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The evolution of sugar signalling in the green lineage

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ABSTRACT

Sugars are not only central metabolites in plants but also act as signalling molecules that coordinate growth, development, and physiology. In the green lineage (viridiplantae), the intermediate of trehalose biosynthesis, trehalose 6-phosphate (Tre6P), has emerged as a central regulator of carbon status. In angiosperms, Tre6P signalling is integrated with energy-sensing mediated by kinases such as SnRK1 and TOR to balance growth with metabolism and environmental factors. Here we review the current knowledge on the functions of sugar signalling components in the green lineage. We put a special emphasis on Tre6P signalling as genomic, transcriptomic, and metabolomic studies across algae, bryophytes, and vascular plants indicate that Tre6P's role as a sugar signal predates the colonization of land and may have been instrumental during terrestrialization and the evolution of vascular systems. Functional studies in mosses, and angiosperms reveal conserved roles of Tre6P in vegetative growth, and the initiation of sexual reproduction, underscoring its potential as a conserved signalling metabolite. Taken together, these insights support the view that Tre6P has acted as a conserved and adaptable hub linking carbon availability to plant development and reproduction throughout plant evolution.

1. Introduction

As photoautotrophic organisms, all plants – from aquatic green algae to land plants – produce sugars by fixing atmospheric CO_2. Efficient usage of the acquired carbon as well as coordinating it with the availability of other nutrients is pivotal for the plant's survival and fitness. We know that in angiosperms, sugars act not only as a source of carbon and energy, but also as important signalling molecules. Our knowledge in other plant lineages, however, remains limited. The main sugar in plants that is used for transport, storage, and stress protection is the non-reducing disaccharide sucrose. Trehalose is the only other non-reducing disaccharide in plants which has similar functions, and is used across all kingdoms of life (including fungi and non-vertebrates) (Paul et al., 2008; Lunn et al., 2014). In angiosperms, the intermediate of trehalose biosynthesis, trehalose 6-phosphate (Tre6P), has been established as an important signalling metabolite integrating metabolic status with developmental decision making (Figueroa and Lunn, 2016; Paul et al., 2020; Fichtner and Lunn, 2021; Wingler and Henriques, 2022).

Additionally, Tre6P is an essential signal and negative feedback regulator of sucrose levels in angiosperms, maintaining sucrose levels within an optimal range (Martínez-Barajas et al., 2011; Yadav et al., 2014; Annunziata et al., 2025). Two other important sugar signalling pathways are the energy-sensing kinase complexes Sucrose-Non-Fermenting 1-Related Kinase 1 (SnRK1) and TARGET OF RAPAMYCIN (TOR) kinase (Margalha et al., 2019; Baena-González and Lunn, 2020). SnRK1 operates as a cellular fuel gauge: under carbon or energy-limiting conditions, it reprograms metabolism and transcription to conserve resources (Baena-González et al., 2007; Broeckx et al., 2016), while TOR promotes anabolism and growth when nutrients and sugars are sufficient (Dobrenel et al., 2016; Burkart and Brandizzi, 2021). SnRK1, homologous to SNF1 in yeast and AMPK in animals, and TOR, homologous to TOR in yeast and mTOR in animals, are conserved energy sensing kinases across eukaryotes. However, their signalling roles and pathways differ between and within kingdoms (Shi et al., 2018; Crepin and Rolland, 2019). It is therefore unknown if their specific signalling mechanisms are conserved across the green lineage or if non-flowering plants have evolved convergent sugar signalling mechanisms.

2. Plant sugar signalling pathways across plant evolution

Tre6P is synthesised by Tre6P synthase (TPS) and dephosphorylated by Tre6P phosphatase (TPP) (Fig. 1a; Cabib and Leloir, 1958). TPS proteins fall into two classes: catalytically active class I TPS proteins

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(Blázquez et al., 1998; Vandesteene et al., 2010; Delorge et al., 2015), which synthesise Tre6P, and catalytically inactive class II TPS(-like) proteins (Vandesteene et al., 2010; Fichtner and Lunn, 2021), which are suggested to act as Tre6P signalling pathway components. SnRK1 is a heterotrimeric kinase complex comprising a catalytic α subunit and two regulatory subunits, β and βγ (Broeckx et al., 2016). The TOR complex 1 (TORC1) is composed of TOR, the regulatory subunits Regulatory-Associated Protein of TOR (RAPTOR) and Lethal with Sec Thirteen 8 (LST8) (Margalha et al., 2019; Henriques et al., 2022).

Extensive crosstalk occurs between these three pathways (Fig. 1a). Tre6P inhibits SnRK1 by directly binding the α subunit and preventing allosteric reorientation and phosphorylation of its activation (T) loop by SnRK1-activating kinases (Zhang et al., 2009; Zhai et al., 2018; Blanford et al., 2024). Class II TPS proteins also physically interact with SnRK1, modify its intracellular localisation and activity (Van Leene et al., 2022), probably dependent on Tre6P levels (Reis-Barata et al., 2025, bioRxiv, preprint). SnRK1, in turn, can inhibit TOR by phosphorylating RAPTOR, particularly under stress conditions (Nukarinen et al., 2016; Jamsheer K et al., 2022). In addition, plant-specific FCS-like zinc finger (FLZ) proteins act as scaffolds at the SnRK1-TOR interface, with several FLZs physically interacting with subunits of both complexes (Nietzsche et al., 2014; Bortlik et al., 2024; Jamsheer et al., 2018a,b, 2019, Jamsheer K et al., 2022).

Over the past five years, several reviews have refined our understanding of sugar signalling and Tre6P biology, and have summarised recent advances in energy signalling focussing on SnRK1 (Peixoto and Baena-González, 2022; Han et al., 2024), or TOR (Henriques et al., 2022). Others took a broader sugar-centred (Yoon et al., 2021; Wingler and Henriques, 2022) or sink-dynamics point of view (Guo et al., 2023; Doidy et al., 2024). The Annual Review by Fichtner and Lunn (2021) highlighted the function of Tre6P as both a sucrose homeostat and developmental signal that integrates source-sink signalling with organ growth. This review also discussed the connection to SnRK1 and the potential for TOR crosstalk, highlighting the vasculature as a hub for TOR/SnRK1 signalling and TPS1 expression. Fichtner (2025) extended these concepts in a recent Tansley Insight establishing cell-specific expression patterns for the different components of these sugar signalling pathways, and positioning Tre6P at the intersection of sugar, hormonal, and developmental control. Several other reviews on sugar signalling include Miret et al. (2024) focussing on the role of sucrose

