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RESEARCH PAPER

Positive pressure does not efficiently repair xylem embolism after drought

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Abstract

Numerous plant species can actively pressurize water in their xylem. It has been hypothesized that regular peaks in positive pressure help plants to remove xylem embolism and to replenish water reservoirs. This may happen after rewatering when plants have suffered from soil water deficit (WD) and/or following diurnal cycles under well-watered (WW) conditions. Using X-ray microcomputed tomography (μCT), we tested these hypotheses in tomato plants by quantifying xylem functionality and internal water pools in stems of 35 plants subjected to WD intensities before and after rewatering and 14 WW plants. Positive xylem pressure was detected in only 30% of the WD plants after rewatering, with a majority of this 30% showing no or rare events of xylem embolism repair. However, all WD tomato plants restored their internal water pools after rewatering, independently of their ability to generate detectable positive xylem pressure. In WW plants, positive xylem pressure was consistently generated and allowed for repair of the few embolized vessels. The ability of tomato plants to rehydrate non-xylary parenchyma tissues after WD and to repair embolisms under WW conditions sheds new light on alternative water-use mechanisms of herbaceous species to recover from drought.

Keywords: Crops, drought recovery, *Solanum lycopersicum*, symplasm, X-ray microcomputed tomography, xylem embolism.

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Introduction

When plants absorb CO_2 via their stomata to photosynthesize, water evaporates from these leaf openings into the atmosphere. This leads to capillary wicking of water molecules in leaf mesophyll cell walls exposed to intercellular gas spaces, creating a gradient of tension that pulls water from the soil towards the transpiring leaves (cohesion–tension theory, Dixon and Joly, 1895). This ingenious root-to-shoot water transport pathway is mainly driven by the energy of the sun and atmosphere, leaving the liquid xylem sap in a metastable state (at subatmospheric pressures) that can lead to gas blockage when drought imposes strong tensions in the water column (Tyree and Sperry, 1989; Schenk *et al.*, 2015). At substantial drought intensities, gas enters the plant vascular system, causing xylem embolism that can (partly) block the water flow, thereby leading to organ desiccation, cell death, and eventually plant mortality (Brodribb *et al.*, 2021; Mantova *et al.*, 2022). Despite this increasing threat in a world facing climate change (Greve *et al.*, 2018; Hammond *et al.*, 2022), major knowledge gaps in how plants respond to water deficit remain (Lens *et al.*, 2022; McDowell *et al.*, 2022; Zheng *et al.*, 2023), especially related to the physiological mechanisms underlying the capacity of the plant to recover from water deficit upon rewatering. We know that plants can recover from drought after rain or rewatering by generating new xylem conduits as long as lethal thresholds are not reached (Lamarque *et al.*, 2018; Gauthey *et al.*, 2022). Other studies showed that embolized conduits can be refilled with water during rehydration (Nardini *et al.*, 2011; Stewart *et al.*, 2025), which requires (near) positive xylem pressures (Zwieniecki and Holbrook, 2009; De Baerdemaeker *et al.*, 2019). Indeed, several publications claimed that plants are able to recover from xylem embolism, a phenomenon commonly called 'xylem repair' or 'xylem refilling' (Nardini *et al.*, 2011; Hacke and Laur, 2016), either following rewatering after soil drought (Trifilò *et al.*, 2014) or under well-watered (WW) conditions during day–night cycles (Canny, 1998). However, these studies relied on methods which either were based on indirect measurements of xylem functionality (Salleo *et al.*, 1996; Trifilò *et al.*, 2014) or were carried out on detached organs (Brodersen *et al.*, 2010; Knipfer *et al.*, 2016), or using cryo-SEM observations (Buchard *et al.*, 1999; Tyree *et al.*, 1999), that were later found to be susceptible to different (but substantial) artefacts (Cochard *et al.*, 2000; Charrier *et al.*, 2016; Lamarque *et al.*, 2018). These methodological artefacts were confirmed by direct *in vivo* observations of xylem functionality [via X-ray microcomputed tomography (μCT)] that demonstrated that xylem repair is not routine in woody and herbaceous species (Cochard and Delzon, 2013), and that this outcome applies for stems, leaves, and roots (Johnson *et al.*, 2018; Lamarque *et al.*, 2018; Harrison Day *et al.*, 2024). However, the debate remains unresolved, as other studies have reported xylem repair following the generation of positive xylem pressure after rewatering in plants subjected to soil drought (Knipfer *et al.*, 2015; Charrier *et al.*, 2016; Gleason *et al.*, 2017; Drobnitch *et al.*, 2021).

In addition to the transpiration-driven water flow, many plants can move water in the xylem via positive xylem pressure (Pickard, 1981; Schenk *et al.*, 2021). Positive xylem pressure is observed in winter-deciduous tree species during springtime to rehydrate their tissues before bud break (Sperry *et al.*, 1987; Niu *et al.*, 2017; Hölttä *et al.*, 2018), and in herbaceous species showing guttation via hydathodes at their leaf margins at the end of the night (Miller, 1985; Kramer and Boyer, 1995; De Swaef *et al.*, 2013). Positive xylem pressure allows plants to move water and solutes to non-transpiring tissues (e.g. roots and apical meristems, Palzkill and Tibbitts, 1977; Weidner *et al.*, 2005), to expand newly developing cells in seedlings (Cosgrove, 1986; McIntyre, 1987; Wegner, 2014), and to facilitate xylem transport in submerged aquatic plants that cannot move sap and nutrients via transpiration (Pedersen, 1993). Finally, positive xylem pressure has been recorded during drought stress recovery, along with the observation of xylem conduit repair as observed in maize, sorghum, and grapevine (Knipfer *et al.*, 2015; Charrier *et al.*, 2016; Gleason *et al.*, 2017; Drobnitch *et al.*, 2021), and/or rehydration of living tissues (Yang *et al.*, 2012, 2015). However, the direct role of positive xylem pressure in both xylem repair and tissue rehydration after drought is scarcely documented and is poorly understood (Schenk *et al.*, 2021).

Positive xylem pressure remains an enigmatic phenomenon in plants, despite observations that go back at least a few hundred years (see Schenk *et al.*, 2021 for a historical overview). After all this time, it is surprising that an overview of the occurrence of positive xylem pressure across a wide taxonomic range of plants is lacking. Furthermore, the underlying mechanisms behind positive xylem pressure remain largely unknown: is water movement driven by osmotic exudation into xylem conduits (Kramer and Boyer, 1995), hydrostatic pressure in parenchyma cells associated with conduits (Pickard, 2003), or both (Schenk *et al.*, 2021)? What is the role of sugar unloading from the phloem (Hölttä *et al.*, 2006)? Is positive xylem pressure developing in roots, stems, or both (Schenk *et al.*, 2021; Michaud *et al.*, 2024)? Also, what is the role of both positive xylem pressure and dynamic symplastic water movement (i.e. cell to cell transport from less negative to more negative water potentials) to remove xylem embolism and refill internal water storage pools during the rehydration process (Steppe *et al.*, 2006, 2015)? Technical challenges that accompany destructive methods to measure positive xylem pressure (Grossenbacher, 1938; Steudle *et al.*, 1993) have impeded us from providing answers, but more recent non-destructive techniques (Clearwater *et al.*, 2007; De Swaef *et al.*, 2013), along with visualization

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techniques of xylem functionality such as μCT (Knipfer *et al.*, 2015; Charrier *et al.*, 2016), have resurrected interest in the topic.

Here, we focus on the potential role of positive xylem pressure in repairing embolized xylem conduits and rehydrating living tissues in stems of tomato plants after drought. We therefore used high-resolution μCT scanning to investigate the stem water relationships of tomato plants, well known for their development of positive xylem pressure (De Swaef *et al.*, 2013). We scanned the tomato plants at different time points under WW conditions and different intensities of soil water deficit (strong enough to generate xylem embolism, WD) before and after rewatering, while monitoring positive xylem pressure development. Our research questions are as follows. (i) Do WD plants develop positive xylem pressure after rewatering, and does this depend on the intensity of the drought applied? (ii) Are the WD plants able to recover from drought-induced loss in hydraulic conductivity by repairing embolized vessels, and what is the role of positive xylem pressure on potential repair in the xylem? (iii) Which tissues rehydrate in the stems of WD plants after rewatering, and is positive xylem pressure involved, or rather an alternative process? (iv) Are WW plants prone to daily xylem embolism formation/repair dynamics?

