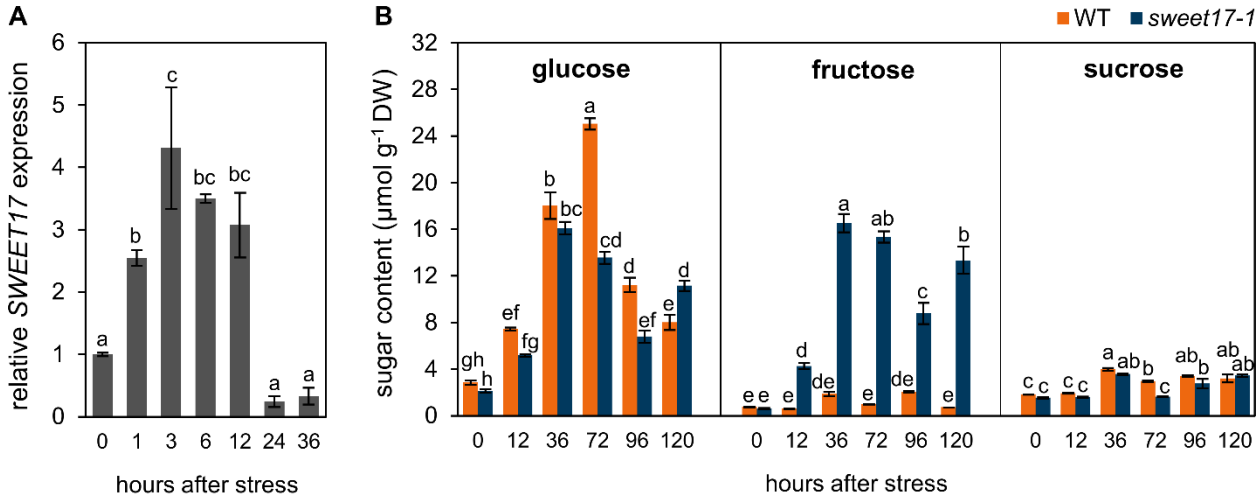
Figure 4: Phenotype of wild type and *sweet17* mutant lines exposed to drought stress at the reproductive stage. Comparison of inflorescence stem and branch development in sweet17 mutant and wild type plants grown at 100% FC (A) and under drought conditions at 50% FC (B), as well as inflorescence height (C), number of primary cauline branches (CI) bigger than 1cm (D) and length of primary cauline branches (CI) (E), seed yield per plant (F) and 500 seed weight (G).Seeds were sown on soil and grown under short day conditions for four weeks and transferred to long day conditions followed by application of drought stress at 50% FC. Pictures were taken and reproductive parameters were analyzed on eight-week-old plants. Center lines in boxplots of reproductive parameters show the median, crosses represent the sample means. Box limits indicate the 25th and 75th percentiles and whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles. Datapoints of n =15 biological replicates in (C-E), n =10 biological replicates (F) or n =5 biological replicates (G) are plotted as shaded circles. Different letters

indicate significant differences between the different lines and conditions according to two-way ANOVA with post-hoc Tukey testing ($p < 0.05$). Scale bars represent 5 cm (A, B).

Figure 5: Expression profiles of central regulators of branching and branch elongation in wild type and *sweet17* lines exposed to drought stress. For gene expression analysis seeds were sown on soil and grown under short day conditions for four weeks and transferred to long day conditions followed by application of drought stress at 50% FC. Primary cauline branches (CI) were cut from the main inflorescence stem of eight-week-old plants and used for RNA-extraction and following gene expression analysis. Expression of *BRC1* (A), *MAX2* (B), *ACE1* (C), *PRE1* (D) and *IBH1* (E) represents expression relative to *PP2AA3* and *SAND* and results were normalized on the expression of the wild type under 100% FC. Values represent the mean of n =3 biological replicates ±SE. Different letters indicate significant differences between the different lines and conditions according to two-way ANOVA wit post-hoc Tukey testing ($p < 0.05$).