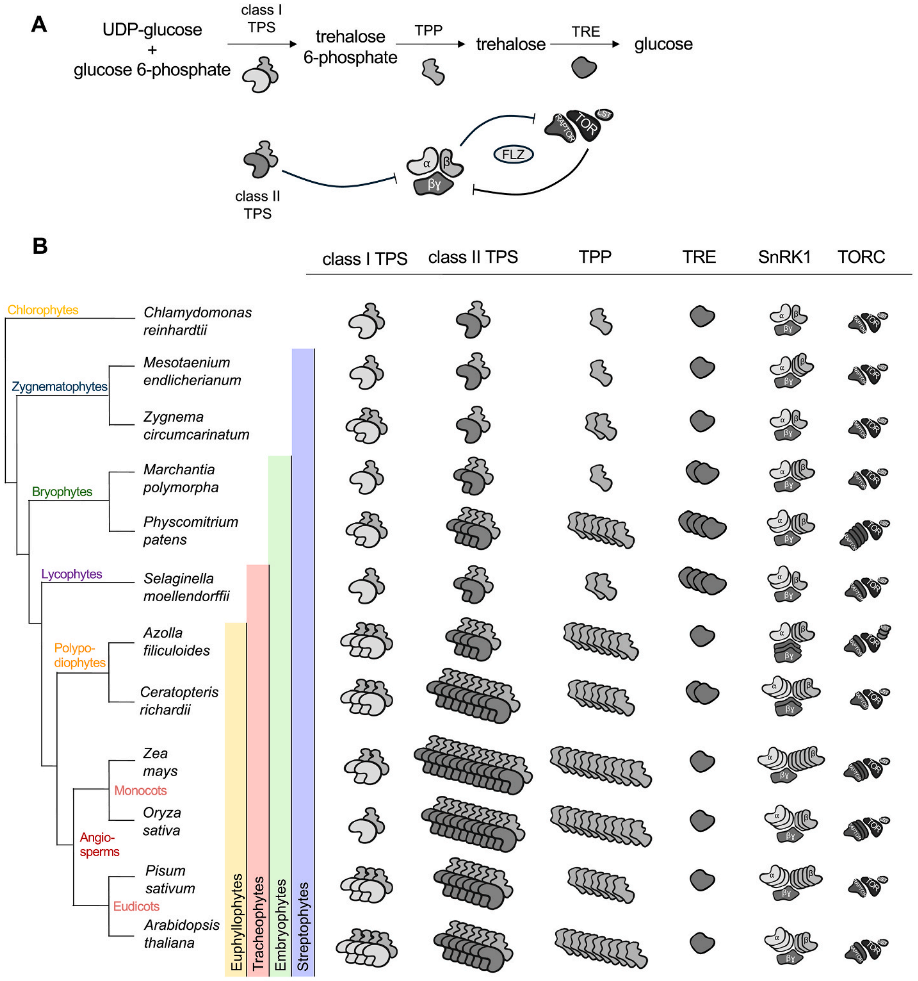

Fig. 1. Predicted protein numbers of trehalose metabolism and central carbon regulators in selected species of the green lineage. (A) Trehalose 6-phosphate (Tre6P) synthesis and degradation via class I TPS (Tre6P synthase), TPP (Tre6P phosphatase) and TRE (trehalase). All TPS proteins have a TPS and an inactive TPP-like domain. Class I TPS proteins synthesise Tre6P while class II TPS proteins are inactive and likely involved in Tre6P signalling, for example via inhibition of SnRK1. SnRK1 and TORC can inhibit each other, partially involving FCS-like zinc finger (FLZ) proteins that act as scaffolds at the SnRK1-TOR interface. (B) Phylogenetic relationship based on Bowman et al. (2017) and de Vries and Archibald (2018), branch length not to scale. Protein shapes are simplified. Sequences were identified via blastp (phytozome.jgi, phycocosm.jgi and fernbase.org) with the arabidopsis sequences as query. Maize TPS, TPP and SnRK1 α protein numbers are based on Tran et al. (2025), Henry et al. (2015) and Wang et al. (2019). Abbreviations: trehalose-6-phosphate synthase, TPS; trehalose-6-phosphate phosphatase, TPP; trehalase, TRE; SNF1-related kinase 1, SnRK1; target of rapamycin complex, TORC. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

homeostasis in crop improvement; Supriya et al. (2025) highlighting the different plant sugar sensors and their crosstalk including HEXOKINASE1, which is an enzyme and sensor for glucose availability; Wang et al. (2025) which focussed on the role of sugars in integrating internal and external cues to regulate shoot branching; Mae-Lin Kerbler et al. (2023) surveyed the TPP family across plants; and Rojas et al. (2023) reviewed Tre6P metabolism in C4 plants. A cross-kingdom review further highlights that Tre6P targets differ between plants and fungi (Liu et al., 2025).

Building on this conceptual foundation, our Perspective explicitly adopts an evolutionary lens. We propose that the Tre6P module has been repeatedly co-opted and rewired on top of deeply conserved SnRK1/TOR networks across major land-plant lineages. We further outline how key evolutionary innovations – such as the origin of vascular tissues, the establishment of long-distance source-sink transport, and the expansion of reproductive sink structures – may have shaped the diversification of sugar signalling pathways.

3. Trehalose 6-phosphate - a conserved regulator of carbon metabolism in the green lineage?

The green lineage (viridiplantae) comprises all green algae and land plants, and can be divided into chlorophytes (most green algae) and streptophytes (streptophyte algae and land plants) (de Vries and Archibald, 2018). Land plants (embryophytes) can be further subdivided into non-vascular (bryophytes) and vascular plants (tracheophytes) (Donoghue et al., 2021). Unlike aquatic environments, terrestrial habitats imposed new challenges requiring extensive physiological and metabolic adaptations (Becker et al., 2025). By developing a vascular system, terrestrial plants evolved to be less water-dependent and capable of growing larger, allowing access to new habitats. These changes required hormone signalling pathways to develop, integrating environmental signals with plant growth responses. For example, there is experimental evidence that the key components of the auxin signalling pathway are not only present but also functionally conserved between the bryophytes *Marchantia polymorpha* (Eklund et al., 2015; Suzuki et al., 2023) and *Physcomitrium patens* (Coudert et al., 2015; Thelander et al., 2022) and angiosperms (Matthes et al., 2019).

Similar to auxin, most plant hormone signalling pathways are already present in rudimentary forms in streptophyte algae (Bowman et al., 2019; Zegers et al., 2024). Signalling pathways then likely expanded as an adaptation to life on land (Blázquez et al., 2020). Gene duplications resulting from tandem duplication, transposition to new chromosomes, or whole-genome duplication (polyploidy) have long been recognized as an important contributor to the evolution of new gene functions (Birchler and Yang, 2022).

When did plants evolve sugar signalling pathways and did these expand with the adaptation to life on land? The genes encoding for Tre6P-related proteins, SnRK1 and TORC are present in the genomes of representative species across the green lineage suggesting sugar signalling – mediated by these pathways – is an ancient trait (Fig. 1, Fichtner et al., 2021). Chlorophyte and streptophyte algal genomes have genes encoding for class I TPS, class II TPS, and a TPP (Fig. 1b) potentially allowing for Tre6P synthesis, degradation, and signalling. Consistent with an ancient function of Tre6P, mutations in *TPP1* in the chlorophyte alga *Chlamydomonas reinhardtii* led to increased Tre6P levels coinciding with accumulation of organic acids (Al Youssef et al., 2023), metabolic changes resembling those caused by elevated Tre6P levels in angiosperms (Figueroa et al., 2016; Fichtner et al., 2017). These data suggest that changes in primary metabolism by Tre6P are somewhat conserved in viridiplantae. Gene expression data from the streptophyte alga *Zygnema circumcarinatum* (CoNekT, https://conekt.sbs.ntu.edu.sg, Proost and Mutwil, 2018; Feng et al., 2024) demonstrates diel dependent fluctuations in transcript abundances of one of its class I *TPS* genes. Expression of this class I *TPS* correlates with light availability, showing higher expression levels in the middle of the day and lower expression levels at night. This pattern suggests that transcript abundance of this *TPS,* and therefore potentially Tre6P levels, responds to changes in photosynthesis and therefore sugar availability. Furthermore, these findings indicate that Tre6P may have evolved as a signal for sugar availability in the green lineage far earlier than previously assumed (Lunn, 2007; Paul et al., 2008). Based on a selection of species representing all major groups of the green lineage (Fig. 1), Tre6P-related genes have very low copy numbers in green algae, while their numbers greatly amplified during land plant evolution, especially with the emergence of vascular tissues and the need for long-distance transport (Fig. 1B–Box 1).

