

## DROUGHT RESISTANCE

## Spraying for yield

Trehalose-6-phosphate (T6P) is an essential signalling molecule in plants. A novel chemical intervention strategy to increase *in planta* T6P levels has now been presented, with remarkable effects on plant yield and drought tolerance.

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Two decades ago, it was discovered that all plant species harbour multigene families of trehalose metabolizing enzymes, which was, at the time, a puzzling observation. Further research on plant trehalose metabolism resulted in the identification of trehalose-6-phosphate (T6P) as an essential regulatory molecule in plants<sup>1</sup>. T6P licenses sugar utilization for plant growth, and its absence halts growth irrespective of the actual sugar level. The molecular functions of T6P and the trehalose multigene family members are poorly understood, but recent studies highlight the importance of modifying T6P levels for regulating productivity and stress tolerance in field crops<sup>2,3</sup>. The controlled expression of a trehalose-6-phosphate phosphatase (TPP) gene in the reproductive organs of maize resulted in increased kernel number and seed yield, particularly under drought conditions<sup>2</sup>. In a separate study, the presence of a functional *OsTPP7* gene allowed seeds of a submergence-tolerant rice variety to germinate in anaerobic conditions<sup>3</sup>. Most of the currently cultivated rice varieties have a truncated, inactive *OsTPP7* and fail to germinate when submerged. In each case, the local modulation of T6P levels promoted allocation of sugar resources to the growing parts, the maize embryo and the rice seedling apical meristem, respectively.

These and other research efforts have revealed the importance of T6P for plant growth and development but so far have not explained the mechanistic details of T6P action as a signalling molecule. No T6P receptor has yet been identified, and we do not have clear understanding of the signalling pathways, with the exception of T6P being an inhibitor of SNF1-related kinase (SnRK1)<sup>4</sup>. SnRK1 responds to low carbon status by activating an energy saving programme and inhibiting plant growth<sup>5</sup>. Sucrose availability promotes T6P biosynthesis, which then inhibits SnRK1, and such inhibition is a prerequisite for sugar utilization and plant growth<sup>1</sup>.

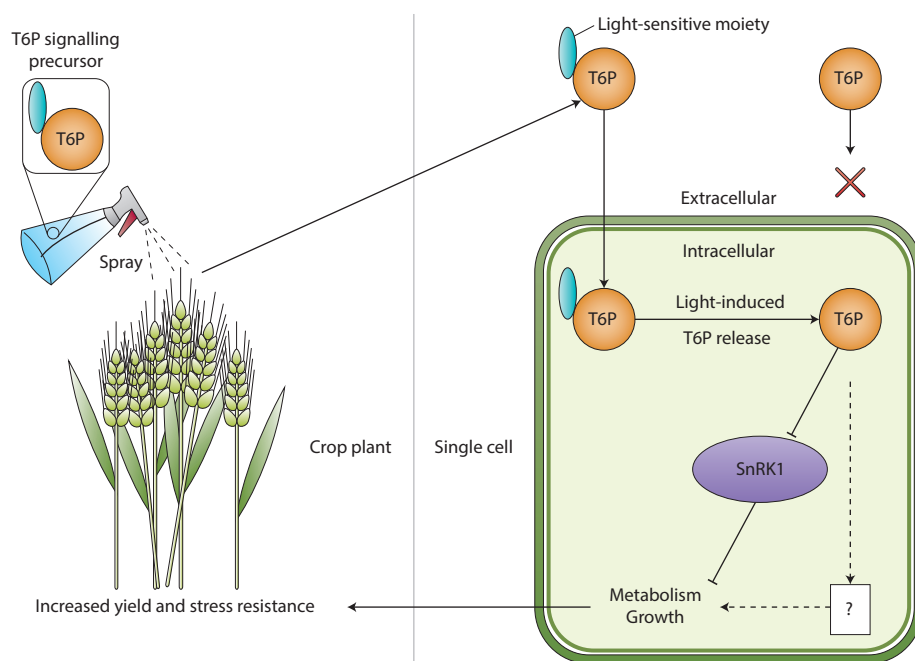
Obviously, the ability to modify T6P levels in plants pays off in the field. With