Figure 6: Branch elongation of excised branches of wild type and *sweet17* lines on agar plates containing different sugars. For analysis of branch elongation on different sugars, wild types and *sweet17* lines were grown under short-day conditions for four weeks and transferred to long-day conditions afterwards. Newly emerging primary cauline branches (CI) on first and second nodes of approximately 5mm length were excised and placed on MS-agar plates containing no sugar (A), 30 mM glucose (B), fructose (C), or sucrose (D). Plates were placed in an upright position in long-day growth conditions and branch length was measured daily for six days and length increase in % was calculated. Values represent the mean of n =13-16 biological replicates ±SE. Asterisks indicate significant differences between the different lines and the wildtype at each individual timepoint according to Student t-test (with * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant).

Figure 7: Importance of SWEET17 in carbohydrate distribution from the pith and in cell-to-cell distribution for branch emergence and elongation.
SWEET17, a vacuolar fructose facilitator, is important for post-phloem transport of carbohydrates to demanding sink tissues such as meristems of developing cauline branches. There, fructose, deriving from sucrose cleavage in the vacuole, stimulates branch outgrowth and elongation by regulation of key integrators like *BRC1* and *ACE1*. Such carbohydrate distribution seems to be especially impaired in situations of reduced carbohydrate supply such as drought stress. Under such conditions, reserve sugars, accumulated in the pith of the inflorescence stem seem to be mobilized and exported from the vacuoles of this tissue via SWEET17 to maintain carbohydrate supply to demanding sinks. This figure was generated using BioRender.com



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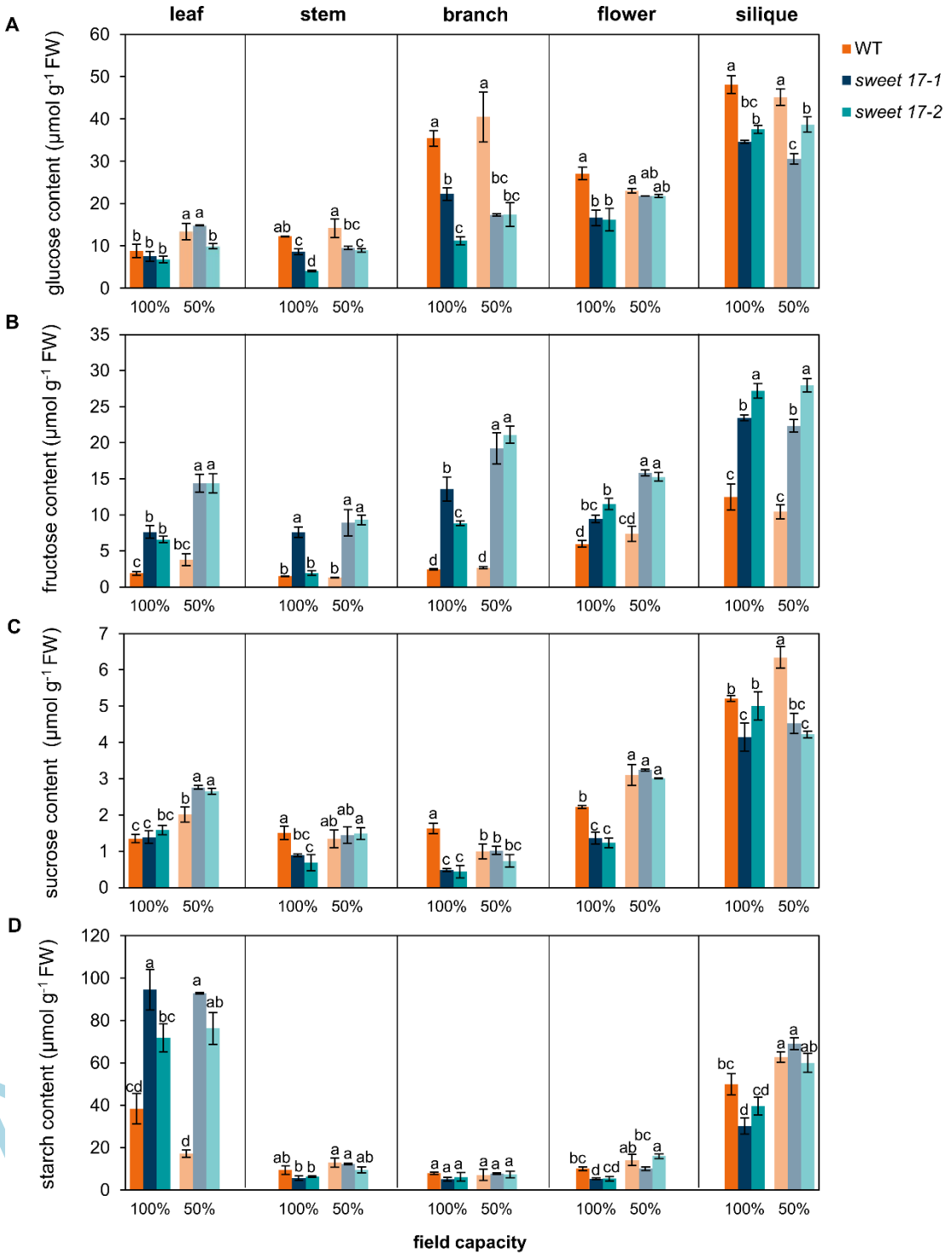

