

SWEET17 and its supportive function in shoot branching

## **Carbohydrate distribution via SWEET17 is critical for Arabidopsis inflorescence branching under drought**

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### **Highlight**

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

### **Keywords**

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

### **Abbreviations**

field capacity FC

fresh weight FW

dry weight DW

1 **Abstract**

2 Sugars Will Eventually be Exported Transporters (SWEETs) are the most recently discovered family of  
3 plant sugar transporters. Functioning as uniporters and thus facilitating the diffusion of sugars across  
4 cell membranes, SWEETs play an important role in various physiological processes such as abiotic  
5 stress adaptation. *AtSWEET17*, a vacuolar fructose facilitator, was shown to be involved in the  
6 modulation of the root system during drought. Moreover, overexpression of a homolog from apple  
7 results in increased drought tolerance of tomato plants. Therefore, SWEET17 appears to be essential  
8 for the plant's drought response. Nevertheless, the role and function of SWEET17 in aboveground  
9 tissues under drought stress to date remains enigmatic. By combining gene expression analysis with  
10 analysis of the sugar profile of various aboveground tissues, we uncovered a putative role of SWEET17  
11 in the carbohydrate supply, and thus cauline branch emergence and growth, particularly during  
12 periods of carbon limitation as occurs under drought stress. SWEET17 thereby being of critical  
13 importance for maintaining efficient reproduction under drought stress.

## 14 Introduction

15 As sessile organisms' vascular plants are constantly exposed to a changing environment and such  
16 environmental conditions can alter either rapidly or gradually. Therefore, plants must constantly  
17 precept, react and adapt to their environment (Kleine et al., 2021; Schwenkert et al., 2022). As plant  
18 metabolism adapts, environmental conditions can affect important factors such as plant biomass  
19 accumulation and thus yield. One abiotic factor which markedly impairs plant growth and  
20 development is drought. Drought stress occurs for a variety of reasons, including low rainfall, high and  
21 low (below freezing) temperatures, high soil salinity or high light intensity. From an agricultural and  
22 physiological perspective, drought stress sets in when water availability decreases due to low soil  
23 moisture or when the rate of transpiration from leaves exceeds the water uptake by the roots (Salehi-  
24 Lisar and Bakhshayeshan-Agdam, 2016). Due to the projected global warming and climate change, the  
25 frequency and intensity of drought stress will increase worldwide (Dai, 2013; Basu et al., 2016; Bashir  
26 et al., 2021). Therefore, the probability of yield loss due to exceptional drought events will increase by  
27 about 20% in the future and already exceeds 70% for several crops such as soybean and corn (Leng  
28 and Hall, 2019). As diverse as the reasons of drought stress are the plants adaptive responses to this  
29 abiotic factor. E.g., plants react to water limitation with an array of morphological, physiological and  
30 biochemical adaptations, all following the general aim to maintain cell-homeostasis by decreasing  
31 cellular water depletion and/or increasing cellular water uptake. Such adaptations may include  
32 increased root formation, onset of stomata closure, relative decrease of shoot growth and sugar  
33 accumulation (Basu et al., 2016; Ahluweila et al., 2021; Bashir et al., 2021; Seleiman et al., 2021).

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

46 Overall, the plant genome harbors numerous individual genes encoding carbohydrate-transport  
47 proteins that can be grouped in three major transporter families: the monosaccharide transporter-

48 like (MST) family, the sucrose transporters (SUT/SUC), and the sugars will eventually be exported  
49 transporter (SWEET) proteins (Doidy et al., 2012; Pommerrenig et al., 2018; Wen et al., 2022). Of these  
50 three families, SWEETs are the most recently described transporter group (Chen et al., 2010) and to  
51 date, common features of all characterized SWEETs are their ability to mediate both influx and efflux  
52 of mono- and/or disaccharides at low sugar affinities (Chen et al., 2015a). SWEET transporters  
53 generally exhibit seven transmembrane domains and most SWEETs locate at the plasma membrane  
54 (Ji et al., 2022). However, three of them, namely SWEET2, SWEET16 and SWEET17 have previously  
55 been shown to localize to the tonoplast (Chardon et al., 2013; Klemens et al., 2013; Chen et al., 2015).  
56 Since the vacuole is the largest cellular organelle and because one of its main functions is the  
57 regulation of dynamic sugar storage and distribution, it does not surprise that especially vacuolar  
58 SWEET transporters show differential expression under abiotic stress conditions (Chardon et al., 2013;  
59 Klemens et al., 2013; Guo et al., 2014; Chen et al., 2015; Ji et al., 2022).

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

## 69 **Materials and Methods**

### 70 **Plant cultivation and harvest**

71 Wild types (Col-0) and two *sweet17* loss of function mutants (*sweet17-1* (SALK\_012485.27.15.x) and  
72 *sweet17-2* (SAIL\_535\_H02); Chardon et al., 2013) were grown under different growth conditions  
73 based on the experimental design and purpose. For soil experiments, seeds were sown on standard  
74 soil (ED-73; Einheitserde Patzer; Sinntal-Altengronau, Germany) and plants were grown under short  
75 day conditions (10h light, 14h dark) with a light intensity of 125  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  at 21°C. To  
76 stimulate plants for initiation of the reproductive growth, four-week-old plants were transferred from  
77 short day to long day conditions (16h light, 8h dark) with the same light intensity and temperature as  
78 present at short days. For growth in hydroponic culture, seeds were germinated on germination  
79 medium, which was filled in detached lids from Eppendorf reaction tubes containing little holes, as  
80 described by Conn et al., (2013). The agar-filled lids were placed floating on plastic boxes containing  
81 liquid germination medium in a way, that developing roots can grow through the agar and extend  
82 directly to the liquid medium. After one week of growth, liquid germination medium was gradually  
83 exchanged with basal nutrient solution in the same composition as described in Conn et al., (2013).  
84 The basal nutrient solution was replaced weekly to ensure constant nutrient levels and pH of the  
85 medium. Plant material was harvested at the timepoints noted in the corresponding figure legends  
86 and if applicable was separated in the different aboveground-tissues leaf, stem, branch, flower and  
87 silique using a scalpel. Branch samples thereby represent first order lateral branches emerging from  
88 cauline leaf buds of the main inflorescence stem. For harvesting branch samples all inflorescences  
89 were removed from the branch. Plant material was directly frozen in liquid nitrogen after harvest and  
90 stored at -80°C until usage.