this in mind, the Paul and Davis laboratories teamed up and devised a chemical strategy for T6P delivery to plants<sup>6</sup>. T6P is a charged, non-membrane-permeable molecule, which precludes its direct use for application. A major breakthrough has been the chemical synthesis of membrane-permeable, photolabile T6P precursor compounds that are taken up by plants either through the roots or the aerial plant surface. Following this, active T6P is released *in planta* by light treatment (Fig. 1).

Four different precursor compounds are taken up by plant roots within one to two days, and they effectively release T6P within hours when subjected to controlled light treatment or when in sunlight. T6P release is further enhanced by UV light supplementation. Application of 1 mM of the chemical precursor to seedlings could boost T6P levels up to 100-fold. T6P levels increase

sufficiently for plants to respond as expected in regard to the expression of metabolism-associated genes, such as *TREHALOSE-6-PHOSPHATE SYNTHASE5 (TPS5)*, *BASIC LEUCIN ZIPPER DOMAIN11 (bZIP11)* and *ASPARAGINE SYNTHETASE1 (ASN1)*, and increased levels of sucrose, glucose and starch. Similar non-toxic photoactive chemical compounds were synthesized using glucose-6-phosphate (Glc6P). Treatment of *Arabidopsis* with the Glc6P compounds did not affect plant starch levels or growth, suggesting that the effect is specific for T6P.

A homogeneously <sup>13</sup>C-labelled T6P precursor compound was prepared and applied to *Arabidopsis* seedlings to confirm T6P release from the precursor compound and to study the kinetics of <sup>13</sup>C-T6P metabolism *in planta*. It was found that addition of <sup>13</sup>C-T6P to seedlings resulted in a rapid (<30 min of UV treatment)



**Figure 1** | A light-sensitive synthetic T6P signalling precursor is taken up by plants and diffuses into a plant cell, where light treatment results in the release of T6P. The T6P specifically interferes with cellular signalling — particularly the inhibition of SnRK1 protein kinase activity — and probably other pathways to interfere with plant metabolism and growth, thus promoting plant stress tolerance and yield.

peaking of endogenous T6P, which might be due to the rising sucrose level observed upon T6P release from the precursor that stimulated endogenous T6P biosynthesis.

In further experiments, the precursor compounds were either sprayed on whole plants or ears of wheat plants during the grain filling period. The resulting enhancement of T6P levels led to an increase in grain yield and starch content of a remarkable 13–20%. Moreover, wheat plants treated with the T6P precursor compound were substantially more tolerant to drought treatment than control plants in resurrection and recovery response experiments.

These are all exciting results but important questions remain. The maize and rice studies<sup>2,3</sup> show the importance of precise temporal and spatial regulation by T6P-hydrolysing enzymes in sink tissues

for effective control of resource partitioning and growth. In the Griffiths *et al.* study<sup>6</sup>, the spatially, and to some extent temporally, uncontrolled immediate boost in T6P levels had a similar effect on yield and drought stress, which makes one wonder about the mechanism involved in resource partitioning using TPP genes and T6P application<sup>7,8</sup>. The key function of T6P as a regulator of plant metabolism and development in the lab and the field is well established. What is urgently needed is insights of T6P signal transduction leading to changes in metabolism and growth. Importantly, the wheat experiments should be extended to field conditions and tested in other crops.

The findings reported by Griffiths *et al.*<sup>6</sup> on the use of T6P precursors, as well as other approaches such as the construction of a synthetic abscisic acid receptor<sup>9</sup>, point the way to chemical intervention strategies,

which specifically target plant signal transduction pathways that contribute to crop traits. □

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#### Competing interests

The author declares no competing financial interests.