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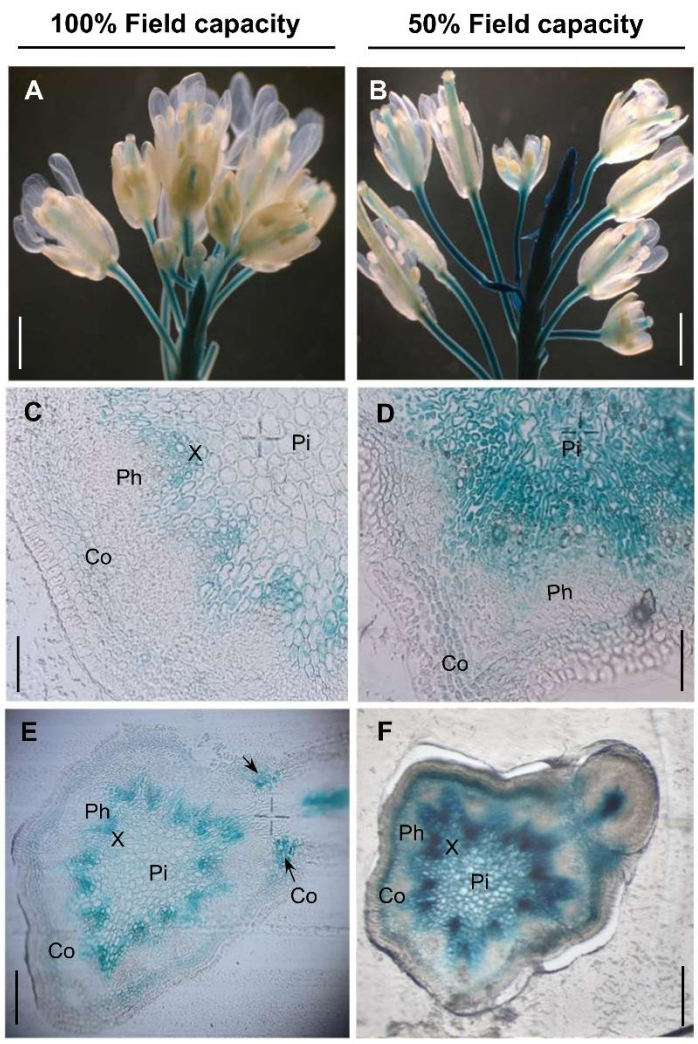