### 91 **Application of drought stress**

92 To analyze the effects of drought stress on plant performance, drought was applied to the soil and  
93 hydroponic cultures based on different methods. For soil experiments, plants were exposed to  
94 drought conditions based on soil field capacity as explained in Valifard et al., (2021). Therefore, plants  
95 were kept at a determined water content in the soil, adjusted to a field capacity of either 100%  
96 (control) or 50%. The water content in the soil was checked and adjusted at 48h intervals until harvest.  
97 To apply drought stress in the hydroponic system, four-week-old plants were exposed to -0.5 MPa  
98 osmotic potential produced by polyethylene glycol 8000 (PEG 8000) according to Michel, (1983).

### 99 **Carbohydrate extraction and quantification**

100 Frozen plant material was ground using a mortar and pestle. Carbohydrates were extracted as  
101 described in (Keller et al., 2021b). Briefly, 50 mg of pulverized plant material were extracted in 80%

102 ethanol at 80°C for 30 minutes. After centrifugation (5min, 14000rpm), the supernatant was  
103 transferred into a new reaction tube and evaporated using a vacufuge concentrator (Eppendorf,  
104 Hamburg, Germany). The pellet remaining after evaporation was resolved in  $\text{d}_2\text{H}_2\text{O}$ . Sediments  
105 remaining from the carbohydrate extraction were washed with 80% ethanol and  $\text{d}_2\text{H}_2\text{O}$  twice and used  
106 for starch digestion. For that, 200  $\mu\text{l}$   $\text{d}_2\text{H}_2\text{O}$  were added to the washed pellet and samples were  
107 autoclaved for 40 minutes at 121°C. For hydrolytic cleavage of the starch, 200  $\mu\text{l}$  of an enzyme mixture  
108 (5 U  $\alpha$ -Amylase; 5 U Amyloglucosidase; 200 mM Sodium-Acetate; pH 4.8) were added to the  
109 autoclaved pellet and the mixture was incubated at 37°C for at least four hours followed by heat  
110 inactivation of enzymes at 95°C for ten minutes. Quantification of the extracted sugars (glucose,  
111 fructose, sucrose) and the hydrolyzed starch was performed using a coupled enzymic test  
112 (spectrophotometric analysis) as described in Stitt et al., (1989).

### 113 **Histological localization of *SWEET17***

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

### 126 **Determination of reproductive growth parameters and yield**

127 For determination of reproductive growth parameters and yield, total inflorescence height as well as  
128 the length of all first order cauline branches (emerging from cauline leaf buds of the main  
129 inflorescence stem) with a minimum length of 1 cm were measured on eight-week-old plants. For  
130 determination of the seed weight per plant, inflorescences of single plants were covered with paper  
131 bags as soon as all flowers turned to siliques. After ripening, seeds of single plants were harvested  
132 separately and the seed weight per plant was determined for ten individual plants of each line. From  
133 those ten individual plants, seeds of five plants were used to count and weight 500 seeds to determine  
134 the 500 seed weight.

135 **RNA extraction**

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

142 **Expression analysis via RT-qPCR**

143 Analysis of gene expression was performed by quantitative real time PCR and was carried out in a CF  
144 X96™ real time cycler (Bio-Rad, Feldkirchen, Germany) using a standard two-step protocol with an  
145 annealing/elongation step at 58°C for 45 seconds. For quantification, the fluorescent dye iQ SYBR®  
146 Green (Bio-Rad Laboratories, Feldkirchen, Germany) was used according to the manufacturer's  
147 guidelines. The calculation of relative gene expression was performed using a modified  $2^{-\Delta\Delta CT}$  method  
148 (Livak and Schmittgen 2001). For transcript normalization the protein phosphatase 2A (PP2AA3;  
149 *AT1G13320*) and the SAND family protein (*AT2G28390*) were used as reference genes (Czechowski et  
150 al., 2005). Primers including their primer efficiencies used for expression calculation are documented  
151 as Supplementary Table 1.

152 **RNA Seq**

153 RNASeq data was extracted from the dataset created for Khan et al. (2022, *preprint*). In brief, leaf discs  
154 from four-week-old Arabidopsis wild type plants were incubated in 3 mM MES containing 100 mM  
155 sugars (mannitol, glucose and fructose) overnight. The next day, leaf discs were harvested and stored  
156 at -80°C. RNA was isolated was using the NucleoSpin® RNA Plant Kit (Macherey-Nagel, Düren,  
157 Germany) according to the manufacturer's guidelines. RNA Sequencing then was performed and  
158 analyzed by Novogene (Cambridge, United Kingdom).

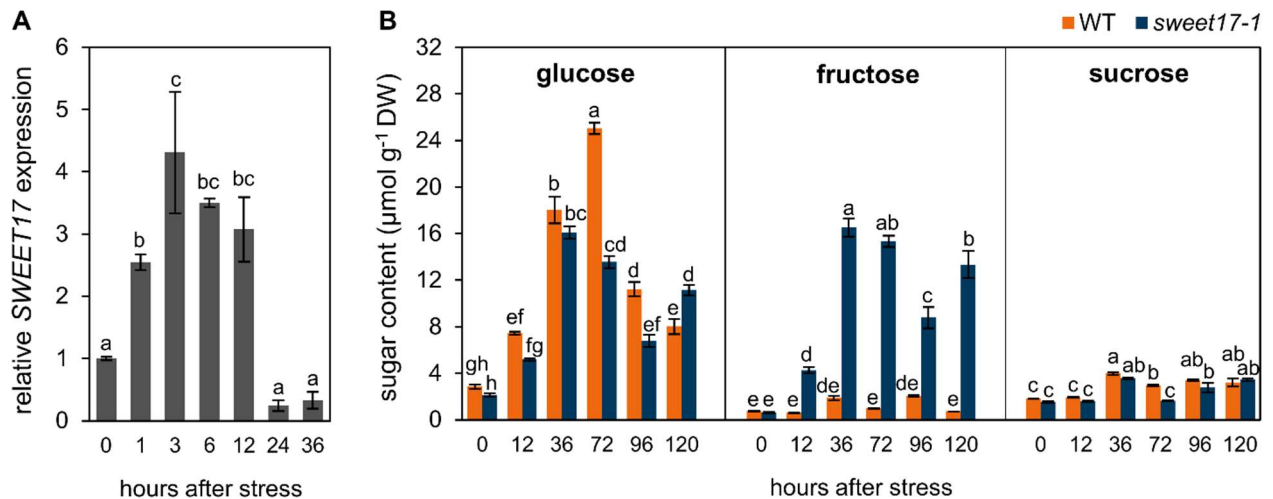
159 **Results**

160 ***SWEET17* is transiently expressed in shoot tissue during drought stress**

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

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





**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 ( $\Psi_s = -0.5$  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  $\pm$  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  $\pm$  SE. Different letters indicate significant differences between the different lines and timepoints according to two-way ANOVA with post-hoc Tukey testing ( $p < 0.05$ ).