Similar to the potential role of Tre6P in sugar signalling in algae, homologs of a SnRK1 α-subunit and TOR kinase also show transcriptional responsiveness to diel fluctuations in the streptophyte alga *Z. circumcarinatum* (CoNekT, https://conekt.sbs.ntu.edu.sg, Proost and Mutwil, 2018; Feng et al., 2024). In contrast to the expanding numbers of *TPS* and *TPP* genes, however, the copy number of SnRK1 and TORC complex components has remained relatively low throughout plant evolution (typically one to three copies per subunit; Fig. 1b). We therefore propose that Tre6P synthesis and signalling via TPS and TPP, rather than modulation of the SnRK1 and TORC1 complexes, provided the cell and tissue-specific fine tuning of sugar signalling required for land plant colonialization.

4. Trehalose 6-phosphate is the metabolic intermediate of trehalose biosynthesis

In land plants, trehalose was long considered of negligible importance due to its low concentrations (Paul et al., 2008; Lunn et al., 2014). Algae and angiosperms possess only one trehalase (TRE), the enzyme catalysing the hydrolysis of trehalose into two glucose moieties. Bryophytes, lycophytes, and ferns, however, have more copies which have potentially arisen from species or clade-specific expansion/duplications (Fig. 1b). Although experimental evidence is currently limited, the increased number of TREs in bryophytes, lycophytes, and ferns may indicate important functions for trehalose in these lineages, for example as an osmoprotectant. Consistent with this idea, certain trehalases from *P. patens* and *M. polymorpha* show high expression levels in desiccation-tolerant spores (PEATMoss, https://peatmoss.plantcode.cup.uni-freiburg.de/expression_viewer/input, Fernandez-Pozo et al., 2020; Marchantia eFP browser, https://bar.utoronto.ca/efp_marchantia/cgi-bin/efpWeb.cgi, Winter et al., 2007). Trehalose is also a key osmolyte and carbon reserve in resurrection plants like the lycophyte *Selaginella lepidophylla* (Anselmino and Gilg, 1913) or the flowering plant *Myrothamnus flabellifolia* (Bianchi et al., 1993), and it is an important regulator of guard cell aperture in arabidopsis (Van Houtte et al., 2013).

In angiosperms, the low copy number of TRE suggests that trehalose may have lost its importance, except in guard cells, as it might have been replaced by other new stress-protection strategies like the deposition of suberin in roots (Zhou et al., 2024). Similarly, the evolution of a more complex vascular network and efficient water transport system in ferns and seed plants (euphyllophytes) (Fang et al., 2022; Ali et al., 2025), together with an increased water retention capacity of seed plant cuticles (Kong et al., 2020), likely enhanced drought tolerance, reducing reliance on trehalose-based protection.

5. Trehalose 6-phosphate as a conserved regulator of vegetative growth?

A study in the moss *P. patens* suggests a function for Tre6P signalling in growth regulation. Phan et al. showed that the knockout of the two catalytically active class I *PpTPS*s severely affected growth as double *Pptps* knockout plants formed significantly smaller colonies (Phan et al., 2020). The growth of colonies and protonema filaments could partially be restored by sucrose or glucose feeding (Phan et al., 2020), supporting

Box 1

The Emergence of Vascular Tre6P Signalling as a Key Innovation in Source-Sink Communication?

In non-vascular plants like bryophytes, assimilates have to move only across short distances. As land plants increased in size and developed specialised organs, they required an effective transport system to distribute carbon and nutrients from source tissues that produce assimilates to sink tissues that rely on imported resources. The independent evolution of the vascular system in lycophytes and euphyllophytes (ferns and seed plants) was a key innovation that enabled long-distance transport of water, nutrients, and sugars (Raven and Edwards, 2001; Lucas et al., 2013). This structural advancement required the parallel evolution of signalling pathways capable of coordinating developmental processes across increasingly large body plans, particularly between source and sink organs (Yu et al., 2015). Consequently, in vascular plants the vasculature has become a central hub for systemic source-sink communication (Lucas et al., 2013; Notaguchi and Okamoto, 2015). The predominant Tre6P synthase, AtTPS1, shows a highly localised expression pattern in *A. thaliana* in the shoot and root vasculature, indicating that Tre6P signalling has become a specialised signal produced primarily in vascular tissues (Fichtner et al., 2020, 2025; Annunziata et al., 2025). If this vascular-specific expression pattern is conserved in other angiosperms, or even more broadly across vascular plants, remains to be tested experimentally. However, meta-analysis of single-cell RNAseq data shows that *TPS* and *TPP* genes of angiosperms might have a conserved expression pattern in vascular tissues. In *Prunus mume*, *Oryza sativa* (rice), *Triticum aestivum* (wheat), and *Plantago major, TPS1*-like transcripts are predominantly expressed in phloem-related cells, while *TPPs* are more broadly expressed in vascular and surrounding tissues (Zang et al., 2011; Huang et al., 2019; T.-Q. Zhang et al., 2021; Y. Guo et al., 2024; Ke et al., 2025) The expression of *TPS* and *TPP* transcripts predominantly in vascular cell clusters across flowering plants points to a specific function of Tre6P metabolism and signalling specifically in the vasculature, suggesting that the coupling of sugar status with long-distance transport and signalling might have been an advantage in land plant evolution (Fig. 2). The vascular-specific expression of TPS1 might also have been an adaptation facilitating source-sink communication (Paul et al., 2017, 2020). When Tre6P became a vascular-specific signal remains unclear. It may have emerged with the first vascular plants, such as the last common ancestor of lycophytes and euphyllophytes, or later during the evolution of vascular tissues in euphyllophytes (Fig. 2).

the hypothesis that the growth defects resulted from a lack of energy or its proper allocation. Phan et al. also suggested a potential connection between Tre6P and hormonal growth regulation. The double *Pptps* knockout mutant was hypersensitive to cytokinins, and produced less caulonema cells, a phenotype that could not be restored by exogenous auxin application. Conversely, auxin treatments altered *TPS* and *TPP* expression patterns (Thelander et al., 2022). A *P. patens* double knockout of the SnRK1 α subunits showed the opposite effect; this mutant was hypersensitive to auxin but unresponsive to cytokinin treatments (Thelander et al., 2004). Similarly, treatments with TORC inhibitors and knocking down components of TORC in *P. patens* impacted vegetative growth (Saliba et al., 2025, bioRxiv, preprint). These studies suggest that (i) Tre6P, SnRK1 and TORC likely have ancient functions in plant growth regulation, (ii) the crosstalk between Tre6P and SnRK1 may be somewhat conserved, and (iii) the Tre6P-SnRK1 module may alter growth by interacting with hormone signalling pathways.

In angiosperms, *TPS1* is expressed predominantly in the vasculature (Fichtner et al., 2020, 2025; Annunziata et al., 2025), placing Tre6P at the interface between source leaves and sink organs. In *A. thaliana,* AtTPS1, the primary, and likely only, source of Tre6P after germination (Paul et al., 2008; Figueroa and Lunn, 2016), is essential for development, as loss-of-function mutants are embryo-lethal (Eastmond et al., 2002). Furthermore, modulating Tre6P levels in *A. thaliana* by constitutive or vascular-tissue specific overexpression of a bacterial *TPS* led to early flowering and increased branching, whereas overexpression of *TPP* homologs showed the opposite effect (Schluepmann et al., 2003; Wahl et al., 2013; Fichtner et al., 2021). Other studies have shown that Tre6P and sucrose are integrated with cytokinin and strigolactone signalling to control bud outgrowth and branching (Bertheloot et al., 2020; Cao et al., 2023; Fichtner et al., 2024; Patil et al., 2022; Salam et al., 2021).