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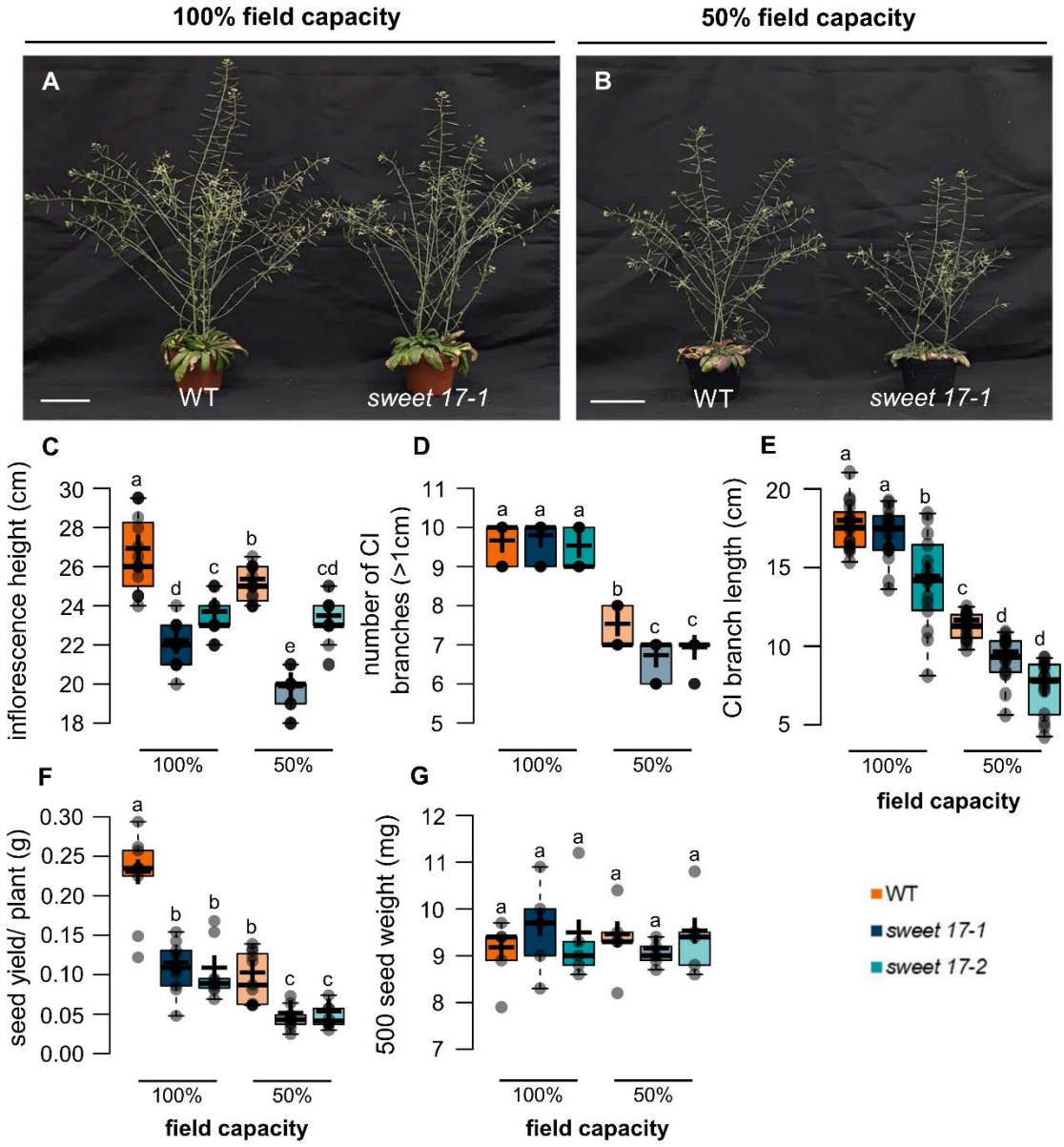