Materials and methods

Growing plants and transfer to the scanning facility

At the Institute of Biology Leiden (Leiden University, the Netherlands), tomato (*Solanum lycopersicum* cv Moneymaker) seeds were sown in Murashige and Skoog medium in multiple batches from February to August 2023. After 3 weeks, the plants with the most developed hypocotyls were transferred into 3.6 litre cylindrical pots in a mixture of potting soil (basis biomix, Lensli® substrates, Bleiswijk, the Netherlands), vermiculite, and sand in a ratio of 25:8:2, along with three teaspoonfuls of osmocote fertilizer. All potted plants were placed in the same growth chamber at 24 °C and 70% relative humidity, with a daily 16 h light and 8 h night cycle and watered every other day until the beginning of the experiments, when the plants were 50 d old.

All experiments were run at Ghent University's Center for X-Ray Tomography (UGCT, Belgium) in three different campaigns of 1 week each: in April, June, and November 2023. To reduce the negative impact of plant transport from the Netherlands to Belgium (2.5 h drive, ~200 km), and allow them to adjust to new conditions, the 50-day-old plants were transported to the UGCT in a room with additional daylight lamps (100 W Erco Optec QR111) 3 d before starting the first scan (see Supplementary Protocol S1 and Supplementary Fig. S1 for information about the preliminary μCT campaigns and the importance of light to generate positive xylem pressure).

Experimental design of the X-ray microcomputed tomography scans and positive xylem pressure measurements

In total, we scanned and measured the xylem pressure in 49 individual plants (14 under WW conditions, 35 under different levels of WD). To obtain a large range of WD intensities, we stopped watering the tomato plants in small subsequent batches from 2 to 3 weeks before the μCT scanning campaigns at the UGCT, for each of the three 1 week campaigns. Right before the first scan (first scan: stem of plants at 10 cm above soil), stem water potential (Ψ_{stem}) was measured on a single mature leaflet covered with light-reflective plastic bags for at least 2 h, using a pressure chamber (Model 1000, PMS Instrument Company, Albany, OR, USA), following the recommended procedures outlined in Rodriguez-Dominguez *et al.* (2022). A few moments before scanning, the leaves from the basal 20 cm of the stem were removed and the leaf scars were immediately sealed with super glue and parafilm. There are two technical reasons for removing the leaves from the basal stem parts: (i) the X-ray source had to be placed as close as possible to the stem to obtain the required resolution allowing us to visualize the dynamics of potential embolism formation/repair in the xylem vessels, and (ii) the stems needed to fit the plants in custom-made carbon-fibre tubes (CarbonWinkel.nl, Tilburg, the Netherlands) to improve the stability and straightness of the plants when they were scanned using the Environmental Micro-CT scanner (EMCT; Dierick *et al.*, 2014). It is possible that leaf removal might have slightly increased the level of native embolism at and around the scanning zone, since vessel length in tomatoes can reach 20 cm (van der Schoot and van Bel, 1989). However, this slight increase can be considered as non-significant, since our results are comparable with the vulnerability curve generated by the optical technique on non-decapitated plants (see later). Likewise, only a subset of the tomato individuals showed leaves around the scanning zone, while the average level of embolism was very similar across WW plants (see the Results). The μCT scanning parameters are detailed in the next section. After the first scan, we decapitated the plant stem at 20 cm from the soil surface, wrapping its cut end with parafilm to avoid dehydration, and immediately scanned the plant again at the same stem region (second scan: cut stem before rewatering). Once out of the μCT stage, we watered the decapitated plants several times at full pot capacity until no more water was absorbed by the soil. To avoid fast dehydration of the cut surface, we put a couple of water droplets on the stem surface with a syringe and installed a silicone tube with a pressure sensor on the top (26PCCFA6D transducer, Honeywell International, Charlotte, NC, USA; or Jumo Midas C08 manometer, Fulda, Germany) according to De Swaef *et al.* (2013). We connected the pressure sensors to a datalogger (CR1000X, Campbell Scientific Ltd, Logan, UT, USA) and recorded the amount of pressure in the water column escaping the stem surface every minute (see Supplementary Fig. S2 for the sensor installation). The third scan (thirrd scan: cut stem after rewatering) was performed at the same stem position as the previous two scans (10 cm above the soil) when the pressure sensors recorded positive xylem pressure (1–3 d after rewatering, depending on the timing of detectable positive pressure across the individuals) or at the end of the 1 week campaign if no positive xylem pressure was recorded (3–5 d after rewatering). The highest positive xylem pressure values (in MPa) during the 3 d after rewatering were taken as reference for the analyses. For a subset of plants (11 out of 49), the pressure sensor was not attached to the plants when water was observed in the silicon tube (i.e. indicating the generation of positive xylem pressure). In this case, we estimated the positive xylem pressure by using the correlation between the amount of water in the silicone tube (always measured) and the recorded pressure for the other plants that were attached to the sensor (y=0.034x+0.0003, P<0.0001, R^2=0.9). At the end of each campaign, we collected the scanned stem segment for each individual and stored it in 70% alcohol for light microscope sectioning and observation at a later stage.

In order to assess the impact of decapitating the stem on the embolism formation/removal dynamics, we also included μCT data of four intact plants (for more details, see later).

X-ray microcomputed tomography scans

The plants, fitted inside the custom-made carbon-fibre tubes, were installed on the stage of the EMCT scanner to scan the stem at ~10 cm above the soil. The tube voltage was set to 90 kV and the tube emission current to 89 μA (target power of 8 W). For every scan, a total of 1600 projections were taken over one full rotation; each projection is acquired by averaging four images with 110 ms exposure time, which resulted in the total scan run duration of 13 min. Reconstructions were semi-

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automated with a Python script in addition to the Octopus reconstruction software package (Vlassenbroeck *et al.*, 2007). The reconstructed data consisted of total stacks of 1093 reconstructed cross-sections with an approximated voxel size of 9×9×9 μm^3. To test whether µCT scanning had any effect on cell death or plant vitality, we installed one non-decapitated plant in the EMCT stage with an active X-ray source for 2 h (corresponding to ∼9 scans), prior to the three 1 week experiments. Subsequently, we brought the plant back to the Naturalis laboratory where we did not observe any damage on the stem scanning point or any growth reduction for the two following months. This confirms that the scans (3 times×13 min per plant) had no significant effect on tomato stem functioning. However, it is still possible that a few inner cells suffered minor (non-recorded) damage.

Light microscopy

In µCT scans, we were able to identify the embolized gas-filled xylem vessels (see next paragraph), appearing black, while the grey water-filled vessels were hard to distinguish from the water-filled surrounding tissue (Steppe *et al.*, 2004). To identify all the vessels in the scanned stem area, the stems were sectioned into 50–80 µm cross-sections (Reichert sliding microtome, Vienna, Austria), stained, mounted on a glass slide, and photographed (AXIO Imager M2 microscope, Zeiss, Oberkochen, Germany), after which all vessels were counted based on light microscopy images for each scanned individual. The sections were treated according to the standard protocol described by Lens *et al.* (2005). In brief, the cross-sections were submerged in household bleach for 1 min, rinsed three times in distilled water, stained for 15 s in an alcian blue/safranin (65–35%) solution (1% alcian blue in H_2O and 1% safranin in 50% ethanol), dehydrated in increasing ethanol solutions (50, 70, and 96%), submerged twice for 2 min in a 96% ethanol solution mixed with Histoclear (50–50%) (Electron Microscopy Science, Hatfield, PA, USA), and finally placed in 100% Histoclear. The cross-sections were mounted on glass slides with Euparal mounting medium (Agar Scientific, Stansted, UK) before taking the digital images.

X-ray microcomputed tomography volume and light microscopy image analysis

For every scanned tomato plant, we obtained three different µCT volumes of the stem at 10 cm above the soil: the first scan on an non-decapitated plant; the second scan on a decapitated plant before rewatering; and the third scan on a decapitated plant after rewatering at the time of positive xylem pressure development (or at the end of the campaign in the case where no positive pressure was generated). By carefully looking at the alignment, size, and shape of the embolized xylem vessels and other defining features in the outer stem parts, we selected one 2D virtual cross-section per 3D volume that best matched the image of the light microscopy section for each of the three scan time points. By doing this, we were able to compare the dynamics of xylem embolism formation–repair at the same stem position for each of the vessels in the scanned individuals.