180

### 181 ***sweet17* mutants exhibit substantial accumulation of fructose during drought stress**

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

188 Three-week-old rosette tissue of both, wild types and *sweet17* mutant plants, exhibited accumulation  
 189 of glucose starting twelve hours after the addition of PEG. Glucose contents peaked at 36 and 72 hours  
 190 after the onset of stress, followed by a decrease of glucose levels at 96 and 120 hours under drought  
 191 in wild types and *sweet17-1* mutants, respectively (Figure 1 B). Although glucose content decreased  
 192 after 96 hours of drought, it was still significantly higher than before onset of the stress treatment in  
 193 both lines (Figure 1 B). Nevertheless, the accumulation of glucose in rosettes of wild types and  
 194 *sweet17-1* mutants under drought stress was comparable (Figure 1 B). Unlike glucose, fructose  
 195 accumulation could only be observed in rosettes of *sweet17-1* mutants under drought stress. At each  
 196 analyzed time point after onset of drought, the fructose content was significantly higher in *sweet17-1*

197 rosettes than in corresponding wild type samples (Figure 1 B). Starting from  $0.76 \mu\text{mol g}^{-1}$  DW in wild  
198 types, fructose increased to a maximum of  $1.87 \mu\text{mol g}^{-1}$  DW and  $2.08 \mu\text{mol g}^{-1}$  DW after 36 and 96  
199 hours under drought, respectively. In contrast, endogenous fructose content in the *sweet17-1* mutant  
200 was  $0.63 \mu\text{mol g}^{-1}$  DW and increased to remarkable  $16.55 \mu\text{mol g}^{-1}$  DW within the first 36 hours after  
201 onset of drought, a value nearly nine-times the wild type level (Figure 1 B). The levels of sucrose and  
202 starch showed comparable changes after exposure to drought stress as observed for glucose contents  
203 in wild types and the *sweet17-1* mutant. For both metabolites, a significant increase was observed in  
204 wild types and *sweet17-1* no later than 36 hours after onset of stress and remained high throughout  
205 the treatment (Figure 1 B and Supplementary Figure 2). Similar to glucose, sucrose and starch contents  
206 tended to be higher in wild types than in *sweet17-1* plants (Figure 1 B, Supplementary Figure S2).  
207 Nevertheless, differences in glucose, sucrose and starch contents between wild types and *sweet17-1*  
208 are minor compared to differences in the fructose content after drought stress (Figure 1 B).

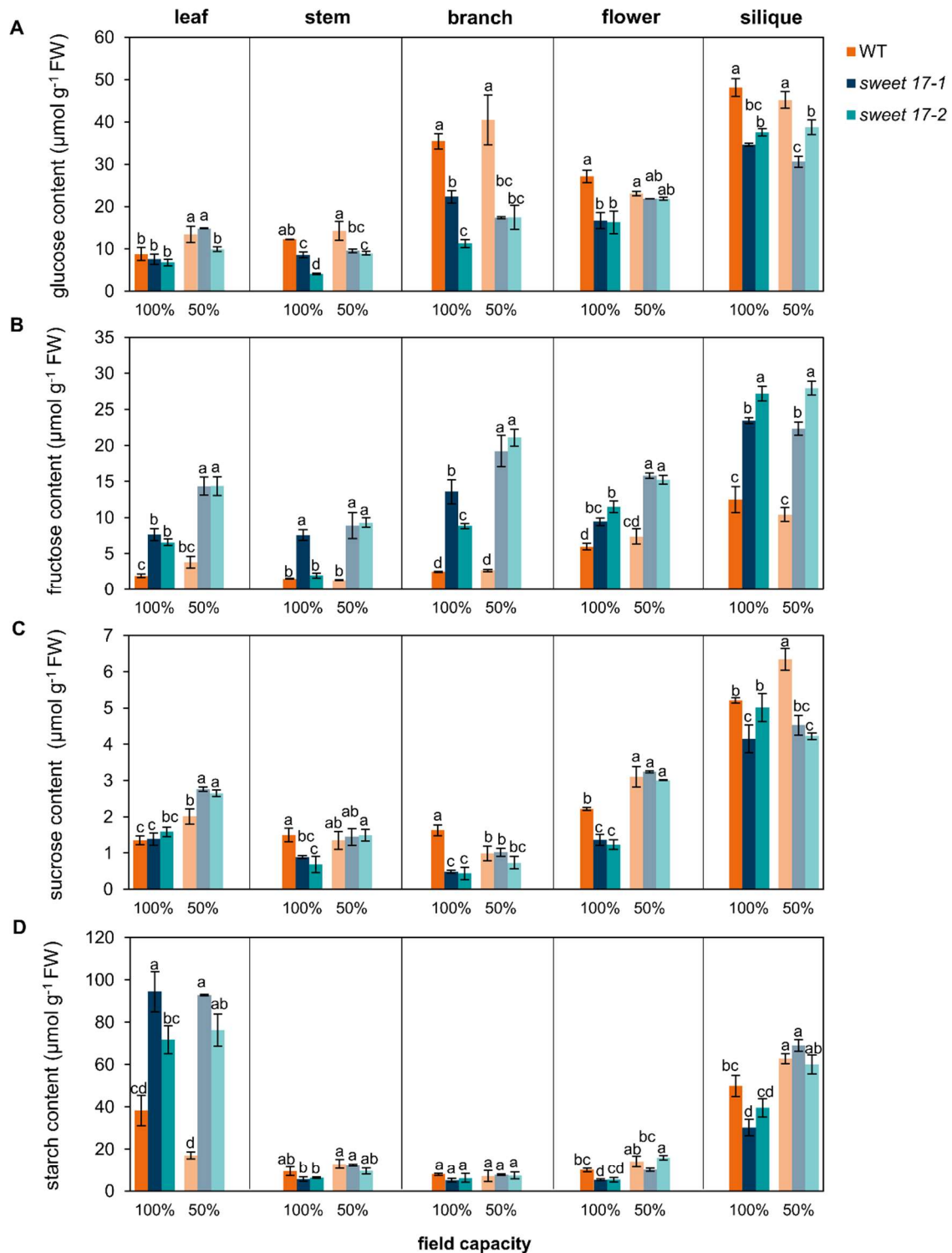
### 209 **Loss of *SWEET17* results in altered sugar profiles in the inflorescence and branches**

210 Since *SWEET17* expression was shown to be upregulated in aboveground tissues under drought stress  
211 (Figure 1 A) and since loss of *SWEET17* severely affects drought related sugar profiles (Figure 1 B), we  
212 wanted to investigate which of the aboveground tissues are most affected by *SWEET17* deficiency  
213 under drought stress. This analysis was of special importance since *SWEET17* expression is highest in  
214 the inflorescence stem (Guo et al., 2014). To this end, *sweet17-1*, *sweet17-2* and wild types were  
215 grown on soil under short day conditions for four weeks and subsequently transferred to long day  
216 conditions to initiate reproductive growth. With the shift in growth conditions, plants were subjected  
217 to 50% field capacity (FC) or 100% FC, respectively for four weeks afterwards. Eight-week-old plants  
218 then were subsequently dissected into the tissues: leaves, stems, branches, flowers and siliques prior  
219 to the extraction of sugars and starch (Figure 2). Our analysis revealed that overall glucose and sucrose  
220 concentrations were highest in the siliques of wild types, while glucose concentrations were lowest in  
221 the leaves and sucrose concentrations were lowest in branches (Figure 2 A and 2 C).

