

development⁶, as well as those that mediate the cell cycle, cell expansion, metabolism and sucrose import⁵. Feast and famine signals are pivotal to adjustment of reproductive load by a mother plant through regulation of kernel abortion and ovary viability under stress. This mechanism provides a vital means for increasing collective sink strength (import capacity) of sucrose-using structures when sugars are plentiful, and decreasing import capacity when resources are limited^{5,7}. If signals of sugar abundance are artificially enhanced for even a short period at crucial stages of development, yield could increase.

The TPP transgenic plant produced by Nuccio *et al.*¹ poses some puzzles because although sucrose levels increase slightly—“up to 20%,” according to the authors—the sucrose signal (mediated by trehalose-6-phosphate (T6P)) should decrease due to depletion of T6P by TPP. This could seemingly lead to mixed messages if signals for sucrose itself are reduced whereas those for its metabolism to hexoses are not. This balance in itself may be the key to the observed results^{6,8}. Alternatively, the extent of the impact for starvation signals from depleted T6P could be attenuated in some other way. How then does the TPP transgenic increase yield under stress? There are several possible explanations, including the specificity of targeted sites and T6P-related signaling.

Developmental context might be crucial. For example, expression of a subset of famine-responsive genes is thought to confer import priority to cells and tissues, which enables post-stress recovery of plant organs⁹. Developing maize kernels do not achieve this ‘essential-sink’ status until one-third of the way through development, after which time they are no longer aborted^{4,5}. Conceivably,

localized TPP overexpression might reduce kernel abortion by promoting an early transition to essential-sink status. Early phases of post-pollination development might also be affected because the rice promoter used in the TPP transgenics targets sites involved later in grain growth. Also, increased sucrose levels in florets of the transgenics could exert a developmental influence owing to changes in sucrose/T6P ratios¹⁰ and probable shifts in sucrose/hexose ratios⁸. Finally, other outcomes of T6P signaling that are not yet defined may have altered development or perception of development.

Questions about the mechanisms underlying TPP-mediated yield increases in maize have

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broader relevance for the impacts of altered T6P signaling in transgenics. What happens when adjacent cells have constitutively different ratios of sucrose and T6P? Work thus far indicates that such an outcome is likely, as ratios change with transgenic perturbation, but otherwise remain tightly coupled during responses to diverse conditions¹⁰. This is important for development of targeted TPP transgenics, because it is not yet known what effect neighboring cells will have on each other when their sucrose levels, sensing and metabolism are different. Another question is the effect in TPP transgenics of the interplay between T6P signaling and other sugar signals that

respond to hexose and glycolytic flux (mediated by hexokinase and TOR systems). The significance of this lies in the extreme sensitivity of plants to sugar signals mediated by T6P. The ratio of sucrose signals to hexose signals may underlie the long-observed correlations between sucrose and hexose “sugar states,” and cell maturation and division⁸. Finally, we need to understand the extent and impact of the sucrose cycling that occurs in transgenics that reduce T6P levels and relieve inhibition of sucrose resynthesis. Such cycling may seem futile, but could increase classic sugar signals by raising flux through hexokinase reactions. Effects could be prominent in and near vascular tissues, such as those targeted in the present study¹.

This work could hold implications for global food supplies. Even food production in mesic areas is increasingly threatened by drought stress, so advances in protecting maize and other grains from such stress will be invaluable.

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

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