In the three selected µCT cross-sections per individual, we: (i) counted the number of gas-filled xylem vessels, (ii) measured the total cross-sectional area of the stem in μm^2, and (iii) measured the hydrated area of the stem (i.e. segmenting the grey hydrated area from any black gas-filled area; in μm^2). In the light microscopy cross-sections, we counted the total number of xylem vessels present in every sample. We calculated the level of xylem embolism as the percentage of embolized vessels (PEV) in every scan:

$$PEV_{1-3} = (n_{\mu CT}/n_{LM}) \times 100 \quad (1)$$

where $n_{\mu CT}$ is the number of embolized vessels counted in the µCT cross-section, and n_{LM} is the total number of vessels counted in the light microscopy cross-section. The xylem vessel embolism induced by decapitating the plant (secon scan) and the number of repaired vessels (third scan) were calculated as:

$$\text{Percentage of decapitation induced embolism} = PEV_2 - PEV_1 \quad (2)$$

$$\text{Percentage of repaired vessels} = PEV_1 - PEV_3 \quad (3)$$

Where PEV_1 is the percentage of embolized vessels before rewatering (first scan), PEV_2 is the percentage of embolized vessels after cutting the plant to install the pressure sensors (second scan), and PEV_3 is the percentage of embolized vessels after rewatering (third scan). The hydrated stem area (H_A) was measured in mm^2 in every scan as:

$$H_A = S_A - E_A \quad (4)$$

where S_A is the stem cross-sectional area and E_A is the embolized area, represented by the all black (i.e. gas-filled) area within each sample, excluding the embolized xylem vessels. The relative increase in hydrated stem area was calculated as:

$$\text{Relative increase in hydrated stem area} = [(H_{A3} - H_{A1})/H_{A1}] \times 100 \quad (5)$$

where H_{A1} is the hydrated stem cross-sectional area (i.e. the grey hydrated area minus any black-gas-filled area) in plants before rewatering (first scan), and H_{A3} is the hydrated stem cross-sectional area after rewatering (third scan). Finally, the vessel diameter from all embolized vessels was estimated from the previously selected 2D slice from the first scan by measuring the area of each vessel with ImageJ and computing the equivalent circle diameter. Subsequently, by carefully comparing the first and the third scans, we differentiated between vessels that remained gas filled and vessels that were repaired after rewatering. This last analysis was limited to WD plants that repaired at least one embolized xylem vessel after rewatering (15 out of 35 plants).

X-ray microcomputed tomography versus the optical vulnerability technique

Once we obtained the level of xylem embolism before rewatering (i.e. PEV_1) in the stems of the tomato plants scanned at different WD intensities, we compared the µCT results with a previously conducted optical vulnerability (OV) experiment on different batches of tomato plants of the same age and grown under the same growth chamber conditions (see details in Bortolami *et al.*, 2024). We observed that the results obtained from µCT for xylem vessels were comparable with the percentage of embolized pixels (PEP) obtained with the optical technique on tomato stems at similar levels of water deficit (Supplementary Fig. S3). This result confirms that the embolized vessels on the µCT scans were drought induced.

Experimental validation in intact (non-decapitated) plants

To assess the impact of stem capitation on the dynamics of xylem embolism and potential repair cycles, we scanned four well-watered plants (Ψ_{stem}= −0.35 MPa) during a day/night cycle in September 2023, without recording the positive xylem pressure. These plants were grown under the same conditions as all the other plants. After the first scan (between 13.00 h and 15.00 h), we wrapped the entire canopy with aluminium foil and a large dark plastic bag in order to prevent transpiration (and potential embolism formation). A second scan was carried out the following morning (between 09 00 h and 11 00 h) to assess the level of embolism

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after one night, while maintaining the imposed dark conditions. After this second scan, the corresponding stem sections were sampled, sectioned, and analysed via light microscopy, and the level of xylem embolism was quantified during the day and after one night as described above.

Statistical analyses

We investigated the effect of water deficit on the ability of tomato plants to generate positive xylem pressure via χ^2 probability test on the number of plants that were or were not generating positive pressure, and a generalized linear mixed model using the stem water potential before rewatering (Ψ_{stem}) as a fixed effect. We tested the differences in the number of embolized vessels and the hydrated stem area with two independent generalized linear mixed models (GLMMs) using positive xylem pressure (absence or presence), watering regime (WW or WD), and rewatering (before or after) as fixed effects, and a Tukey test for the two-by-two comparisons. Since the decapitation-induced xylem embolism was limited but not entirely absent (i.e. 3±0.4% PEV), we used a GLMM on PEV levels with cutting (before or after) as a fixed effect to verify that cutting the plant did not affect xylem embolism development ($F_{1,95}$=0.16, P=0.69). Moreover, we demonstrated that decapitation-induced embolism was not related to decreasing Ψ_{stem} or increasing native PEV, it did not significantly influence the xylem vessel repairing computation, and it also did not induce a loss in xylem pressure generation and xylem repair (Supplementary Fig. S4). We tested the difference in diameter between vessels that remained gas filled and vessels that were repaired after rewatering with a GLMM using the vessel functionality as a fixed effect and the plant as a random effect, as multiple vessels were measured on the same virtual µCT cross-section. The relationships between the embolism before rewatering, positive xylem pressure, stem size, the percentage of repaired xylem vessels, and the relative increase in hydrated stem area were tested using linear regression models. All the analyses were done in SAS software (SAS 9.4; SAS Institute), using the GLIMMIX, FREQ, and REG procedures.

Results

Soil water deficit decreases positive xylem pressure development

We performed measurements of positive xylem pressure after (re)watering in 14 WW control plants and 35 water-stressed plants at different WD intensities (ranging from the onset to almost complete xylem embolization, Fig. 1). All WW plants showed positive xylem pressure, reaching the maximum pressure peaks at 0.012±0.002 MPa (average ±SE, Fig. 1), while only 31% of WD plants showed detectable positive pressure after rewatering, reaching 0.007±0.001 MPa (average ±SE, Fig. 1). Ψ_{stem} measured before rewatering had a significant effect on the amount of positive pressure generated across all plants ($F_{1,47}$=18.2, P<0.001, Fig. 1A), and on the proportion of plants in the WW and WD batches that showed positive pressure (χ^2<0.0001, Fig. 1B). However, Ψ_{stem} before rewatering did not affect the amount of positive xylem pressure in WD ($F_{1,33}$=0.02, P=0.9) or WW plants ($F_{1,12}$=0.36 P=0.6).

Quantification of xylem vessel embolism and stem cross-sectional area via X-ray microcomputed tomography

Tomato stems were scanned at 10 cm above the soil using µCT to compare the level of xylem embolism and the hydrated cross-sectional area of the stems before rewatering (referring to the first scan in non-decapitated individuals, Fig. 2A, C, E, G, I, K) and after rewatering (referring to the third scan in

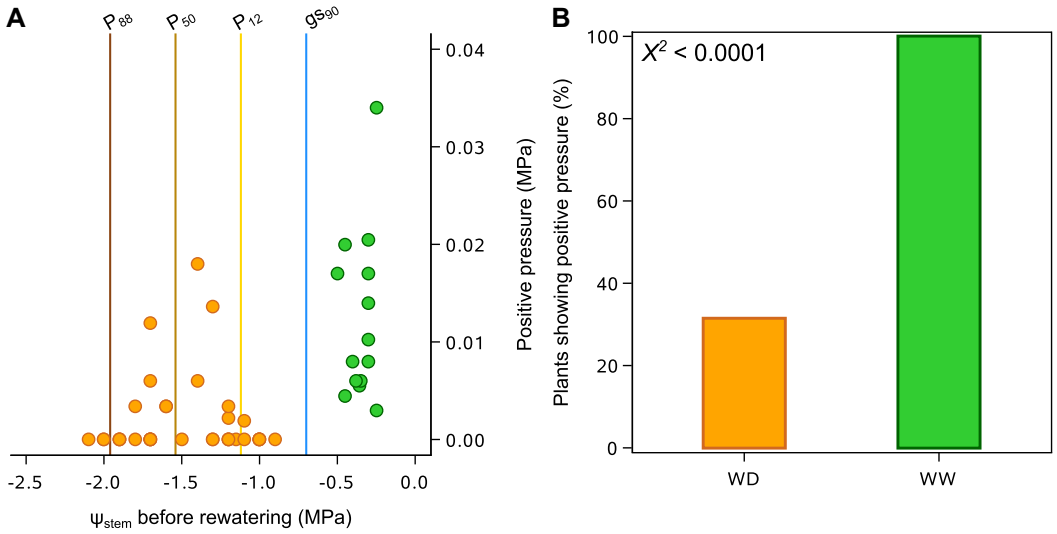


Fig. 1. Soil water deficit (WD) decreases the ability to develop positive xylem pressure in *S. lycopersicum*. (A) Relationship between the Ψ_{stem} reached before rewatering (MPa) and the maximum recorded positive xylem pressure (MPa) in the 3 d following rewatering in plants under well-watered (WW, green dots) and WD (orange dots) conditions. The vertical blue line indicates the point of stomatal closure (g_{s90}), and the yellow, brown, and red vertical lines refer to the different levels of embolism development in the stem xylem (P_{12}, P_{50}, and P_{88}, respectively) measured via the optical vulnerability technique. g_{s90}, P_{12}, P_{50}, and P_{88} values were obtained from Bortolami et al. (2024). (B) Frequency of plants showing detectable positive xylem pressure under WD (orange bar) and WW (green bar) conditions. The significance of the χ^2 test is indicated.