The regulatory link between Tre6P and shoot branching also appears to be conserved in monocots such as rice and maize. In rice, knockout of *OsSTP15* was reported to increase tiller number, likely due to elevated sucrose and Tre6P levels in leaves (Li et al., 2024). In maize (*Zea mays*), the transcription factors *GT1* (*GRASSY TILLERS 1*) and *TB1 (TEOSINTE BRANCHED 1)* have been suggested to act upstream of the Tre6P pathway, sucrose transport and catabolism to suppress bud outgrowth by modulating carbon signalling and allocation (Dong et al., 2019).

Besides meristems, roots represent another major sink tissue that depends on the import of carbon from source organs to sustain development and growth (Paul and Foyer, 2001). Roots, which have evolved at least twice independently in land plants, are essential organs for water uptake and nutrients (Raven and Edwards, 2001; Kudoyarova et al., 2015). Recently, it was suggested in a preprint that altering Tre6P levels specifically within the vasculature of *A. thaliana* roots leads to significant changes in root size (Goebel et al., 2025; bioRxiv, preprint). Furthermore, it was shown that an increase in Tre6P levels in lateral root founder cells leads to an increase in root branching through coordinated inhibition of SnRK1 and activation of TOR (Morales-Herrera et al., 2023, 2024). A role for Tre6P in modulating root growth and development might not be restricted to euphyllophytes as the lycophyte *Selaginella moellendorffii* shows high expression of *SmTPS1* (Ferrari et al., 2020) specifically within roots (from CoNekT, https://conekt.sbs.ntu.edu.sg, Proost and Mutwil, 2018), suggesting that Tre6P signalling might also have a function in lycophyte roots.

The ferns *Azolla filiculoides* and *Ceratopteris richardii* both harbour three class I TPSs. The TPS with the highest sequence similarity to AtTPS1 is expressed in all fern tissues but shows a strong sporophyte-dominant tendency. Highest expression was detected in vegetative and non-vegetative fronds. In contrast to *S. moellendorffii*, where *SmTPS1* was strongly expressed in roots, expression of the fern *TPS* genes was the lowest in roots (Ali et al., 2025). However, some of the fern *TPP* genes show expression in the roots, suggesting that Tre6P is present in fern roots. In angiosperms, shoot-derived Tre6P has a strong influence on root growth (Goebel et al., 2025; bioRxiv, preprint), which might also be the case in ferns. As lycophyte roots developed independently from euphyllophyte roots (Singh et al., 2023), it is possible that the role and site of action of Tre6P signalling may be very different in these lineages. Based on these findings, we propose that Tre6P signalling may have been co-opted independently in different lineages and sink tissues to coordinate growth and development with carbon availability.

6. Trehalose 6-phosphate as a conserved regulator of sexual reproduction?

The initiation of sexual reproduction and the allocation of resources to reproductive structures poses a considerable commitment of carbon in a plant's life cycle and thus requires tight regulation (Dorken et al., 2025). While it is generally assumed that Tre6P and its related genes play a key role in coordinating carbon status with reproductive processes in angiosperms (Paul et al., 2017, 2020), we propose that this role is evolutionarily conserved and was crucial to ensure the reproductive success of early land plants.

Most of what is known about Tre6P signalling in reproduction is based on studies in angiosperms, particularly in *A. thaliana* and monocot crops like maize. Beyond its vascular expression pattern, AtTPS1 is also expressed in the flanks of the shoot apical meristem (Wahl et al., 2013; Fichtner et al., 2021). When the embryo-lethal *tps1-2* null mutant was rescued past the embryonic stage using a chemically inducible *AtTPS1* construct, the resulting adult plants either failed to flower or flowered severely delayed (Van Dijken et al., 2004; Wahl et al., 2013; Zeng et al., 2025). This link between Tre6P and flowering in *A. thaliana* was further resolved by showing that induction of the florigen *FLOWERING LOCUS T* (*FT*) in leaves depends on a functional *TPS1*, linking photoperiodic and sugar signalling to fine tune plant development (Wahl et al., 2013). Mutations in *KIN10* and *SNF4*, the regulatory βγ subunit of SnRK1, suppress the embryo-lethality and non/late-flowering phenotype of *tps1-2* plants (Zacharaki et al., 2022), providing genetic evidence that these two signalling pathways converge to modulate flowering time. However, the role of Tre6P extends beyond floral initiation. After successful fertilisation, the developing seeds need to be supplied by maternal tissues with essential nutrients, including sugars, and are therefore strong carbon sinks (Patrick and Offler, 2001). The regulation of seed filling in angiosperms is governed by a combination of hormonal and metabolic signalling pathways (Weber et al., 2005). As discussed in Miret et al. (2024), Tre6P and SnRK1 are key regulators of seed and grain filling in angiosperm species especially cereals (e.g. Martínez-Barajas et al., 2011; Nunes et al., 2013; Nuccio et al., 2015; Oszvald et al., 2018; Li et al., 2022) and have been associated with domestication traits in cereal crops (Paul et al., 2020).

To understand if this regulatory module is conserved, one must consider the evolution of land plants, which alternate between gametophyte and sporophyte generations. While angiosperms are sporophyte-dominant, bryophytes are gametophyte-dominant (Becker et al., 2025). Independent of these differences in life cycle, the metabolic cost of generating a new reproductive structure remains high. Besides the aforementioned alterations in vegetative growth, class I *Pptps* null mutant *P. patens* plants fail to produce sporophytes (Phan et al., 2020), the structure in which spores are formed and dispersed from after fertilisation (Ligrone et al., 2012). This suggests that Tre6P regulates the production of the reproductive generation (sporophyte), similar to its regulatory role in the reproductive transition in angiosperms (flowering). Based on *P. patens* single nucleus RNA-seq data, one class I *PpTPS* is specifically expressed in daughter cells of the single meristematic apical cell*, ergo* very early in gametophore development (Hata et al., 2025). Additionally, a class II *TPS* and a *TPP* are strongly expressed in cells of the gametophore that undergo differentiation and organogenesis (Hata et al., 2025). In *M. polymorpha*, the single *TPS1* homolog is highly expressed in the sexual reproductive organs (antheridiophores and archegoniophores) and in spores (Higo et al., 2016; Bowman et al., 2017; Hisanaga et al., 2021), further suggesting a role for Tre6P in sexual reproduction in bryophytes. In the sporophyte-dominant lycophyte *S. moellendorffii*, *SmTPS1* is highly expressed in strobili (Chan et al., 2008; Ferrari et al., 2020), the structures that produce spores. These spores germinate into gametophytes, which subsequently develop into a new sporophyte generation after fertilisation, suggesting a role for Tre6P in sexual reproduction across lineages.

Other sugar signalling components also show strong expression in sexual organs. In *M. polymorpha*, one of the genes encoding for a SnRK1 β subunit is highly expressed in sperm cells, while the gene encoding another β subunit is highly expressed in antheridia (Higo et al., 2016; Julca et al., 2021). Similar to *SmTPS1*, the transcripts of SnRK1 subunit genes are abundant in strobili of *S. moellendorffii* (from CoNekT, https://conekt.sbs.ntu.edu.sg, Proost and Mutwil, 2018). These expression data indicate an essential role for sugar signalling in reproductive structures of lycophytes and bryophytes.