222 As observed earlier, glucose contents were increasing in leaf-tissues upon drought treatment in wild  
223 types as well as in *sweet17* mutants and overall glucose level were comparable between all lines  
224 (Figure 2 A). In stems, branches, flowers and siliques no increase of glucose could be observed in any  
225 of the plant lines after growth at 50% FC. In addition, *sweet17* mutants exhibited lower glucose  
226 contents than wild types in those tissues (Figure 2 A). Regarding fructose, highest contents could  
227 always be observed in *sweet17* mutants, especially upon drought stress at 50% FC (Figure 2 B), while  
228 wild types did not show any accumulation of fructose under drought in any of the analyzed tissues  
229 (Figure 1 B, Figure 2 B). The biggest differences in fructose contents between wild type and *sweet17*  
230 plants could be observed in stems and branches under control, as well as under drought conditions.

231 Thereby, the concentration of fructose was already five- to 5.5-fold higher in *sweet17-1* stems and  
232 branches than in corresponding wild type tissues under unstressed conditions and increased to  
233 approximately seven-times the concentration of wild types under drought stress, indicating an  
234 important role of the transporter in these tissues particularly under drought (Figure 2 B).

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



**Figure 2: Sugar and starch content in aboveground tissues of Arabidopsis wild type and *sweet17* mutants in response to drought stress.**

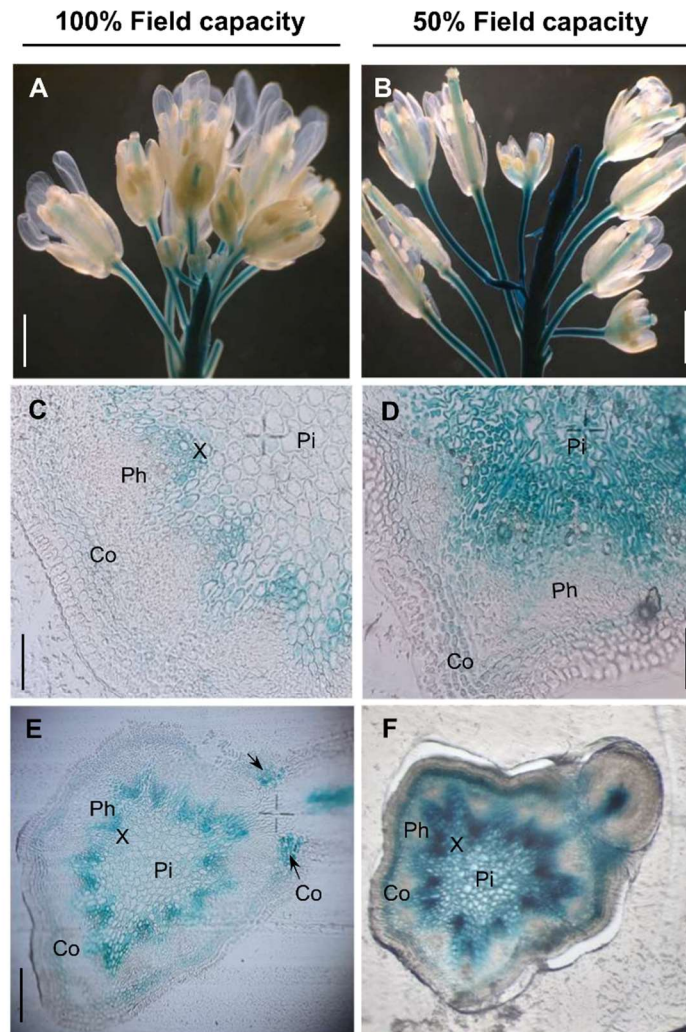
Seeds were sown on soil and grown under short day conditions for four weeks and then were transferred to long day conditions followed by application of drought stress at 50% FC. After eight weeks of growth plants were dissected in leaf, stem, branch, flower and siliques and contents of glucose (A), fructose (B), sucrose (C) and starch (D) were measured. Starch contents were determined as hydrolyzed glucose. Bars represent the mean from  $n = 3$  biological replicates  $\pm$  SE. Different letters indicate significant differences between the different lines and conditions according to two-way ANOVA with post-hoc Tukey testing ( $p < 0.05$ ).