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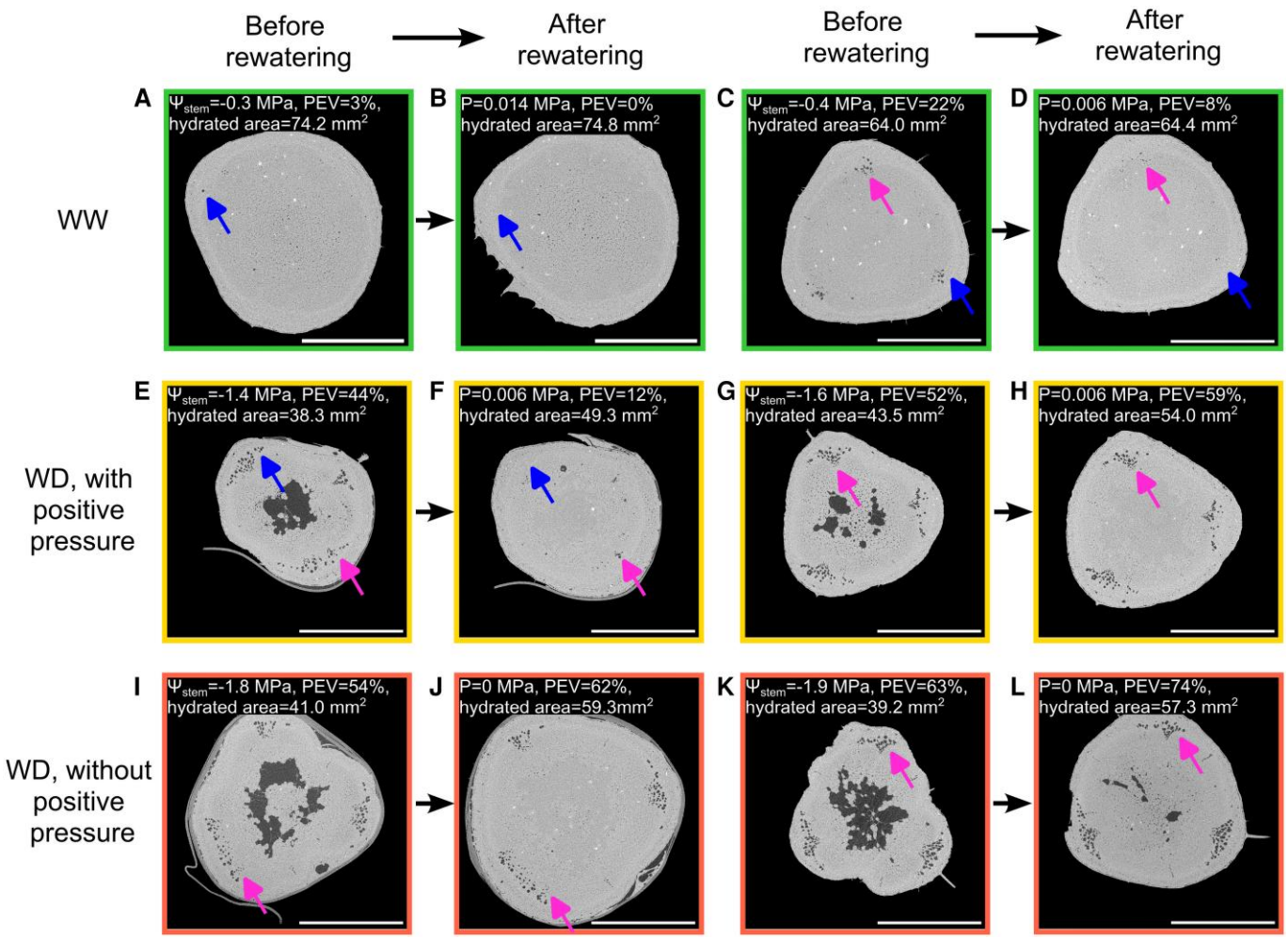


Fig. 2. Cross-sections of the μCT volume of tomato stems in six individuals before and after rewatering show different embolism repair dynamics. After the first μCT scans in plants before decapitation (A, C, E, G, I, K), the stems were cut, rewatered, and scanned again after 1–5 d (B, D, F, H, J, L). Significant xylem embolism repair is detected in the WW plants (green, A–D) and rarely in the WD plants with positive xylem pressure after rewatering (yellow, E–H), but never in the WD plants without detectable xylem pressure after rewatering (red, I–L). The selected cross-sections show the same location in the stem for the six individuals before and after rewatering (10 cm above the soil). The Ψ_{stem} (MPa) before rewatering, the amount of positive xylem pressure (P, MPa) after rewatering, the proportion of embolized vessels (PEV, %), and the hydrated stem area (mm^2) are indicated for the three individuals. Scale bars correspond to 5 mm. The blue arrows indicate the xylem vessels able to change their status from gas-filled (black) to water-filled (grey), while pink arrows indicate xylem vessels remaining embolized after rewatering.

decapitated individuals, Fig. 2B, D, F, H, J, L). We observed that for all the WW plants, the majority of the few embolized vessels were repaired in almost all (13 out of 14) individuals (Fig. 2A–D). More specifically, the embolism before rewatering in WW plants declined from an average (±SE) of 5±1% of embolized vessels (PEV) to 2±1% PEV after showing detectable positive xylem pressure (Fig. 3A, B). To cross-validate this result, we also scanned four WW plants that remained intact during a day/night cycle (Supplementary Fig. S5), without recording the amount of positive xylem pressure. We observed that the PEV changed from 1.5% (during the day) to 0.8% (after one night) on average. For the water-stressed plants subjected to different WD intensities (n=35), we subdivided them into two subgroups: WD plants developing positive xylem pressure after rewatering (n=11, coloured yellow in Figs 2 and 3), and plants that did not show detectable positive pressure after rewatering (n=24, coloured red in Figs 2 and 3). Based on the 11 WD plants showing positive xylem pressure after rewatering, five of them were able to substantially repair xylem embolism, ranging from an average of 53.3±9% PEV before rewatering to 20±9% PEV after rewatering (Figs 2E, F, 3B), while the six remaining WD plants showed no or slight differences in the number of embolized vessels before and after rewatering (Fig. 2G, H, yellow dots near the 1–1 line in Fig. 3B). Overall, these 11 WD plants ranged from an average of 43±6% PEV before rewatering to 29±6% PEV after rewatering (Fig. 3A). For the 24 WD plants where we did not record positive xylem pressure (Figs 2I–L, 3), no substantial differences in

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xylem embolism were found after rewatering: only nine were able to slightly repair xylem embolism (never more than 10% PEV, red dots below the 1–1 line in Fig. 3B), while the majority of them even showed a small increase in xylem embolism (Fig. 2I–L, red dots above the 1–1 line in Fig. 3B). Overall, these 24 WD plants without detectable positive xylem pressure increased their embolism levels from 43±4% PEV before rewatering to 45±5% PEV after rewatering (Fig. 3A). We found that only the watering regime (WW and WD) had a significant effect on PEV levels ($F_{1,94}$=37, P<0.0001), while neither the presence or absence of positive xylem pressure nor rewatering influenced PEV. PEV results are summarized in Supplementary Fig. S6. We noticed that decapitation did not significantly alter PEV, or the capacity of the plant to develop