7. Trehalose 6-phosphate as a modulator of floral development

Beyond regulating reproductive transitions, Tre6P signalling plays crucial roles in the development of reproductive structures. The maize mutant *ramosa3* (*ra3*), which is deficient in the TPP-encoding *RA3*, exhibits increased inflorescence branching (Klein et al., 2022; Satoh-Nagasawa et al., 2006; Sun et al., 2024). This branching phenotype is largely independent of RA3's catalytic activity, as complementation with a catalytically inactive RA3 version can partially rescue the mutant. This suggests RA3 and its paralog TPP4 having a regulatory "moonlighting" function beyond their enzymatic role (Claeys et al., 2019). In barley (*Hordeum vulgare*), a similar module involving *HvTPS1* and *HvSRA* (*SISTER OF RAMOSA3*) has been proposed to act as a determining factor of inflorescence branching (Vardanega et al., 2025).

Similar roles for TPPs in regulating reproductive development have been observed in heterodichogamous woody perennials. Heterodichogamy is a mating system where a species has two distinct reciprocal flowering morphs. This strategy has likely evolved to prevent inbreeding and can be found in a diverse range of flowering plant genera (Endress, 2020; Renner, 2001). Recently, new insights into the genetic mechanisms of heterodichogamy have correlatively linked this trait to be in part regulated by genes of the trehalose pathway. In walnuts (*Juglans*) a *TPP* gene was found to be a strong functional candidate for conferring heterodichogamy (Groh et al., 2025). The proposed mechanism involves increased tissue-specific *cis* expression of the gene likely driven by multiple tandem repeats in its 3' UTR. This would lead to decreased Tre6P levels in developing male flowers of female-first individuals delaying male flower development (Groh et al., 2025). In *Cyclocarya paliurus*, another heterodichogamous member of the *Juglandaceae*, analysis of differential methylation and transcriptional profiles of flowers links another *TPP* gene to the temporal separation of female and male flowers (Wang et al., 2025). In summary, the trehalose pathway genes have been found to be involved in regulating floral timing and architecture in a diverse range of angiosperm species. This sparks the hypothesis that the trehalose pathway has been co-opted multiple times during angiosperm evolution additionally to mediate transitional decisions and timing.

In addition to Tre6P, also SnRK1 signalling is important for correct floral organ development. For example, in *A. thaliana*, the SnRK1 βγ subunit is essential for proper mitochondria and peroxisome biogenesis and ROS signalling in pollen, enabling pollen hydration and germination on the stigma (Gao et al., 2016).

8. Conclusions and future perspectives

Taken together, the findings collated here highlight the potential role for Tre6P as a central link between carbon availability and (reproductive) development across the green lineage. The Tre6P pathway appears to have been repeatedly co-opted to fine tune timing, architecture, and development of vegetative and reproductive growth strategies across plant species (Fig. 2). It can be speculated that Tre6P likely played a regulatory role earlier than previously assumed, maybe even predating the split between chlorophytes and streptophytes. Its integration with phytohormones, SnRK1, and TORC may have been essential for coordinating carbon status with growth and stress responses during terrestrialization. The duplication and neofunctionalization of class II TPS might have enabled fine tuning of the cross talk between the different sugar signalling pathways, while the expansion of the TPPs provided additional flexibility, enabling plants to deploy Tre6P turnover and signalling in growth-related processes across specific organs, cell types, and developmental stages. This expansion of regulatory capacity via Tre6P, while keeping the central energy-sensing kinases SnRK1 and TOR, and Tre6P synthases (class I TPSs) comparatively stable, may have been crucial for translating carbon status into appropriate developmental outputs throughout plant evolution.

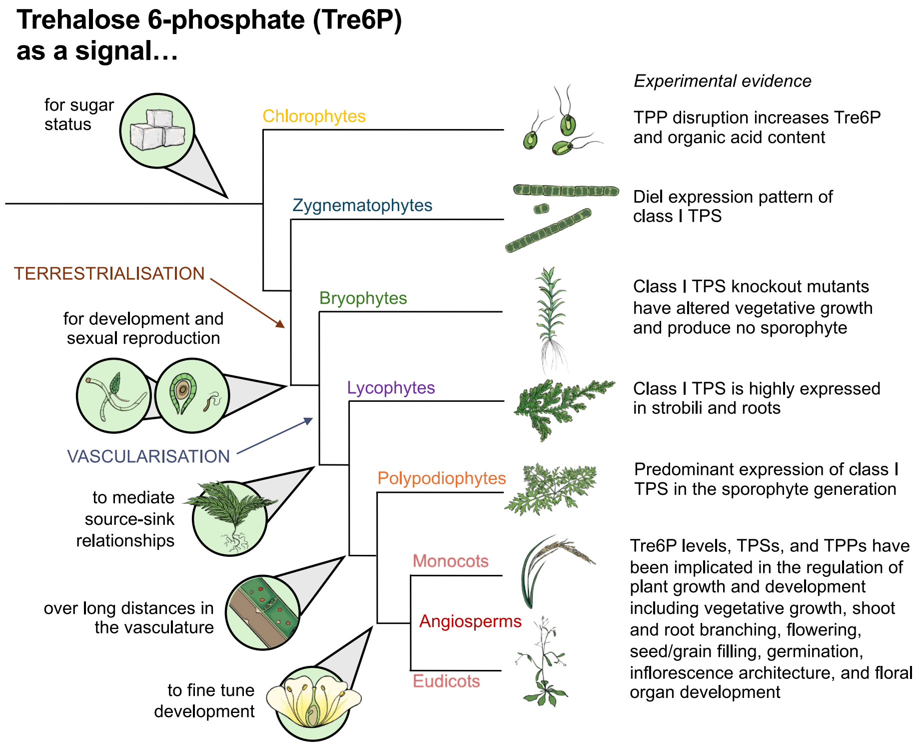

Fig. 2. Possible trajectory of trehalose 6-phosphate (Tre6P)-signalling **evolution.** We postulate that the function of Tre6P as a signal for sugar availability pre-dates the chlorophyte/streptophyte split. With the transition from water to land, Tre6P potentially was recruited to facilitate developmental and reproductive signalling. In vascular plants, Tre6P was then used to organise coordinated root and shoot development. We speculate that with the evolution of vasculature, mediation of the source-sink relationship over long distances was partially also mediated by Tre6P-signalling. In ferns (polypodiophytes) and seed plants (here represented by but not exclusive to angiosperms), the function of Tre6P was potentially adapted to meet the need for fine-tuned organ development, as for example in flowers. Statements on the right-hand side are generalisations based on the evidence discussed in the main text.

CRediT authorship contribution statement

Hannah L. Lepper: Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Linus F. Börnke:** Writing – review & editing, Writing – original draft, Conceptualization. **Lucas Müller:** Writing – review & editing, Writing – original draft, Conceptualization. **Anika Maerten:** Writing – original draft. **Jesús Praena:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization. **Franziska Fichtner:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Funding acquisition, Conceptualization.

Gene IDs

A list with all gene IDs can be found in Supporting Table S1.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jplph.2025.154653.

Data availability

No data was used for the research described in the article.

References

Al Youssef, W., Feil, R., Saint-Sorny, M., Johnson, X., Lunn, J.E., Grimm, B., Brzezowski, P., 2023. Singlet oxygen-induced signalling depends on the metabolic status of the Chlamydomonas reinhardtii cell. Commun. Biol. 6 (529), 1–16. https://doi.org/10.1038/s42003-023-04872-5.