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

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

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





**Figure 3: Expression pattern of *SWEET17* in Arabidopsis stem tissues.**

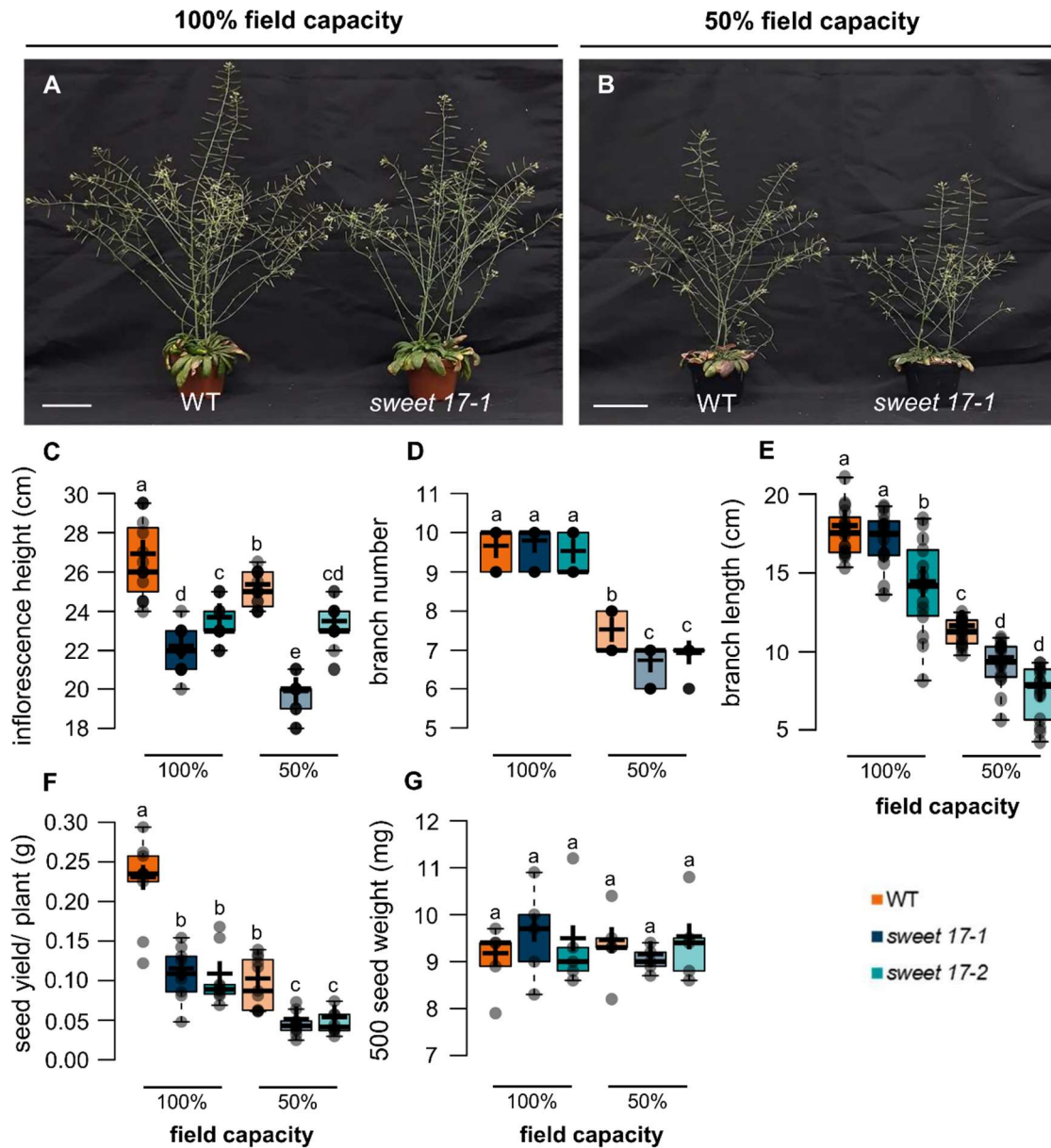
Histochemical localization of Pro*SWEET17*::b-GLUCURONIDASE (GUS) activity in eight-week-old inflorescence stem of Arabidopsis plants grown at 100% FC (A, C, E) and under drought stress at 50% FC (B, D, F). Seeds were sown on soil and grown under short day conditions for four weeks and transferred to long day conditions followed by application of drought stress at 50% FC. GUS signal was detected in the pith (Pi), xylem parenchyma (X) and cortex (Co) (C,D) especially in places of 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 4µm (C, D, E) and 5.5µm (F) thickness were analyzed. Scale bars represent 250 µm (A, B), 30 µm (C, D), 100 µm (E, F).

265

266 ***sweet17* mutants exhibit decreased number of branches and lower seed yield per plant**

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

273 We observed that mutant plants exhibited an overall shorter inflorescence under both, well-watered  
274 and drought stress conditions, when compared to corresponding wild type plants (Figure 4 A-C).  
275 However, under drought stress, wild type and mutant plants showed reduced inflorescence heights  
276 when compared to control conditions, with *sweet17* inflorescences being significantly shorter than  
277 that of wild types (Figure 4 C). Unlike inflorescence height, the number of branches did not differ  
278 between wild type and mutants under control conditions (Figure 4 D). When exposed to drought  
279 stress, the branch number was significantly reduced in all lines (Figure 4 D). However, this decrease  
280 was more pronounced in *sweet17* mutants (Figure 4 D). Similar behavior was observed for the branch  
281 length (Figure 4 E). While only *sweet17-2* mutants showed significantly shorter first order cauline  
282 branches than wild types at 100% FC, at 50% FC branch length was reduced in all lines. There, both  
283 *sweet17* mutant lines showed significantly reduced branch lengths when compared to the wild type  
284 (Figure 4 E). Therefore both, branch number and branch length appeared to be negatively affected in  
285 *sweet17* mutants under drought stress, as both parameters are comparable between all lines at 100%  
286 FC but are significantly lower in *sweet17* mutants under drought compared to corresponding wild  
287 types (Figure 4 D and Figure 4 E). Under control conditions, in *sweet17* mutants a lower inflorescence  
288 height resulted in a decreased seed yield per plant (Figure 4 F), while showing similar 500 seed weight  
289 (Figure 4 G) as wild types. A decrease of seed yield could also be observed in wild types under drought  
290 conditions (Figure 4 F). This negative effect was more severe in *sweet17* mutants (Figure 4 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), branch number (D) and length (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 25<sup>th</sup> and 75<sup>th</sup> percentiles and whiskers extend 1.5 times the interquartile range from the 25<sup>th</sup> and 75<sup>th</sup> 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 5cm (A, B).

