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In Brief

Escaping the drought: the OST1-VOZ1 module regulates early flowering in tomato

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The decision to flower is a critical developmental step in plants, as it marks the transition from the vegetative to the reproductive stage. In agriculture, the timing of flowering is crucial and any interference such as drought can reduce yield. In general, plants regulate drought responses through the abscisic acid (ABA) signaling pathway (Zhu, 2016), often leading to accelerated flowering and a shortening of the plant life cycle, a process known as drought escape. ABA downstream targets include OPEN STOMATA 1 (OST1), a kinase that is produced in guard cells and controls ABA-induced stomatal closure. In Arabidopsis (*Arabidopsis thaliana*), ABA- and drought-induced stomatal closure are impaired in *ost1* mutants, but no obvious developmental phenotypes have been reported.

In a new publication, **Leelyn Chong, Rui Xu, Pengcheng Huang,** and colleagues (Chong et al., 2022) reveal that OST1 plays an important part in drought-induced flowering in tomato (*Solanum lycopersicum*). Using BLAST, the authors identified SlOST1, a tomato protein with high sequence identity to Arabidopsis OST1. They then used genome editing to create tomato mutants defective in *SlOST1*. Following exposure to drought stress, wild-type plants were able to recover when rewatered, but the *slost1*-mutant plants did not. The *slost1* plants also suffered from higher water loss and had a lower leaf surface temperature, indicative of open stomata. Strikingly, they flowered later than wild-type plants. Since SlOST1 is a kinase, the authors set out to investigate SlOST1 phosphorylation targets. Using a phosphoproteomics approach they had developed in an earlier study (Hsu et al., 2018), the authors identified the transcription factor VASCULAR PLANT ONE-ZINC FINGER 1 (SlVOZ1) as a potential SlOST1 substrate, which they confirmed using recombinant SlOST1 and SlVOZ1 proteins and by showing direct interaction between these proteins in vivo. This observation raised an obvious question: how does phosphorylated VOZ1 differ from the unphosphorylated protein? The authors noticed that SlVOZ1 is quickly degraded when incubated with tomato protein extracts. By contrast, phosphorylated SlVOZ1 appeared resistant to degradation, suggesting that phosphorylation of SlVOZ1 is crucial for its stability. Experiments conducted in vitro and in protoplasts then showed that ABA treatment increases SlVOZ1 phosphorylation, a step that is mediated by SlOST1. When the authors examined the localization of SlVOZ1, they detected phosphorylated SlVOZ1 predominantly in the nucleus; in addition, ABA treatment enhanced this translocation from the cytosol.

Chong, Xu, Huang, and coworkers then turned to SlVOZ1 and generated mutants in *SlVOZ1* via genome editing. They discovered that, compared with wild-type plants, *slvoz1* mutants were late flowering under long-day growth conditions and exhibited several phenotypes typical of decreased drought tolerance. Finally, by using DNA affinity purification sequencing (DAP-seq), luciferase reporter assays, and electrophoretic mobility shift assays, they were able to demonstrate that SlVOZ1 directly binds to the promoter of *SINGLE FLOWER TRUSS* (*SFT*) to activate its transcription. SFT is the tomato ortholog of Arabidopsis FLOWERING LOCUS T, also known as the flowering hormone florigen.

SFT has been implicated in influencing fruit yield in tomato (Krieger et al., 2010) and these results reveal important details about flowering and its response to drought stress. By combining different in vivo and in vitro methods, Chong, Xu, Huang et al. provide a probable mechanism by which tomato plants respond to drought: The ABA signaling pathway activates the kinase

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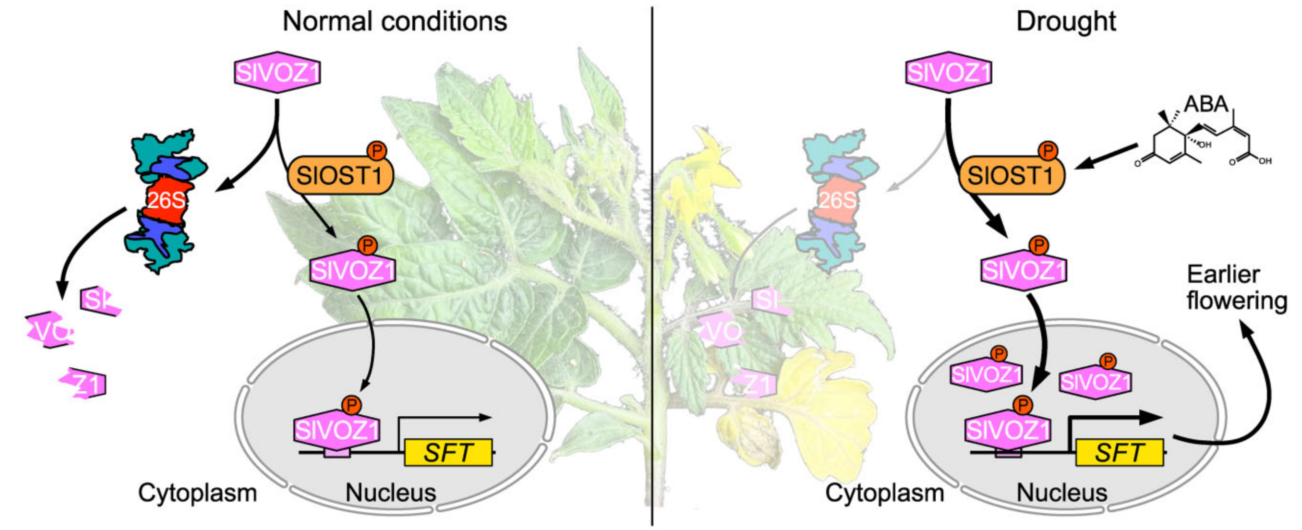

Figure The OST1-VOZ1 module regulates drought and flowering in tomato. Drought induces ABA production, which activates the kinase OST1, in turn phosphorylating VOZ1. The phosphorylated form of VOZ1 is more stable, translocates to the nucleus, and activates *SFT* transcription. Adapted from Chong et al. (2022).

OST1, which phosphorylates the transcription factor VOZ1. Phosphorylated VOZ1 then translocates from the cytosol to the nucleus and activates *SFT* transcription (see Figure). It remains to be established whether other flowering genes are also regulated by the OST1-VOZ1 module. Finally, it will be interesting to see how general the role of OST1 in flowering transition is in different plant species. The data provided by Chong, Xu, Huang, and coworkers give new insights into flowering in tomato, as flowering time regulation is not only a survival strategy of plants growing under poor conditions, but has also become of high importance for the genetic improvement of crops.

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