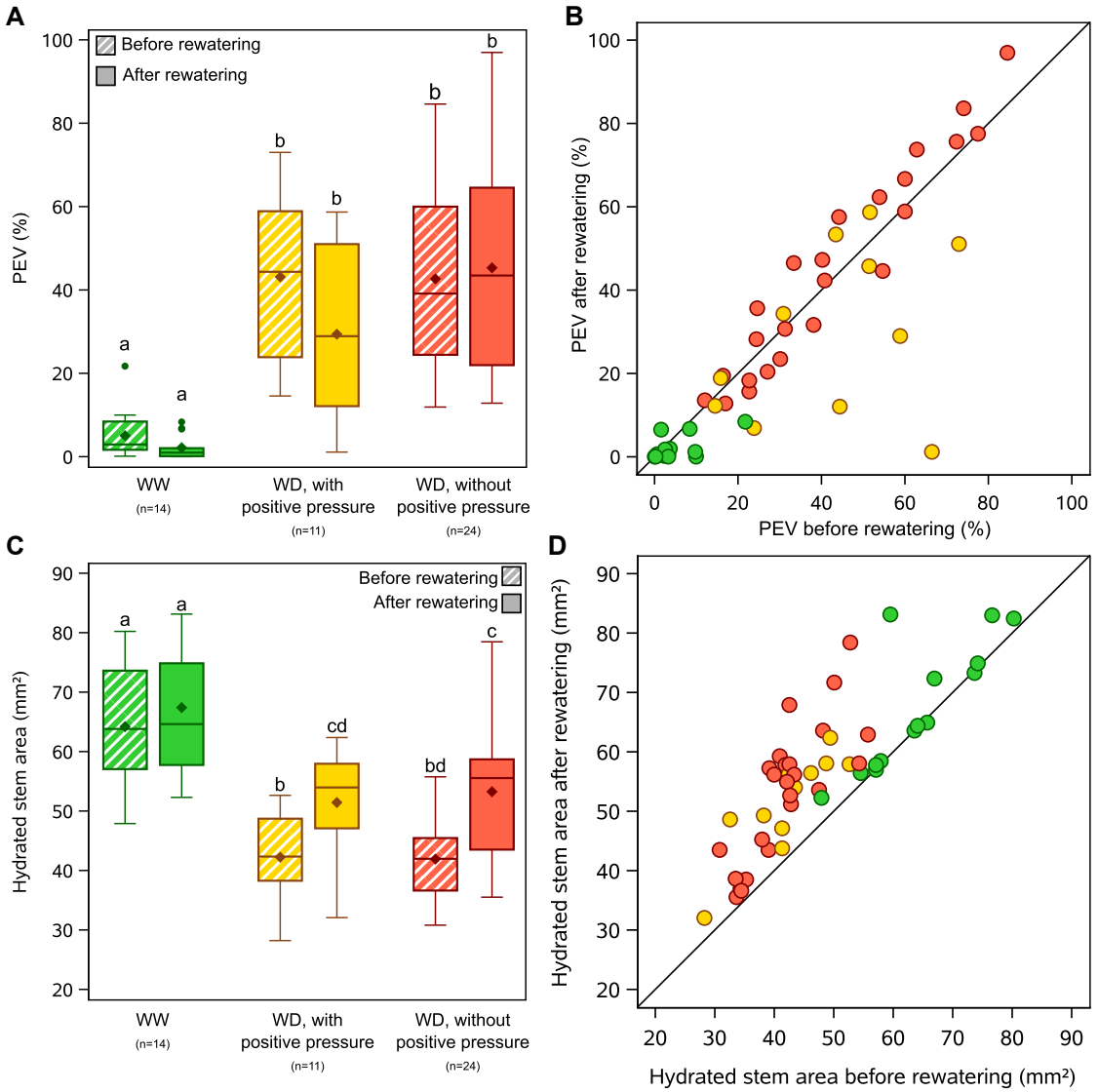


Fig. 3. Embolized xylem vessels and hydrated area of tomato stems. (A) Percentage of embolized vessels (PEV) slightly dropped in WW plants (green) and WD plants showing positive xylem pressure (yellow) after rewatering, but further increased in WD plants not developing detectable positive pressure (red). PEV was counted in the µCT cross-sections from the first scans (i.e. PEV before rewatering, striped boxes) and third scans (i.e. PEV after rewatering, full boxes). (B) Relationship between PEV before and after rewatering (%) counted in the µCT cross-sections. Symbols represent individual WW plants (green), WD plants showing positive xylem pressure (yellow), and WD plants without detectable positive pressure (red). Circles below the black 1–1 relationship line represent individuals with xylem embolism repair after rewatering, which is most prominent in some of the WD plants that were capable of developing xylem pressure. (C) Hydrated stem area (mm^2) in the µCT cross-sections from the first and third scans, showing a significant increase in stem area after rewatering in the WD individuals. Box colours and patterns are the same as in (A). (D) Relationship between the hydrated stem area before and after rewatering (mm^2) measured in the µCT cross-sections, showing a subtle to substantial increase in stem area in the WD plants after rewatering and a status quo in most WW plants. Symbols represent individual plants with the same colour code as (B). The black line represents the 1–1 relationship. In (A) and (C), boxes and bars show the medians, quartiles, and extreme values, diamonds within boxes correspond to means, and circles outside boxes correspond to outlier values.

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root pressure or xylem repair (Supplementary Fig. S4). However, the decapitation-induced embolisms are more relevant in WD plants compared with WW plants (Supplementary Fig. S4). In terms of hydrated stem cross-sectional area (Fig. 3C, D), all WD plants slightly to substantially increased their hydrated stem surface upon rewatering, while most WW plants maintained the status quo. Indeed, WW plants showed the lowest increase, ranging from 64±2 mm^2 to 67±3 mm^2 (Fig. 3C, D). WD plants with detectable positive pressure after rewatering increased their hydrated stem area from 42±2 mm^2 before rewatering to 51±3 mm^2 after rewatering (Fig. 3C, D). Similarly, WD plants without detectable positive pressure increased their hydrated area from 42±1 mm^2 to 53±2 mm^2 after rewatering (Fig. 3C, D). The watering regime ($F_{1,94}$=50.1, P<0.0001) and rewatering ($F_{1,94}$=20.2, P<0.0001), but not the presence of positive xylem pressure, had a significant effect on the hydrated stem area.

The dynamics of xylem vessel repair upon rewatering

By comparing the scans from all the individuals, we observed that gas embolism spread in the xylem occurs in a radial direction from the inner primary xylem vessels towards the later formed secondary xylem vessels during decreasing Ψ_{stem} (Supplementary Fig. S7). In contrast, subtle xylem vessel repair (in plants with or without positive xylem pressure) showed more complex spatial dynamics (Fig. 4). In nine WD plants (out of 15 showing some degree of xylem vessel repair), we observed vessel repair only in the vessels closer to the cambium, while the majority of vessels positioned further away from the cambium remained embolized (as in Fig. 4A, B). In five other WD plants, subtle xylem embolism repair was more randomly scattered, as shown in Fig. 4C and D. One WD plant almost completely removed the gas embolism from the xylem after rewatering, making it impossible to reconstruct the dynamic sequence of events from a gas-filled to a water-filled xylem (Fig. 4E, F). These different spatial repair dynamics were not related to the level of embolism repair or the detection/intensity of positive pressure (Fig. 5). When comparing vessel lumen diameter between vessels that remain embolized versus vessels that were repaired after rewatering, no significant difference was observed ($F_{1,2702}$=0.01, P=0.92, Supplementary Fig. S8).

The potential impact of positive xylem pressure, stem size, and xylem embolism before rewatering on vessel repair and water storage refilling upon rewatering

We observed that there was no linear relationship between the capacity of plants to repair their xylem vessels and to increase their stem hydrated area upon rewatering (Fig. 5). We then analysed several intrinsic traits that might have influenced this large variability in the ability of the plants to recover from embolism in the stem after rewatering (Fig. 6). Higher values of detectable positive xylem pressure only slightly influenced (positively) the capacity of the plant to remove embolism from the xylem vessels (P=0.04, R^2=0.12, standardized regression coefficient β=0.34, Fig. 6A), but did not influence the stem hydrated area changes (P=0.6, Fig. 6D). Smaller stems did not influence the chance of xylem vessel repair after rewatering but decreased the capacity of the stem to rehydrate its area (Fig. 6B, E). Finally, higher levels of embolism before rewatering positively influenced the relative increase in hydrated stem area but not xylem vessel repair (Fig. 6C, F).

Discussion

In this study, we show four main results: (i) periods of WD strongly reduce the capacity of tomato plants to generate positive xylem pressure after rewatering (Fig. 1); (ii) positive xylem pressure in WD plants after rewatering is not linked with the occasionally observed xylem vessel repair (Figs 2, 3), but WD plants are much better able to replenish their internal stem water storage, mostly in the pith region (Figs 2, 3); (iii) under WW conditions and sufficient light intensity, positive xylem pressure in tomato plants can almost completely repair the few embolized vessels in stems (Figs 1–3); and (iv) decapitation did not significantly affect embolism formation and repair based on comparison of scans within the same decapitated WW and WD individuals (Supplementary Fig. S4) and using μCT observations on four non-decapitated WW individuals (Supplementary Fig. S5). These results suggest that positive xylem pressure in tomato plants can prevent the xylem from reaching the point of exponential embolism spread during WW conditions, possibly driven by atmospheric drought. Additionally, the recovery of the stem hydraulic capacitance after WD suggests water flow via the non-xylary, symplastic pathway towards the pith cells (Figs 4–6).