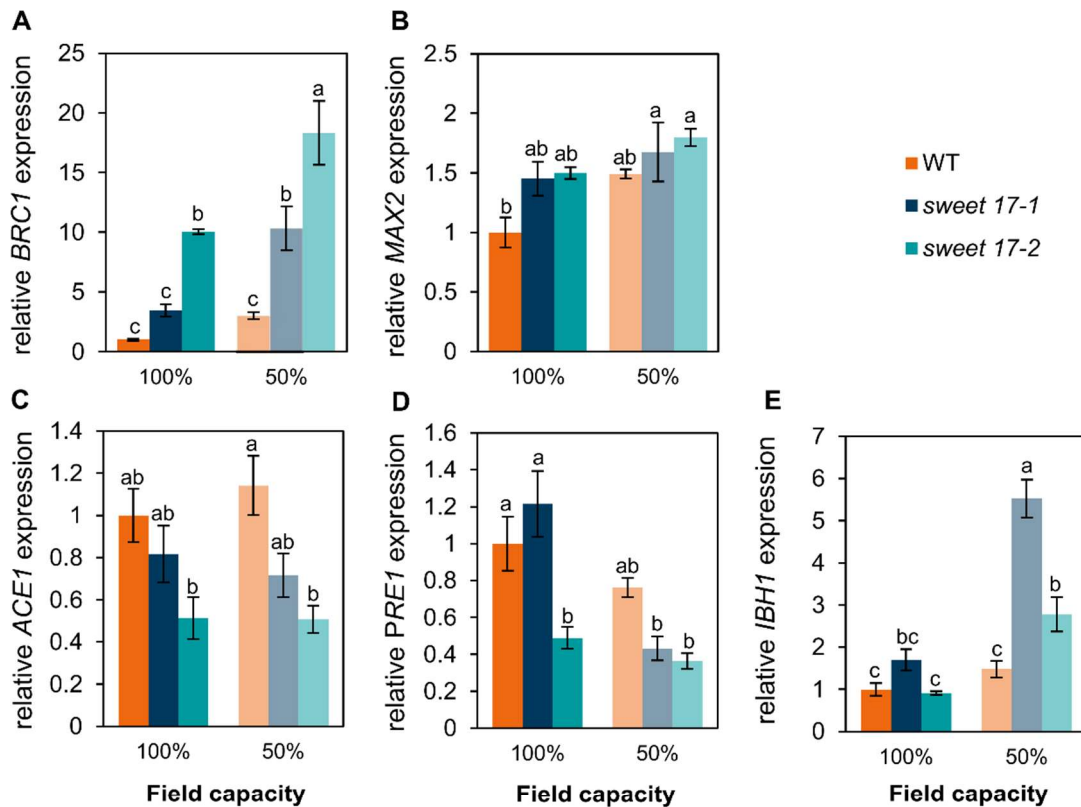


292 **Expression of key regulators of branching and branch elongation are altered in *sweet17* mutants**

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

299 One of these transcription factors is *BRANCHED1 (BRC1)*, an inhibitor of bud outgrowth that maintains  
300 bud dormancy (Aguilar-Martinez et al., 2019). Interestingly, *BRC1* expression was already higher in  
301 *sweet17-2* mutants compared with wild types under unstressed conditions and further increased  
302 under drought, resulting in significantly higher *BRC1* expression in *sweet17* mutants compared with  
303 the corresponding wild types (Figure 5 A). The expression of *BRC1* can be directly regulated via sugar  
304 availability or via sugar induced expression changes of upstream regulators like *MORE AXILLARY*  
305 *GROWTH2 (MAX2)*, which is involved in the strigolactone-dependent regulation of branching  
306 (Stirnberg et al., 2002). Drought in tendency induced the expression of *MAX2* in wild types (Figure 6  
307 B). However, although not significant, *MAX2* expression was higher in *sweet17* than in wild type plants  
308 under both control and drought conditions (Figure 5 B).

309 In Arabidopsis, a series of bHLH (basic helix-loop-helix) transcription factors including *ACTIVATOR FOR*  
310 *CELL ELONGATION1-3 (ACE1-3)*, *PACLOBUTRAZOL-RESISTANT1 (PRE1)* and *INCREASED LEAF*  
311 *INCLINATION1 BINDING bHLH1 (IBH1)* have been identified as regulators of cell elongation in response  
312 to environmental factors and developmental stages (Wang et al., 2018; Ikeda et al., 2012; Zhiponova  
313 et al., 2014). The expression of *ACE1* and *PRE1*, both being inducer of cell elongation, were already  
314 significantly reduced in *sweet17-2* mutants under control conditions (Figure 5 C and 5 D). Under  
315 drought, *ACE1* expression did not change in any of the analyzed lines, therefore *sweet17-2* still  
316 showing significantly reduced expression values when compared to the corresponding wild types  
317 (Figure 5 C). The expression of *PRE1* was significantly reduced in *sweet17-1* mutants under drought  
318 stress, while expression in wild types and *sweet17-2* was not affected. Therefore, although not  
319 significant, both mutant lines showed a lower expression of *PRE1* under drought stress when  
320 compared to wild types (Figure 5 C). Expression profiles of *IBH1* did not differ between *sweet17*  
321 mutants and wild types under unstressed conditions (Figure 5 E). However, under drought stress *IBH1*  
322 expression was significantly induced in both *sweet17* mutants leading to significantly higher  
323 expression values than in wild types (Figure 5 E).



**Figure 5: Expression profiles of central regulators of branching and branch elongation in wildtype 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. Lateral branches 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 WT under 100% FC. Values represent the mean of n=3 biological replicates  $\pm$ SE. Different letters indicate significant differences between the different lines and conditions according to two-way ANOVA with post-hoc Tukey testing ( $p < 0.05$ ).

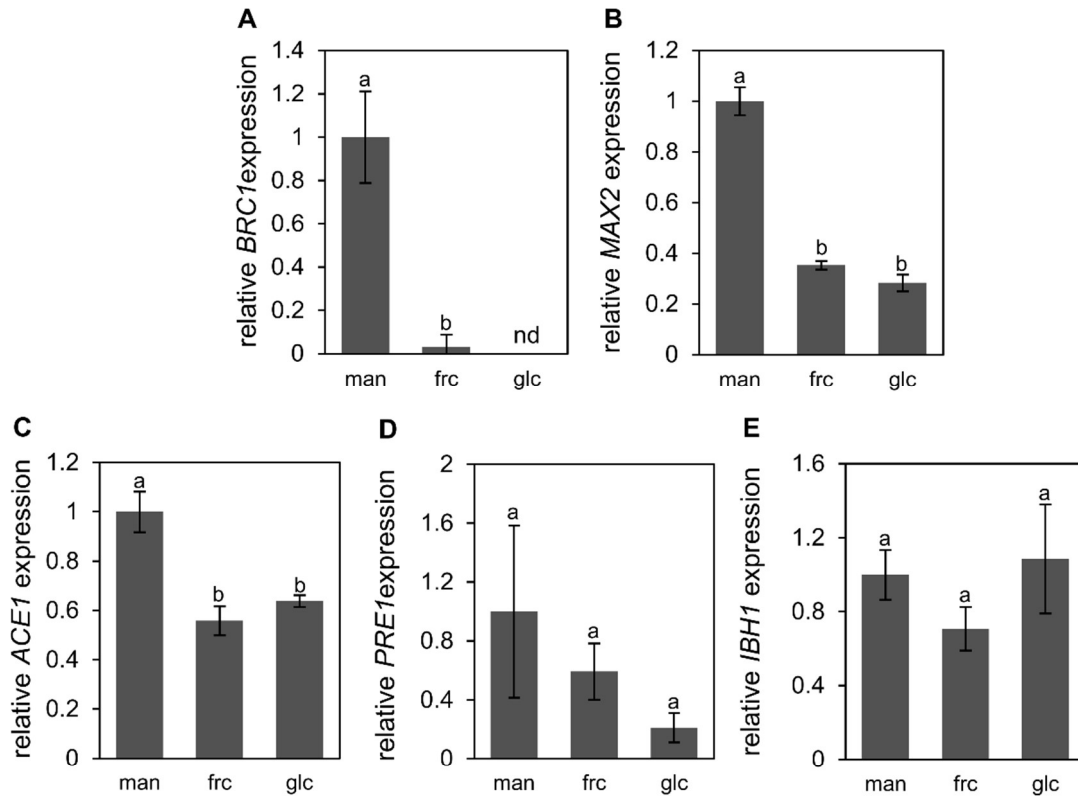
324

### 325 Expression of branching- and branch elongation regulators is influenced by monosaccharide levels

326 Given that the expression of key factors regulating branching and branch elongation differs between  
 327 wild types and *sweet17* mutant plants, it is reasonable to speculate that fructose, the sole transport  
 328 substrate of SWEE17 (Chardon et al., 2013), exerts a signaling function in the developmental process  
 329 of branching. Therefore, to verify this hypothesis we extracted data from RNA-Seq analysis of  
 330 Arabidopsis wild type leaf discs subjected to mannitol (as control) or fructose (Khan et al., 2022  
 331 *preprint*). In addition, extracted from the same dataset, we analyzed the effect of glucose, as another  
 332 abundant monosaccharide, on global gene expression in Arabidopsis.