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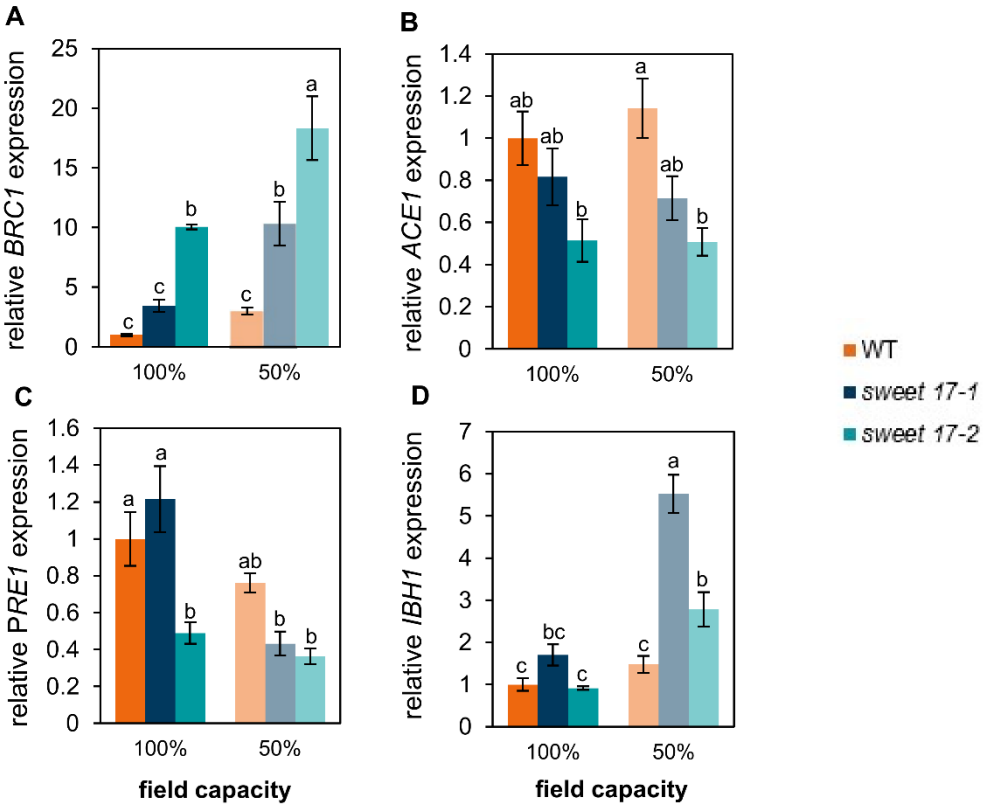

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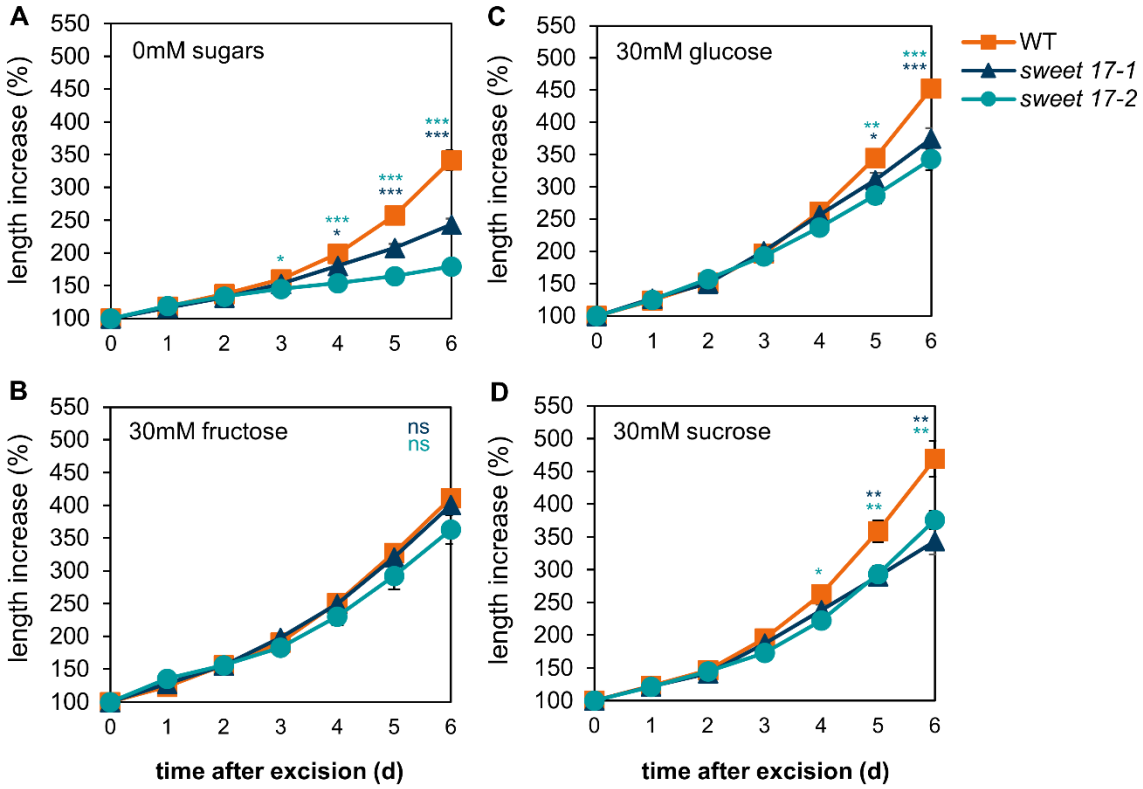