Positive xylem pressure does not efficiently promote xylem embolism repair after soil water deficit in tomato plants

Based on our observations that soil WD strongly hampered the ability of tomato plants to develop positive xylem pressure after rewatering, we can convincingly state that positive xylem pressure is not an efficient mechanism in tomato stems to repair drought-induced xylem embolism. Out of the 35 individuals that were subjected to different WD intensities and subsequent rewatering, 11 showed detectable positive xylem pressure, of which only five individuals were able to substantially repair the xylem embolism generated by drought at 10 cm above the soil (Fig. 3). Among these five individuals subjected to WD, it is unknown whether the repaired vessels were connected to the functional root-to-shoot water transport or rather were blocked by embolized vessels in upper stem parts. Our results agree with the consensus that xylem repair is not routine in herbaceous or woody plants after soil water drought (Cochard and Delzon, 2013; Johnson *et al.*, 2018; Lamarque *et al.*, 2018; Stewart *et al.*, 2026), and contradict the observations in the herbaceous monocots sorghum (Drobnitch *et al.*, 2021) and

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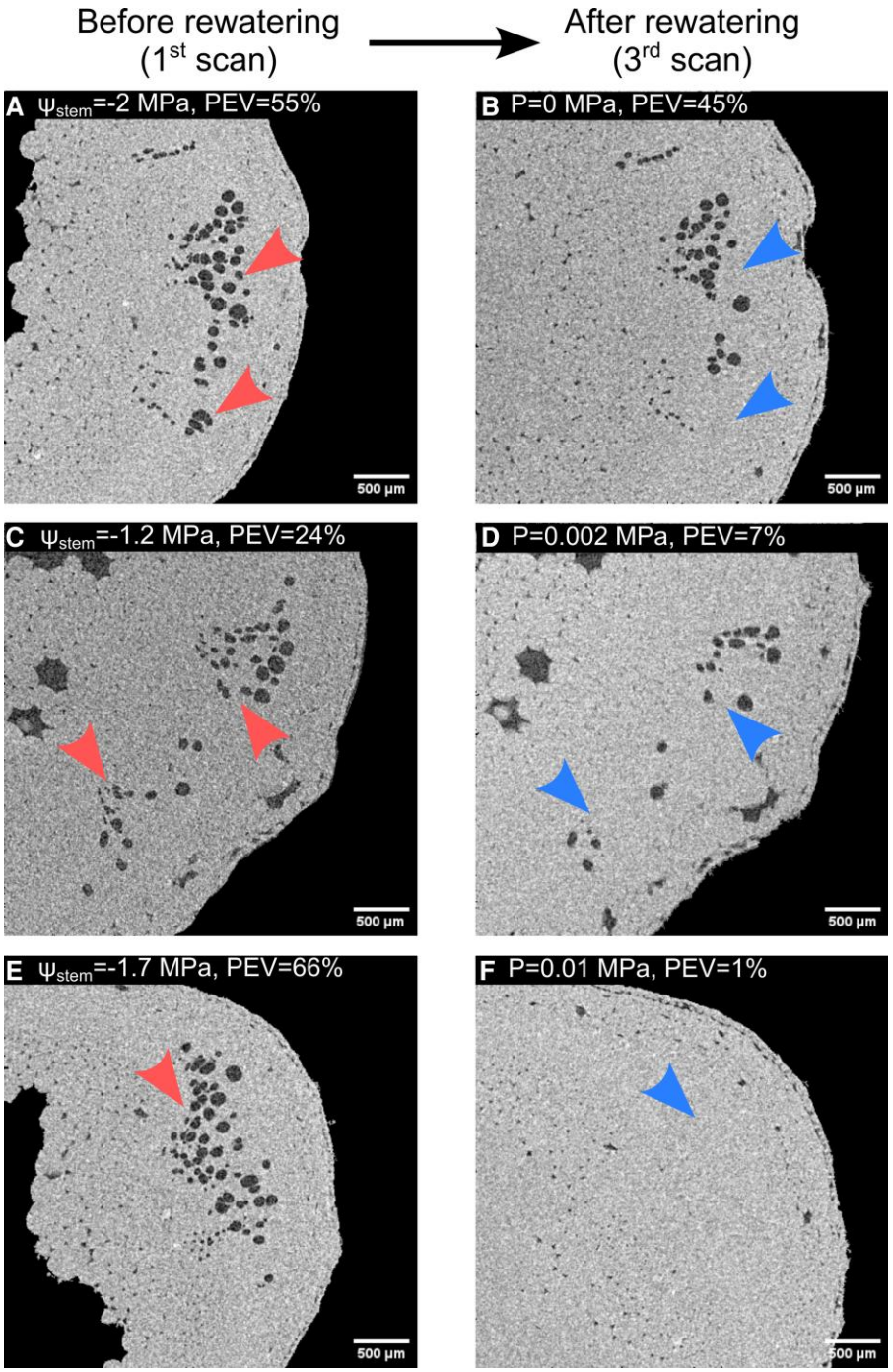


Fig. 4. Dynamics of xylem embolism repair in tomato. 2D reconstructions of cross-sections from µCT volumes of tomato stems showing repair of xylem embolism. The scans were taken at the same spot in three different plants before (A, C, E) and after (B, D, F) rewatering. The arrows indicate xylem vessels that changed their status from gas-filled (red arrows) to water-filled (blue arrows) after rewatering. Vessel repair showed roughly two different patterns among the 15 WD plants that were able to (partly) recover from xylem embolism: most of the plants (nine) repaired only the most recently formed vessels (A, B), and five plants showed a random pattern of embolism repair (C, D). In one remaining WD individual, xylem embolism repair was almost completed (E, F). The Ψ_{stem} (MPa) before rewatering, the amount of positive xylem pressure (P, MPa) after rewatering, and the number of embolized vessels (PEV, %) are indicated for every sample. Scale bars correspond to 500 µm.

maize (Gleason *et al.*, 2017), and in the woody eudicot *Vitis* spp. (Knipfer *et al.*, 2015; Charrier *et al.*, 2016) where positive pressure was enhanced by rewatering after WD (compared with WW conditions) and associated with xylem vessel repair (Knipfer *et al.*, 2015; Charrier *et al.*, 2016). It is worth noting that we are lacking µCT scans on intact WD plants that would

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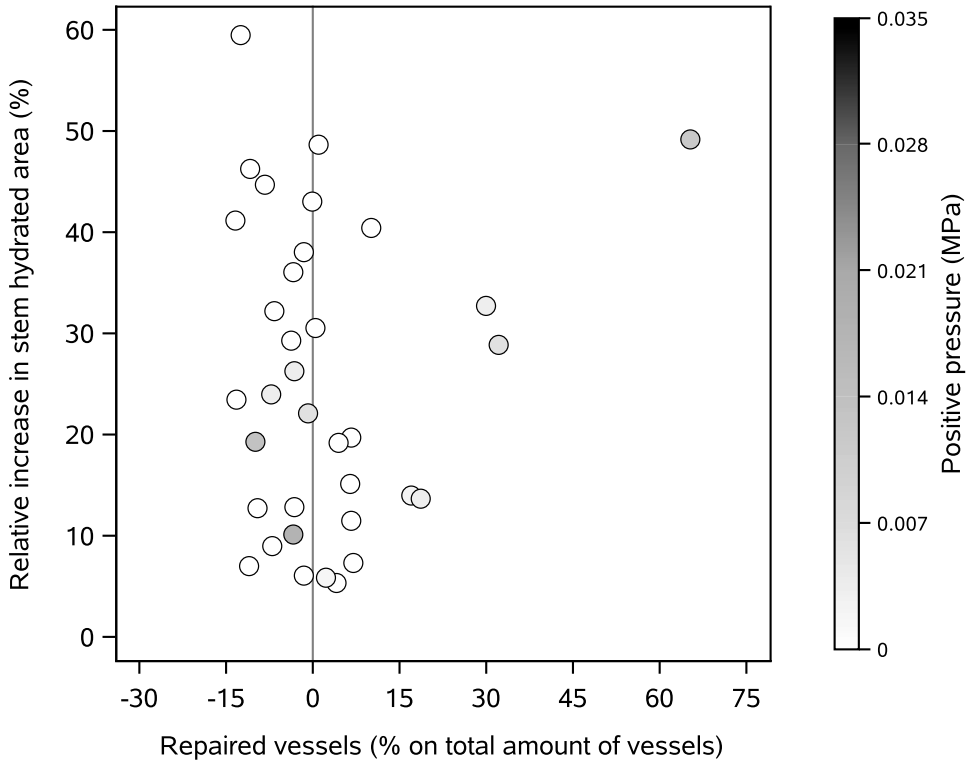


Fig. 5. No link between the capacity of WD plants to repair embolized xylem vessels and to recover their stem area. Relationship between the number of repaired vessels (% compared with the total number of vessels) and the relative increase in stem hydrated area (%) after rewatering. Circles represent single replicates, and their colour indicates the recorded positive xylem pressure after rewatering from white (no pressure recorded) to black (maximum: 0.035 MPa).

have nicely complemented our main results based on decapitated plants. However, since stem decapitation did not influence positive pressure generation or xylem repair dynamics (Supplementary Fig. S4), we assume that any potential decapitation artefact did not have a major impact on the main results during the 1 week μCT experiment.