Ali, Z., Wen Tan, Q., Ken Lim, P., Chen, H., Pfeifer, L., Julca, I., Min Lee, J., Classen, B., Vries, S., Vries, J., Vinter, F., Alvarado, C., Layens, A., Mizrachi, E., Saddik Motawie, M., Joergensen, B., Ulvskov, P., Peer, Y., Chuan Ho, B., et al., 2025. Comparative transcriptomics in ferns reveals key innovations and divergent evolution of the secondary cell walls. Nat. Plants 1028–1048. https://doi.org/10.1038/s41477-025-01978-y.

Annunziata, M.G., Feil, R., Lohse, M., Figueroa, C.M., Hartman, M.D., Esmailpour, M., Nikoloski, Z., Koehl, K., Stitt, M., Lunn, J.E., Fichtner, F., 2025. The sucrose: trehalose 6-phosphate nexus is conserved in flowering plants with different phloem loading and carbon storage strategies. J. Exp. Bot. https://doi.org/10.1093/jxb/eraf401.

Anselmino, O., Gilg, E., 1913. Über das Vorkommen von Trehalose in Selaginella lepidophylla. Ber. Deut.Pharm. Ges. 23, 326–330.

Baena-González, E., Lunn, J.E., 2020. SnRK1 and trehalose 6-phosphate – two ancient pathways converge to regulate plant metabolism and growth. In: Current Opinion in Plant Biology, 55. Elsevier Ltd, pp. 52–59. https://doi.org/10.1016/j.pbi.2020.01.010.

Baena-González, E., Rolland, F., Thevelein, J.M., Sheen, J., 2007. A central integrator of transcription networks in plant stress and energy signalling. Nature 448. https://doi.org/10.1038/nature06069.

Becker, A., Chen, X., Dresselhaus, T., Gutsche, N., Müller-Schüssele, S.J., Sprunck, S., Theißen, G., de Vries, S., Zachgo, S., 2025. Sexual reproduction in land plants: an evolutionary perspective. In: Plant Reproduction, 38. Springer Science and Business Media Deutschland GmbH. https://doi.org/10.1007/s00497-025-00522-4. Issue 2.

Bertheloot, J., Barbier, F., Boudon, F., Perez-Garcia, M.D., Péron, T., Citerne, S., Dun, E., Beveridge, C., Godin, C., Sakr, S., 2020. Sugar availability suppresses the auxin-induced strigolactone pathway to promote bud outgrowth. New Phytol. 225, 866–879. https://doi.org/10.1111/nph.16201.

Bianchi, G., Gamba, A., Limiroli, R., Pozzi, N., Elster, R., Salamini, F., Bartels, D., 1993. The unusual sugar composition in leaves of the resurrection plant Myrothamnus flabellifolia. Physiol. Plantarum 87, 223–226.

Birchler, J.A., Yang, H., 2022. The multiple fates of gene duplications: deletion, hypofunctionalization, subfunctionalization, neofunctionalization, dosage balance constraints, and neutral variation. Plant Cell 34 (7), 2466–2474.

Blanford, J., Zhai, Z., Baer, M.D., Guo, G., Liu, H., Liu, Q., Raugei, S., Shanklin, J., 2024. Molecular mechanism of trehalose 6-phosphate inhibition of the plant metabolic sensor kinase SnRK1. Sci. Adv. 10.

Blázquez, M.A., Nelson, D.C., Weijers, D., 2020. Evolution of plant hormone response pathways. Annu. Rev. Plant Biol. 71, 327–353. https://doi.org/10.1146/annurev-arplant-050718.

Blázquez, M.A., Santos, E., Flores, C.-L., Martínez-Zapater, J.M., Salinas, J., Gancedo, C., 1998. Isolation and molecular characterization of the Arabidopsis TPS1 gene, encoding trehalose-6-phosphate synthase. Plant J. 13 (5), 685–689. https://doi.org/10.1046/j.1365-313X.1998.00063.x.

Bortlik, J., Lühle, J., Alseekh, S., Weiste, C., Fernie, A.R., Dröge-Laser, W., Börnke, F., 2024. DOMAIN OF UNKNOWN FUNCTION581-9 negatively regulates SnRK1 kinase activity. Plant Physiol. 194, 1853–1869. https://doi.org/10.1093/plphys/kiad594.

Bowman, J.L., Briginshaw, L.N., Fisher, T.J., Flores-Sandoval, E., 2019. Something ancient and something neofunctionalized—evolution of land plant hormone signaling pathways. In: Current Opinion in Plant Biology, 47. Elsevier Ltd, pp. 64–72. https://doi.org/10.1016/j.pbi.2018.09.009.

Bowman, J.L., Kohchi, T., Yamato, K.T., Jenkins, J., Shu, S., Ishizaki, K., Yamaoka, S., Nishihama, R., Nakamura, Y., Berger, F., Adam, C., Aki, S.S., Althoff, F., Araki, T., Arteaga-Vazquez, M.A., Balasubrmanian, S., Barry, K., Bauer, D., Boehm, C.R., et al., 2017. Insights into land plant evolution garnered from the Marchantia polymorpha genome. Cell 171 (2), 287–304. https://doi.org/10.1016/j.cell.2017.09.030 e15.

Broeckx, T., Hulsmans, S., Rolland, F., 2016. The plant energy sensor: evolutionary conservation and divergence of SnRK1 structure, regulation, and function. In: Journal of Experimental Botany, 67. Oxford University Press, pp. 6215–6252. https://doi.org/10.1093/jxb/erw416. Issue 22.

Burkart, G.M., Brandizzi, F., 2021. A tour of TOR complex signaling in plants. Trends Biochem. Sci. 46 (5), 417–428. https://doi.org/10.1016/J.TIBS.2020.11.004.

Cabib, E., Leloir, L.F., 1958. The biosynthesis of trehalose phosphate. J. Biol. Chem. 231, 259–275.

Cao, D., Chabikwa, T., Barbier, F., Dun, E.A., Fichtner, F., Dong, L., Kerr, S.C., Beveridge, C.A., 2023. Auxin-independent effects of apical dominance induce changes in phytohormones correlated with bud outgrowth. Plant Physiol. 192 (2), 1420–1434. https://doi.org/10.1093/plphys/kiad034.

Chan, A.P., Melake-Berhan, A., O'Brien, K., Buckley, S., Quan, H., Chen, D., Lewis, M., Banks, J.A., Rabinowicz, P.D., 2008. The highest-copy repeats are methylated in the small genome of the early divergent vascular plant Selaginella moellendorffii. BMC Genom. 9. https://doi.org/10.1186/1471-2164-9-282.

Claeys, H., Vi, S.L., Xu, X., Satoh-Nagasawa, N., Eveland, A.L., Goldshmidt, A., Feil, R., Beggs, G.A., Sakai, H., Brennan, R.G., Lunn, J.E., Jackson, D., 2019. Control of meristem determinacy by trehalose 6-phosphate phosphatases is uncoupled from enzymatic activity. Nat. Plants 5 (4), 352–357. https://doi.org/10.1038/s41477-019-0394-z.

Coudert, Y., Palubicki, W., Ljung, K., Novak, O., Leyser, O., Jill Harrison, C., 2015. Three ancient hormonal cues co-ordinate shoot branching in a moss. eLife 2015 (4). https://doi.org/10.7554/eLife.06808.001.

Crepin, N., Rolland, F., 2019. SnRK1 activation, signaling, and networking for energy homeostasis. Curr. Opin. Plant Biol. 51, 29–36. https://doi.org/10.1016/J.PBI.2019.03.006.

de Vries, J., Archibald, J.M., 2018. Plant evolution: landmarks on the path to terrestrial life. New Phytol. 217 (4), 1428–1434. https://doi.org/10.1111/nph.14975.