333 Expression of the three transcription factors *BRC1*, *MAX2* and *ACE1* were regulated by both fructose  
 334 and glucose treatment, which generally led to a marked downregulation of their expression (Figure 6  
 335 A-C). Expression of *BRC1* was at such low levels after glucose feeding that it could not be detected in

336 RNASeq analysis (Figure 6 A). Although not significant, *PRE1* showed an in tendency similar regulation  
337 with decreased expression levels after supply with either glucose or fructose (Figure 6 D). In contrast,  
338 *IBH1* expression was not affected by fructose and glucose treatment (Figure 6 E). Overall, a marked  
339 pattern of regulation of three of five key regulators of branching and branch elongation could be  
340 observed upon feeding external sugars.



**Figure 6: Expression of central regulators of branching and branch elongation in response to different sugars.**

Gene expression data was extracted from RNASeq performed by Khan et al. 2022. Therefore, leaf discs from four-week-old Arabidopsis plants were incubated in 3mM MES containing 100mM mannitol, 100mM fructose or 100mM glucose for 24 hours. Expression data in form of fpkm values of *BRC1* (A), *MAX2* (B), *ACE1* (C), *PRE1* (D) and *IBH1* (E) were extracted from the dataset and normalized on the fpkm value under mannitol treatment. Values represent the mean of n=3 biological replicates  $\pm$ SE. Different letters indicate significant differences between the different conditions according to one-way ANOVA with post-hoc Tukey testing ( $p < 0.05$ ).

341

## 342 Discussion

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

353 Plant sugar sensing is a well described process and leads to the adjustment of the expression of a wide  
354 number of genes (Rolland et al., 2002, 2006). The best characterized plant sugar sensing system is  
355 represented by the sensor protein HEXOKINASE1 (Xiao et al., 2000; Moore et al., 2003), which  
356 connects changes of the cytosolic glucose concentration to altered transcription efficiency of nuclear  
357 located genes (Cho et al., 2006). Thus, it is not surprising that especially the subcellular composition  
358 of sugars affects the development of both, soil-located and aboveground plant organs (see e.g., Tjaden  
359 et al., 1994, Patzke et al., 2019, Valifard et al., 2021). Detailed analyses of various mutants revealed  
360 that especially the activity of vacuolar sugar transporters is important for the control of the cytosolic  
361 sugar levels (Wormit et al., 2006; Wingenter et al., 2010; Poschet et al., 2011; Klemens et al., 2013).

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

371 Since SWEET17 was shown to act as a fructose facilitator, loss-of-function of this transporter, which  
372 preferentially acts as a vacuolar exporter under unfavorable conditions (Guo et al., 2014; Chandran  
373 2015), results in accumulation of fructose in the vacuole and thus a higher total cellular fructose  
374 content (Figure 1 B, Figure 2 B; Chardon et al., 2013). The opposite reaction was observed in SWEET17-

375 overexpressor plants, which showed significantly lower fructose contents in comparison to the wild  
376 type, especially when grown in a challenging environment (Guo et al., 2014).

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

384 Interestingly, only *sweet17* mutants were able to accumulate fructose under drought stress conditions  
385 (Figure 1 B, Figure 2). As fructose accumulating in vacuoles mainly originates from sucrose cleavage  
386 via vacuolar invertases, those findings indicate an essential function of the vacuolar invertase during  
387 adaptation to drought. Latter conclusion is fully in line with the generally important function of  
388 vacuolar invertase for sucrose hydrolysis in *Arabidopsis* under various conditions (Vu et al., 2020).  
389 Moreover, as shown in mono- and dicot species, drought induces vacuolar invertase gene expression  
390 and the resulting enzyme activity is a critical element of the response to drought stress (Kakumanu et  
391 al., 2012; Chen et al., 2021). Vacuolar sucrose, cleaved by invertases, originates from an increased  
392 activity of vacuolar sugar transporters like TST1 and TST2, which's expression is known to be  
393 upregulated under drought stress (Supplementary Figure 1; Wormit et al., 2006). In wild types  
394 invertase cleavage products glucose and fructose can sufficiently be exported from the vacuole via  
395 sugar porters like SWEET17 (Chardon et al., 2013; Valifard et al., 2021) and ESL1 (Yamada et al., 2010;  
396 Slawinski et al., 2021), while in the vacuole of *sweet17* plants fructose remains to be trapped to a  
397 higher extend, leading to the observed fructose levels (Figure 1 B, Figure 2 B).

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

404 Both *SWEET17* transcript and *SWEET17* protein were also detected in the cortex (Figure 3 C; Guo et  
405 al., 2014; Aubry et al., 2022; Hoffmann et al., 2022) and the pith (Figure 3 D; Hoffmann et al., 2022) of  
406 the stem, whereby expression of *SWEET17* in the pith is promoted under drought stress. Key  
407 characteristics of pith cells are their large size, large vacuoles and the fact that pith cells they are