It remains an open question why we observed the variability in detectable positive xylem pressure and the associated differences in xylem repair among the WD plants after rewatering, and why the stress intensity does not directly influence the recovery capacity. This question is linked to the incomplete understanding of the mechanism(s) underlying positive xylem pressure. As reviewed by Schenk *et al.* (2021), two non-mutually exclusive mechanisms can contribute to water movement under pressure: (i) the osmotic exudation due to a gradient in osmotic water potential from the soil to the vessel-associated cells in the xylem; and/or (ii) the hydraulic pressure through activation of aquaporins and H^+-ATPase pumps. It has been recently shown that tomato plants increase suberin deposition in the cell walls of the root exodermis following WD (Cantó-Pastor *et al.*, 2024). Although we have not investigated the root anatomy, a thickened exodermis might decrease the osmotic-driven soil-to-xylem water flow even after rewatering when the soil osmotic potential is near zero. Moreover, WD might have caused an irreversible disruption of the soil–root conductance by destroying fine roots and root hairs (Koch *et al.*, 2025), with a potential subsequent loss in xylem pressure generation. Furthermore, stomatal closure in tomato plants happens very early at the onset of drought, thereby strongly reducing photosynthesis even during mild drought conditions (Bortolami *et al.*, 2024). As WD conditions are prolonged, this may lead to a shortage in the movement of soluble sugars towards the roots and stems, which in turn may increase the osmotic potential (i.e. becoming less negative) in the vessel-associated cells and/or inactivate the aquaporins and H^+-ATPase pumps in the different root compartments. Our observation that WW plants growing in darker daytime conditions generated substantially lower values of positive xylem pressure (Supplementary Fig. S1, confirmed by Papanov *et al.*, 2020) supports this hypothesis, since photosynthesis and phloem flux are light dependent (Sellier and Mammeri, 2019; Miyoshi *et al.*, 2023). The potential role of phloem unloading in developing positive xylem pressure is consistent with its light dependency (Papanov *et al.*, 2020). Interestingly, the fact that nearly all the decapitated WW plants were able to generate positive xylem pressure after the stem–leaf continuum was disrupted highlights the involvement of redundant mechanisms in addition to phloem unloading. In conclusion,

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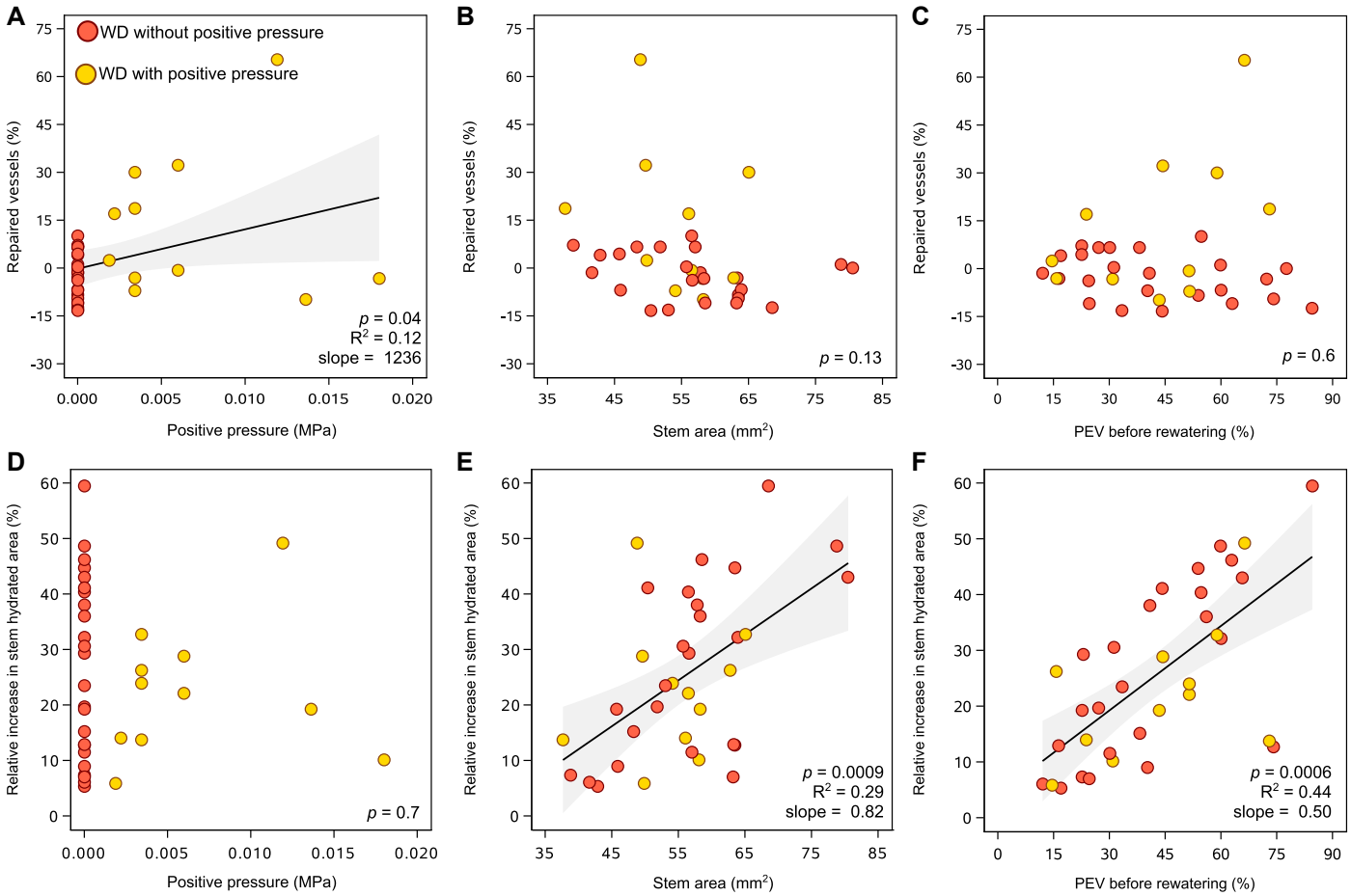


Fig. 6. The potential role of three selected functional traits on vessel repair and relative increase in stem area after rewatering in WD plants. (A) Positive xylem pressure (MPa) has a slight positive effect on xylem embolism repair after rewatering (number of repaired vessels compared with the total number of vessels). (B) No correlation between stem area (mm^2) and percentage of repaired vessels after rewatering. (C) No correlation between xylem embolism before rewatering (PEV) and percentage of repaired vessels after rewatering. (D) No correlation between positive xylem pressure (MPa) and relative increase in stem hydrated area (%). (E) Larger stem area (mm^2) is correlated with a higher relative increase in stem hydrated area after rewatering. (F) Higher xylem embolism before rewatering (% PEV) is linked with a higher relative increase in stem hydrated area after rewatering. For every panel, symbols represent single replicates, colours represent WD plants with positive xylem pressure (yellow) and WD plants without detectable positive xylem pressure (red), and lines refer to the linear regressions, with shaded areas showing the 95% confidence intervals. For the significant relationships, the *P*-values, R^2, and the slope of the linear regression analyses are indicated within each panel. For the non-significant relationships, only the *P*-values are indicated.

positive xylem pressure in tomato plants is heavily impacted by soil WD due to a range of potential changes in root anatomy (e.g. suberin deposited in outer root layers), availability of soluble sugars, sufficient light conditions, and/or other unknown variables, meaning that there are several potential reasons why rewatering does not consistently result in detectable positive xylem pressure and vessel embolism repair.

Rehydration of stem water pools after water deficit is substantial, and unlikely to be related to positive xylem pressure

Our results clearly show that the extra xylary tissue can be rehydrated more easily than xylem vessels upon rewatering WD plants (Fig. 3). The expansion of these stem tissues following rewatering agrees with studies finding a clear relationship between stem (or petiole) diameter and water potential (Bourbia and Brodribb, 2023; Peters *et al.*, 2025; Harrison Day *et al.*, 2026). This emphasizes the role of stem capacitance and internal water storage pools during tomato recovery from drought. Hydraulic capacitance in plant organs relates to the amount of water they can internally store or release per unit of water potential variation, and has been highlighted as an important functional plant trait related to drought tolerance (Steppe and Lemeur, 2007; Epila *et al.*, 2017; Salomón *et al.*, 2017; De Boeck and Steppe, 2025). This holds especially true for herbaceous plants and stem succulents such as cacti that have stems with abundant living parenchyma tissues (Nobel *et al.*, 1992; Corso *et al.*, 2020; Verbeke *et al.*, 2023), and also in leaves where the decline in water content outside