Delorge, I., Figueroa, C.M., Feil, R., Lunn, J.E., Van Dijck, P., 2015. Trehalose-6-phosphate synthase 1 is not the only active TPS in Arabidopsis thaliana. Biochem. J. 466 (2), 283–290. https://doi.org/10.1042/BJ20141322.

Dobrenel, T., Caldana, C., Hanson, J., Robaglia, C., Vincentz, M., Veit, B., Meyer, C., 2016. TOR signaling and nutrient sensing. In: Annual Review of Plant Biology, 67. Annual Reviews Inc, pp. 261–285. https://doi.org/10.1146/annurev-arplant-043014-114648.

Doidy, J., Wang, Y., Gouaille, L., Goma-Louamba, I., Jiang, Z., Pourtau, N., Le Gourrierec, J., Sakr, S., 2024. Sugar transport and signaling in shoot branching. J. Mol. Sci. 2024, 13214. https://doi.org/10.3390/ijms252313214.

Dong, Z., Xiao, Y., Govindarajulu, R., Feil, R., Siddoway, M.L., Nielsen, T., Lunn, J.E., Hawkins, J., Whipple, C., Chuck, G., 2019. The regulatory landscape of a core maize domestication module controlling bud dormancy and growth repression. Nat. Commun. 10 (1), 3810. https://doi.org/10.1038/s41467-019-11774-w.

Donoghue, P.C.J., Harrison, C.J., Paps, J., Schneider, H., 2021. The evolutionary emergence of land plants. In: Current Biology, 31. Cell Press, pp. R1281–R1298. https://doi.org/10.1016/j.cub.2021.07.038. Issue 19.

Dorken, M.E., van Kleunen, M., Stift, M., 2025. Costs of reproduction in flowering plants. In: New Phytologist, 247. John Wiley and Sons Inc, pp. 55–70. https://doi.org/10.1111/nph.70166. Issue 1.

Eastmond, P.J., Van Dijken, A.J.H., Spielman, M., Kerr, A., Tissier, A.F., Dickinson, H.G., Jones, J.D.G., Smeekens, S.C., Graham, I.A., 2002. Trehalose-6-phosphate synthase 1, which catalyses the first step in trehalose synthesis, is essential for Arabidopsis embryo maturation. Plant J. 29 (2), 225–235. https://doi.org/10.1046/j.1365-313x.2002.01220.x.

Eklund, D.M., Ishizaki, K., Flores-Sandoval, E., Kikuchi, S., Takebayashi, Y., Tsukamoto, S., Hirakawa, Y., Nonomura, M., Kato, H., Kouno, M., Bhalerao, R.P., Lagercrantz, U., Kasahara, H., Kohchi, T., Bowman, J.L., 2015. Auxin produced by the indole-3-pyruvic acid pathway regulates development and gemmae dormancy in the liverwort Marchantia polymorpha. Plant Cell 27 (6), 1650–1669. https://doi.org/10.1105/tpc.15.00065.

Endress, P.K., 2020. Structural and temporal modes of heterodichogamy and similar patterns across angiosperms. In: Botanical Journal of the Linnean Society, 193. https://academic.oup.com/botlinnean/article/193/1/5/5741356.

Fang, Y., Qin, X., Liao, Q., Du, R., Luo, X., Zhou, Q., Li, Z., Chen, H., Jin, W., Yuan, Y., Sun, P., Zhang, R., Zhang, J., Wang, L., Cheng, S., Yang, X., Yan, Y., Zhang, X., Zhang, Z., et al., 2022. The genome of homosporous maidenhair fern sheds light on the euphyllophyte evolution and defences. Nat. Plants 8, 1024–1037. https://doi.org/10.1038/s41477-022-01222-x.

Feng, X., Zheng, J., Irisarri, I., Yu, H., Zheng, B., Ali, Z., De Vries, S., Keller, J., Fürst-Jansen, J.M.R., Dadras, A., Zegers, J.M.S., Rieseberg, T.P., Dhabalia Ashok, A., Darienko, T., Bierenbroodspot, M.J., Gramzow, L., Petroll, R., Haas, F.B., Fernandez-Pozo, N., et al., 2024. Genomes of multicellular algal sisters to land plants illuminate signaling network evolution check for updates. Nat. Genet. 56, 1018–1031. https://doi.org/10.1038/s41588-024-01737-3.

Fernandez-Pozo, N., Haas, F.B., Meyberg, R., Ullrich, K.K., Hiss, M., Perroud, P.F., Hanke, S., Kratz, V., Powell, A.F., Vesty, E.F., Daum, C.G., Zane, M., Lipzen, A., Sreedasyam, A., Grimwood, J., Coates, J.C., Barry, K., Schmutz, J., Mueller, L.A., Rensing, S.A., 2020. PEATmoss (Physcomitrella expression atlas tool): a unified gene expression atlas for the model plant physcomitrella patens. Plant J. 102 (1), 165–177. https://doi.org/10.1111/tpj.14607.

Ferrari, C., Shivhare, D., Hansen, B.O., Pasha, A., Esteban, E., Provart, N.J., Kragler, F., Fernie, A., Tohge, T., Mutwil, M., 2020. Expression atlas of Selaginella moellendorffii provides insights into the evolution of vasculature, secondary metabolism, and roots. Plant Cell 32, 853–870. https://doi.org/10.1105/TPC.19.00780.

Fichtner, F., 2025. Trehalose 6-phosphate – a central regulator at the crossroads of sugar signalling, metabolism, and development. In: New Phytologist. John Wiley and Sons Inc. https://doi.org/10.1111/nph.70533.

Fichtner, F., Barbier, F.F., Feil, R., Watanabe, M., Annunziata, M.G., Chabikwa, T.G., Höfgen, R., Stitt, M., Beveridge, C.A., Lunn, J.E., 2017. Trehalose 6-phosphate is involved in triggering axillary bud outgrowth in garden pea (Pisum sativum L.). Plant J. 92 (4), 611–623. https://doi.org/10.1111/tpj.13705.

Fichtner, F., Dissanayake, I.M., Lacombe, B., Barbier, F., 2021. Sugar and nitrate sensing: a multi-billion-year story. In: Trends in Plant Science, 26. Elsevier Ltd, pp. 352–374. https://doi.org/10.1016/j.tplants.2020.11.006. Issue 4.

Fichtner, F., Humphreys, J.L., Barbier, F.F., Feil, R., Westhoff, P., Moseler, A., Lunn, J.E., Smith, S.M., Beveridge, C.A., 2024. Strigolactone signalling inhibits trehalose 6-phosphate signalling independently of BRC1 to suppress shoot branching. New Phytol. 244 (3), 900–913. https://doi.org/10.1111/nph.20072.

Fichtner, F., Lunn, J.E., 2021. The role of trehalose 6-Phosphate (Tre6P) in plant metabolism and development. Annu. Rev. Plant Biol. 72, 737–760. https://doi.org/10.1146/annurev-arplant-050718.

Fichtner, F., Olas, J.J., Feil, R., Watanabe, M., Krause, U., Hoefgen, R., Stitt, M., Lunn, J.E., 2020. Functional features of TREHALOSE-6-PHOSPHATE SYNTHASE1, an essential enzyme in Arabidopsis. Plant Cell 32 (6), 1949–1972. https://doi.org/10.1105/tpc.19.00837.