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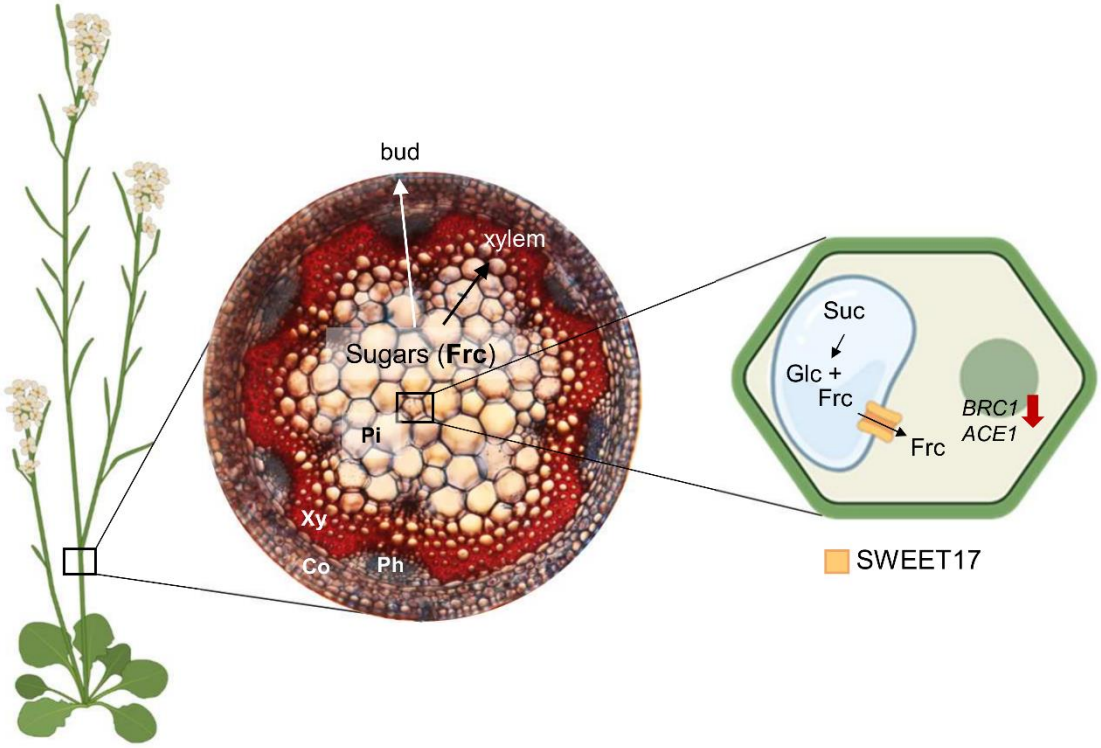

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