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the xylem is an important intrinsic cue at the beginning of drought stress (Scoffoni *et al.*, 2014, 2017). However, the role of hydraulic capacitance during the recovery phase from drought remains incompletely known. Outside-xylary water is mostly thought of as an internal water reservoir that can temporarily delay water shortage periods (Gleason *et al.*, 2014; Degraeve *et al.*, 2021; Pereira *et al.*, 2024). Interestingly, we observed that all WD tomato plants were able to (almost completely) recover their stem area and rehydrate their parenchyma cells (especially in the central pith), independently of their capacity to develop detectable positive xylem pressure. Such water redistribution usually occurs at night under WW conditions, when cells that have been depleted during the day due to transpirational water loss are rehydrated, thereby restoring their turgor pressure, which in turn enables cell division and plant growth (Steppe *et al.*, 2006, 2015). This cell-to-cell water movement is typically governed by a water potential gradient, with water flowing from regions of less negative (or zero to positive) water potential (e.g. the xylem) towards regions of more negative water potential (e.g. extracellular spaces and living tissues, Steppe *et al.*, 2006, 2015). This mechanism of symplastic water movement is in line with our observations related to stem area rehydration and recovery: more stressed plants also restore water pools more efficiently (Fig. 5F), confirming that more negative water potentials attract more water into gas-filled parenchyma cells. Our results mostly suggest that this symplastic water pool is not connected to the root-to-leaf water flow as plants can: (i) more easily rehydrate the empty (air) space in the stems and not the xylem vessels (Fig. 5) and (ii) in the rare cases of vessel repair, this is not systematically related to a precise spatial pattern (Fig. 4). Moreover, since larger stems (and therefore a larger amount of hydrated tissue) are not related to a better vessel repair (Fig. 6B), we can exclude that the water flowing via the cell-to-cell pathway might require a longer time (our experiment is based on a 1 week window) to build up enough turgor in the cells to develop positive pressure and subsequent vessel recovery.

Summarizing, this dynamic water exchange between xylem vessels and the surrounding tissues highlights the complexity of xylary and non-xylary water pathways, especially in critical survival stages such as the recovery period. For instance, Stewart *et al.* (2025) showed that barnyard grass (a herbaceous monocot) can repair xylem embolism before recovery of the surrounding tissues, while *Pleopeltis polypodioides* (an epiphytic resurrection fern) rehydrates the non-vascular tissues before showing tracheid embolism repair (Prats and Brodersen, 2021), suggesting that recovery strategies can be lineage specific. While the regular embolism spread through the xylem vessel network (from the inner to the outer vessels) demonstrates that the primary xylem is more vulnerable to embolism (Supplementary Fig. S7), the random spatial arrangement of the few repaired vessels suggests that multiple water pathways (both symplastic and aploplastic) are involved with temporal and spatial dynamics that remain obscure (Fig. 4; Steppe *et al.*, 2012; Hubeau and Steppe, 2015). For instance, the vessels that are closer to the cambium could be rehydrated by the phloem via transversal rays, while the inner xylem conduits could be rehydrated by water coming from the inner parenchyma cells in the pith area, and both could receive water from downstream vessels that are still functional. We conclude that these dynamic water movements in non-xylary tissues of herbaceous species are often ignored (Skelton *et al.*, 2017), and advocate that they probably play a more important role in plant survival of forbs and grasses than anticipated.

Positive xylem pressure repairs subtle losses in daily xylem conductivity in tomato stems under well-watered conditions

Although cycles of substantial embolism formation and repair on a daily basis have been documented in the literature (Salleo *et al.*, 2004; Nardini *et al.*, 2011; Venturas *et al.*, 2017), there is increasing evidence that widespread levels of embolism in the field are not routine and are mainly limited to periods of severe drought (Cochard and Delzon, 2013; Delzon and Cochard, 2014; Lens *et al.*, 2022). This does not, however, contradict observations of mild levels of xylem embolism throughout the growing season under normal natural conditions, as reported for herbaceous (<20% loss of stem conductivity, Lens *et al.*, 2016) and various temperate tree species (<20% loss of stem conductivity, Wason *et al.*, 2018; Guan *et al.*, 2022). Indeed, we found subtle levels of xylem embolism (on average 5% of embolized vessels) in the stems of tomato plants even under controlled WW conditions. We acknowledge here that cutting leaves close to the scanning zone due to practical constraints might have slightly increased the level of native embolism in our plants during the first scan. However, when comparing the results with the optical technique, we can confirm that these changes are subtle (Supplementary Fig. S3). Moreover, the overall decapitation effect was limited, especially in WW plants (Supplementary Fig. S4), and the validation of the results by scanning intact (i.e. non-decapitated) WW plants during a night/day cycle confirms that plant decapitation did not significantly influence our results. After positive xylem pressure had consistently been detected in the WW individuals, the average percentage of embolized vessels slightly dropped from 5% to 2%. This indicates that positive xylem pressure does not completely repair the subtle levels of xylem embolism. Does this mean that it is not relevant for a tomato plant to partly recover from these minor losses in xylem hydraulic conductivity?

Although we did not assess whether the few repaired vessels were actually functionally contributing to the root-to-shoot water transport system or whether the repaired vessels would be more vulnerable to recurrent embolism (Hacke *et al.*, 2001; Bouda *et al.*, 2019), we argue that partly recovering from daily minor losses in xylem conductivity is important under, both declining and high soil water content. First,

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when soil water content decreases, subtle embolism repair dynamics during the night-time may have important consequences for the spread of gas in the 3D conduit network. Like most vascular species, tomato plants present a sigmoidal vulnerability curve (Supplementary Fig. S3), indicating that the spread of gas in the vascular tissue exponentially increases at a certain threshold, which is defined by the pressure inducing 12% loss of hydraulic conductivity (P_{12}). In this context, even repairing 3% of the vessels might be an important avoidance strategy to delay reaching the P_{12} threshold, thereby avoiding a rapid embolism spread in the vasculature. Second, when soil water content is sufficiently high, plants might benefit from partly repairing the embolized vessels during atmospheric water deficit periods [i.e. when the atmospheric vapour pressure deficit (VPD) increases]. It has been observed that when VPD increases (i.e. with high temperatures and low relative air humidity), xylem embolism can spread in the vascular tissue even under sufficient soil moisture (Schönbeck *et al.*, 2022). Consequently, nocturnal positive pressure peaks could be important in sensitive species by repairing the few most vulnerable vessels that embolized during the warmest hours of the previous day (Jacobsen and Pratt, 2012; Venturas *et al.*, 2017), thereby removing part of the VPD-induced embolism and preventing the vascular system from reaching P_{12}. This theory is also reinforced by our observation that after removing the day/night cycles, xylem pressure generation was greatly reduced.

Conclusion

Our results show that most tomato plants subjected to soil WD cannot repair embolized xylem vessels after rewatering, but they can rehydrate the inner part of their stems (pith parenchyma cells) that may or may not be linked to the transpiration pathway. We also demonstrate that positive xylem pressure can consistently repair some of the few embolized vessels that arose during the day under WW conditions due to evaporative demands. The combination of both (subtle) xylem vessel repair and (substantial) internal water storage replenishment in tomato stems indicates that refilling of gas-filled cells happens via two non-mutually exclusive mechanisms: (i) fine-scale adjustment of xylem conductance directly driven by positive xylem pressure (especially in WW plants, but strongly hampered in WD plants after rewatering); and (ii) substantially rehydrating non-xylary parenchyma tissues via different sources of dynamic cell-to-cell water flow (becoming the more dominant process after post-drought rewatering). These findings demonstrate how water-use strategies in vulnerable crops support drought recovery, with important implications for the agro-industry in securing tomato yields both in greenhouses and in the field.

Supplementary data

The following supplementary data are available at *JXB* online.

Fig. S1. Positive effect of light intensity on the generation of positive xylem pressure under well-watered conditions.

Fig. S2. Photograph of pressure sensors installed on decapitated plants.

Fig. S3. Vulnerability curve comparison of tomato stems between X-ray μCT observations and the optical technique.

Fig. S4. Decapitation did not influence tomato stem repair dynamics.

Fig. S5. Cross-sections of the μCT volume of tomato stems in intact (i.e. non-decapitated) individuals following a day/night cycle.

Fig. S6. Point-by-point PEV during the μCT experiment.

Fig. S7. Vessel embolism dynamics in tomato stems follow a radial direction from the inner towards the outer xylem.

Fig. S8. Vessel diameter is not correlated with embolism repair.

Protocol S1. Preliminary μCT campaigns highlighting the positive impact of light on developing positive xylem pressure.

Dataset S1. Dataset from μCT reconstruction analyses, light microscopy, water potential, and positive pressure records.

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Author contributions

GB, FL, KS, JVdB, and ML: planned and designed the research; GB, SB, MB, IF, TG, IJ, PK, ML, LdL, NAPZ, AT, ST, RV, JVA, BvH, and MvU: performed experiments; GB: analysed the data; GB, FL, KS, and JVdB: wrote the manuscript with contributions from all authors.

Conflict of interest

The authors declare no competing interest.

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Data availability

Collected data are available in the supplementary data. The raw μCT volumes and light microscopy pictures can be shared on request to the corresponding author.

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