408 surrounded by vasculature (Lev-Yadun, 1994; Zhong et al., 2000), making them an ideal storage tissue.  
409 In addition, pith cells harbor a variety of sugar transporters, as e.g. carbohydrate transporters of the  
410 EARLY RESPONSE TO DEHYDRATION SIX-LIKE (ERDL) and SUCROSE TRANSPORTER (STP) families,  
411 known to be expressed in the inflorescence stem, show high expression levels in the pith of this organ  
412 (Shi et al., 2021; Dinant and Le Hir, 2022). Therefore, the pith and in particular its subcellular sugar  
413 distribution may play an important role in plant developmental processes, such as the development  
414 of the vascular system, a process that is clearly influenced by sugar signaling and thus by sugar  
415 availability and distribution (Dinant and Le Hir, 2022). In accordance with suggestions by Dinant and  
416 Le Hir (2022), increased *SWEET17* expression in the pith allows fructose to be mobilized from vacuoles  
417 and serve as carbohydrate source for local sinks such as the xylem tissue (Spicer 2014; Aubry et al.,  
418 2022). However, not only vascular tissue but also buds of cauline branches represent local sinks. Thus,  
419 increased expression of *SWEET17* could support bud outgrowth and branch development. This  
420 hypothesis gains support by strong *SWEET17* expression in the cortex, especially where branches are  
421 connected to the main stem (Figure 3 E and 3 F). This expression pattern resembles *SWEET17*  
422 expression in the outgrowing region of lateral roots where fructose specifically mobilized from  
423 vacuoles via *SWEET17* is involved in controlled initiation of lateral root formation (Valifard et al., 2021).  
424 During drought experiments *sweet17* mutants showed impaired biomass accumulation because of a  
425 limited water uptake ability due to lower root biomass (Valifard et al., 2021). Low water availability  
426 usually results in metabolic impairments such as decreased photosynthesis (Pinheiro and Chaves,  
427 2011) and altered long distance transport (Keller et al., 2021). Together these factors result in  
428 inhibition of growth and therefore accumulation of sugars in leaf blades (Chaves and Oliveira, 2004)  
429 as observed in drought affected *sweet17* mutants (Figure 2). While sugars are synthesized and  
430 accumulate in source tissues, sink tissues like roots or siliques rely on carbohydrate distribution via  
431 the phloem, which is impaired under drought stress. In accordance, *sweet17* mutants accumulated  
432 higher carbohydrate contents in the leaves, while siliques showed lower contents of glucose and  
433 sucrose than the corresponding wild types under drought (Figure 2), highlighting a possible  
434 involvement of *sweet17* in carbohydrate distribution to branches and reproductive organs.

435 Shoot branching, like root development (Takahashi et al., 2013), is stimulated by the availability of  
436 sugars (Rabot et al., 2012; Mason et al., 2014; Barbier et al., 2015; Fichtner et al., 2017; Barbier et al.,  
437 2019). Sugar availability, as well as auxin-, strigolactone- and cytokinin levels exert influence on the  
438 process of branching (Thimann and Skoog 1933; Dun et al., 2012; Rameau et al., 2015; Balla et al.,  
439 2016; Dierck et al., 2016; Barbier et al., 2019). All these factors trigger changes in *BRANCHED1* (*BRC1*)  
440 expression, a central regulator of shoot branching, because it inhibits bud outgrowth and maintains  
441 bud dormancy (Aguilar-Martinez et al., 2019). *BRC1* expression under both, control and drought



442 conditions were found to be higher in *sweet17* mutants when compared to corresponding wild types  
443 (Figure 5 A). This went along with a lower number of stem branches in mutant plants under drought  
444 (Figure 4 B and 4 D) and because *BRC1* expression was shown to be downregulated by external sucrose  
445 (Mason et al., 2014), it is reasonable to expect additional regulation by the supply of fructose and  
446 glucose, as shown above (Figure 6 A). In addition, the upstream integrator of the branching response  
447 named MORE AXILLARY GROWTH2 (*MAX2*) (Stirnberg et al., 2002), which's expression is known to be  
448 negatively affected by sucrose (Barbier et al., 2015) and the external supply of glucose and fructose  
449 (Figure 6 B), was in tendency found to be increased in *sweet17* mutants (Figure 5 B). Thus, increased  
450 fructose mobilization by high expression of *SWEET17*, as occurring under drought, leads to  
451 suppression of *BRC1* and *MAX2*, which in sum stimulates branching. Because *MAX2* expression and  
452 signaling are directly influenced by factors such as strigolactone concentration (Chevalier et al., 2014;  
453 Khuvung et al., 2022) it is not surprising that observed *MAX2* expression differences between wild  
454 types and *sweet17* mutants are not significant (Figure 5 B). Anyhow *MAX2* expression supports the  
455 observed *BRC1* regulation and branching differences between wild types and *sweet17* mutants (Figure  
456 4 and Figure 5 A).

457 Elongation and growth of plant cells is regulated by a tri-antagonistic series of helix-loop-helix (bHLH)  
458 transcription factors including ACTIVATOR FOR CELL ELONGATION1-3 (*ACE1-3*), PACLOBUTRAZOL-  
459 RESISTANT1 (*PRE1*) and INCREASED LEAF INCLINATION1 BINDING bHLH1 (*IBH1*) (Bai et al., 2012; Ikeda  
460 et al., 2012; Zhiponova et al., 2014; Wang et al., 2018). Expression of these factors differed significantly  
461 between wild types and *sweet17* mutants, especially under drought treatment (Figure 5 C- 5 E).  
462 Thereby, reduced expression of the positive regulators *ACE1* and *PRE1* as well as an increased  
463 expression of the cell elongation inhibitor *IBH1* resulted in a decreased branch length in *sweet17*  
464 mutants, especially under drought stress (Figure 5 C- E). As the expression of the tri-antagonistic  
465 signaling cascade can be influenced by various environmental factors (Bai et al., 2012), it is reasonable  
466 to expect regulation of these genes by sugar availability, as for *ACE1* significantly and for *PRE1* in  
467 tendency observed above (Figure 6 C and 6 D). Sugar regulation of the corresponding signaling genes,  
468 as well as differences in their expression between wild types and *sweet17* plants reinforce the idea of  
469 a possible involvement of *SWEET17* not only in shoot branching but also in branch elongation.

470 Overall, our results reveal high expression of *SWEET17* in the pith and cortex in areas of branch  
471 emergence of the inflorescence stem (Figure 1 A and Figure 3), high differences in the sugar profile of  
472 the main inflorescence stem and cauline branches between wild types and *sweet17* mutants (Figure  
473 2), as well as differential expression of sugar regulated branching and branch elongation regulators  
474 (Figure 5 and Figure 6). In summary, these results suggest a supportive role of *SWEET17* in shoot  
475 branching. Fewer branches as well as a limited branch length in *sweet17* mutants resulted in lower

476 seed yield per plant, indicating an important function of SWEET17 for plant productivity. We believe  
477 that in wild types grown under drought conditions - in which sugar availability in sink tissues is limited  
478 by impaired photosynthesis and reduced functionality of the carbohydrate transport circuit (Li et al.,  
479 2017; Liang et al., 2020; Keller et al., 2021) - SWEET17 might lead to increased mobilization of sugars  
480 from the vacuoles of the pith to maintain carbohydrate supply to lateral bud formation. An idea  
481 supporting the assumption that SWEET proteins increase sugar mobilization to sink tissues during  
482 abiotic stress and therefore maintaining crop productivity (Anjali et al., 2021).



## Supplementary Data

Fig. S1. Drought-induced expression of *TST2* and *TST1*.

Fig. S2. Drought-induced changes in starch content of *sweet17-1* mutant plants.

Table S1. List of Primers used in this study.

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## Author Contribution

M.V., I.K. and A.K.: 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

## Conflict 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.

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