In the Search for the SWEETest Pear

If you close your eyes and think about the most delicious fruit you have ever tasted, it is likely that one specific characteristic will come to mind (and mouth!): its sweetness. Humans have a natural appreciation of plant sugars, and it is no surprise that enhanced sugar content is among the most desired traits by fruit producers. Indeed, we have long been selecting for increased sugar contents in many crops, and sweetness is recognized as one of the main factors driving fruit consumer preferences (Jaeger et al., 1998; Patrick et al., 2013). Fruit sweetness is largely determined by a plant’s capacity to metabolize and translocate soluble sugars (such as Glc, Fru, and Suc) from photosynthetic sources to the fruit. For this reason, numerous studies have focused on uncovering the identity and mode of action of the molecular players involved in sugar allocation in plants (Klee and Tieman, 2018). Surprisingly, little is known about the mechanisms controlling fruit sugar accumulation in pear, one of the most important horticultural crops worldwide.

In this issue of *Plant Physiology*, Li et al., (2020) investigate the basis of sweetness in two varieties of Ussurian pear (*Pyrus ussuriensis*), ‘Nanguo’ (NG) and its clonal bud sport variety (BNG). BNG was identified from a NG tree in the 1980s, and it is valued for producing sweeter tasting fruit than NG. Until now, the mechanism underlying this much-sought trait was unknown. To shed light on this topic, Li et al., (2020) compared the total soluble solids of NG and BNG fruits during different stages of development. They observed that one particular carbohydrate accumulated at significantly higher levels in BNG relative to NG fruits, namely Suc (colloquially known as table sugar). At the time of commercial harvest, BNG fruits were loaded with as much as three times the amount of Suc typically found in NG fruits.

To uncover the genetic basis behind the higher Suc accumulation in the BNG pears, Li et al. (2020) compared the transcriptomes of NG and BNG fruits at the time of commercial harvest. One gene in particular, *PuSWEET15*, showed an ~11-fold higher expression in BNG fruits compared to NG fruits. *PuSWEET15* is a putative member of the Sugars Will Eventually be Exported Transporter (SWEET) family of transmembrane sugar transporters, which are widely studied for their involvement in Suc allocation in many plant species (Chen et al., 2015). Expression of *PuSWEET15* increases during fruit development only in the BNG variety, peaking at the time of commercial harvest. Further genetic analysis demonstrated that *PuSWEET15* overexpression culminated in increased Suc concentrations in NG fruits, whereas its silencing led to reduced levels of the carbohydrate in BNG. Finally, functional characterization of *PuSWEET15* indicated that this gene encodes a functional membrane-bound Suc transporter, whose action is essential for Suc accumulation in pear fruits.

To address the cause of higher *PuSWEET15* expression in the BNG pears, the authors searched the fruit transcriptome for BNG-upregulated transcription factors (TFs) that could potentially bind the *PuSWEET15* promoter. Their analysis led to the identification of *PuWRKY31*, a TF gene with increased expression in BNG during fruit development. By utilizing different molecular biology methods, they were able to show that *PuWRKY31* was capable of physically interacting with the *PuSWEET15* promoter to upregulate its expression. Overexpressing *PuWRKY31* in NG

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**Figure 1.** Transcriptional cascade regulating sweetness in pear fruits. In this issue of *Plant Physiology*, Li et al. (2020) demonstrate that Suc accumulation in Ussurian pear fruits is affected by epigenetic modifications at the promoter of *PuWRKY31*. In BNG fruits (regarded as the sweetest variety of the NG Ussurian pear), higher expression of the *PuHLS1* histone acetyltransferase is associated with increased acetylation levels of *PuWRKY31* histones, leading to up-regulation of *PuWRKY31* transcription. *PuWRKY31* is a TF that binds to the promoter of *PuSWEET15*, a transmembrane Suc transporter, to induce its expression, resulting in higher Suc levels in the BNG fruits.
led to higher expression of PuSWEET15 and, consequently, higher Suc concentrations in the NG fruit. PuWRKY31 belongs to the WRKY superfamily of transcriptional regulators, which are associated with a plethora of plant physiological programs ranging from pathogen defense to senescence (Rushton et al., 2010). The findings of Li et al. (2020) provide the first direct evidence of WRKY participation in plant sugar transport.

To gain insight into the genetic regulation of PuWRKY31, authors compared the coding sequence, promoter sequence, and methylation levels of the PuWRKY31 promoter in NG and BNG fruits. Since no significant differences were observed, they suspected that the expression pattern of PuWRKY31 was correlated with epigenetic modification on its associated histones. Indeed, by chromatin immunoprecipitation methods, they identified a significantly higher level of acetylation in PuWRKY31-associated histones in BNG fruits. Acetylation is an epigenetic modification frequently associated with actively transcribed genomic regions (Bártová et al., 2008); thus, this finding provides a plausible explanation for why PuWRKY31 is highly expressed in the BNG variety. The cause for such modification in histone acetylation status may be correlated with the activity of PuHLS1, a histone acetyltransferase whose expression was also found to be higher in BNG than in NG fruits. Li et al. (2020) were able to demonstrate that PuHLS1 interacts with the coding sequence of PuWRKY31, providing an initial insight into the epigenetic mechanisms regulating PuWRKY31 expression.

Sweetness is possibly the most remarkable sensorial trait of any edible fruit. Thus, it is important that we understand the genetic mechanisms regulating sugar accumulation in fruits, especially those with high horticultural value, such as pears. This work by Li et al. (2020) has uncovered a transcriptional cascade controlling Suc accumulation in Ussurian pear fruit. Although it remains to be understood why PuHLS1 is highly expressed in BNG fruits, and whether its activity is directly involved with the increased acetylation status of PuWRKY31-associated histones, the authors’ proposed model (Fig. 1) already provides a useful resource that will aid scientists and fruit producers in their search for the sweetest pear.

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