Figueroa, C.M., Feil, R., Ishihara, H., Watanabe, M., Kölling, K., Krause, U., Höhne, M., Encke, B., Plaxton, W.C., Zeeman, S.C., Li, Z., Schulze, W.X., Hoefgen, R., Stitt, M., Lunn, J.E., 2016. Trehalose 6-phosphate coordinates organic and amino acid metabolism with carbon availability. Plant J. 85, 410–423. https://doi.org/10.1111/tpj.13114.

Figueroa, C.M., Lunn, J.E., 2016. A tale of two sugars: Trehalose 6-phosphate and sucrose. Plant Physiol. 172 (1), 7–27. https://doi.org/10.1104/pp.16.00417.

Gao, X.Q., Liu, C.Z., Li, D.D., Zhao, T.T., Li, F., Jia, X.N., et al., 2016. The Arabidopsis KINβγ subunit of the SnRK1 complex regulates pollen hydration on the stigma by mediating the level of reactive oxygen species in pollen. PLoS Genet. 12 (7), e1006228.

Goebel, M., Foster, J., Westhoff, P., Skorzinski, N., Lepper, H., Njo, M.F., et al., 2025. Systemic and local regulation of root growth by vascular trehalose 6-phosphate is correlated with re-allocation of primary metabolites between shoots and roots. bioRxiv 11, 2025.

Groh, J.S., Vik, D.C., Davis, M., Monroe, J.G., Stevens, K.A., Brown, P.J., Langley, C.H., Coop, G., 2025. Ancient structural variants control sex-specific flowering time morphs in walnuts and hickories. Science 387 (6729). https://doi.org/10.1126/science.ado5578.

Guo, D., Liu, P., Liu, Q., Zheng, L., Liu, S., Shen, C., Liu, L., Fan, S., Li, N., Dong, J., Wang, T., 2023. Legume-specific SnRK1 promotes malate supply to bacteroids for symbiotic nitrogen fixation. Mol. Plant 16 (9), 1396–1412. https://doi.org/10.1016/J.MOLP.2023.08.009.

Guo, Y., Chen, X., Li, J., Wang, Q., Zhang, S., Liu, N., Zhang, Y., Zhang, T., 2024. Single-cell RNA sequencing reveals a high-resolution cell atlas of petals in Prunus mume at different f lowering development stages. Horticulture Research 11. https://doi.org/10.1093/hr/uhae189.

Han, C., Wang, H., Shi, W., Bai, M.Y., 2024. The molecular associations between the SnRK1 complex and carbon/nitrogen metabolism in plants. New Crops 1, 100008. https://doi.org/10.1016/J.NCROPS.2023.12.003.

Hata, Y., Hetherington, N., Battenberg, K., Hirota, A., Minoda, A., Hayashi, M., Kyozuka, J., 2025. snRNA-seq analysis of the moss Physcomitrium patens identifies a conserved cytokinin-ESR module promoting pluripotent stem cell identity. Dev. Cell 60 (13), 1884–1899.e7. https://doi.org/10.1016/j.devcel.2025.02.006.

Henriques, R., Calderan-Rodrigues, M.J., Crespo, J.L., Baena-González, E., Caldana, C., 2022. Growing of the TOR world. J. Exp. Bot. 73 (20), 6987–6992. https://doi.org/10.1093/jxb/erac401.

Henry, C., Bledsoe, S.W., Griffiths, C.A., Kollman, A., Paul, M.J., Sakr, S., Lagrimini, L.M., 2015. Differential role for trehalose metabolism in salt-stressed maize. Plant Physiol. 169, 1072–1089. https://doi.org/10.1104/pp.15.00729.

Higo, A., Niwa, M., Yamato, K.T., Yamada, L., Sawada, H., Sakamoto, T., Kurata, T., Shirakawa, M., Endo, M., Shigenobu, S., Yamaguchi, K., Ishizaki, K., Nishihama, R., Kohchi, T., Araki, T., 2016. Transcriptional framework of male gametogenesis in the liverwort Marchantia polymorpha L. Plant Cell Physiol. 57 (2), 325–338. https://doi.org/10.1093/pcp/pcw005.

Hisanaga, T., Fujimoto, S., Cui, Y., Sato, K., Sano, R., Yamaoka, S., Kohchi, T., Berger, F., Nakajima, K., 2021. Deep evolutionary origin of gamete-directed zygote activation by KNOX/BELL transcription factors in green plants. eLife 1–25. https://doi.org/10.7554/eLife.

Huang, J., Huang, Z., Zhou, X., Xia, C., Imran, M., Wang, S., Xu, C., Zha, M., Liu, Y., Zhang, C., 2019. Tissue-specific transcriptomic profiling of Plantago major provides insights for the involvement of vasculature in phosphate deficiency responses. Mol. Genet. Genom. 294 (1), 159–175. https://doi.org/10.1007/s00438-018-1496-4.

Jamsheer K, M., Jindal, S., Sharma, M., Awasthi, P., S, S., Sharma, M., Mannully, C.T., Laxmi, A., 2022. A negative feedback loop of TOR signaling balances growth and stress-response trade-offs in plants. Cell Rep. 39 (1). https://doi.org/10.1016/j.celrep.2022.110631.

Jamsheer, K.M., Sharma, M., Singh, D., Mannully, C.T., Jindal, S., Shukla, B.N., Laxmi, A., 2018. FCS-like zinc finger 6 and 10 repress SnRK1 signalling in Arabidopsis. Plant J. 94 (2), 232–245. https://doi.org/10.1111/tpj.13854.

Jamsheer, K.M., Shukla, B.N., Jindal, S., Gopan, N., Mannully, C.T., Laxmi, A., 2018. The FCS-like zinc finger scaffold of the kinase SnRK1 is formed by the coordinated actions of the FLZ domain and intrinsically disordered regions. J. Biol. Chem. 293 (34), 13134–13150. https://doi.org/10.1074/jbc.RA118.002073.

Jamsheer, K.M., Singh, D., Sharma, M., Sharma, M., Jindal, S., Mannully, C.T., Shukla, B.N., Laxmi, A., 2019. The FCS-LIKE ZINC FINGER 6 and 10 are involved in regulating osmotic stress responses in Arabidopsis. Plant Signal. Behav. 14 (6). https://doi.org/10.1080/15592324.2019.1592535.

Julca, I., Ferrari, C., Flores-Tornero, M., Proost, S., Lindner, A.C., Hackenberg, D., Steinbachová, L., Michaelidis, C., Gomes Pereira, S., Misra, C.S., Kawashima, T., Borg, M., Berger, F., Goldberg, J., Johnson, M., Honys, D., Twell, D., Sprunck, S., Dresselhaus, T., Mutwil, M., 2021. Comparative transcriptomic analysis reveals conserved programmes underpinning organogenesis and reproduction in land plants. Nat. Plants 7 (8), 1143–1159. https://doi.org/10.1038/s41477-021-00958-2.

Ke, Y., Pujol, V., Staut, J., Pollaris, L., Seurinck, R., Eekhout, T., Grones, C., Saura-Sanchez, M., Van Bel, M., Vuylsteke, M., Ariani, A., Liseron-Monfils, C., Vandepoele, K., Saeys, Y., De Rybel, B., 2025. A single-cell and spatial wheat root atlas with cross-species annotations delineates conserved tissue-specific marker genes and regulators. Cell Rep. 44 (2), 115240. https://doi.org/10.1016/j.celrep.2025.115240.

Klein, H., Gallagher, J., Demesa-Arevalo, E., 2022. Recruitment of an ancient branching program to suppress carpel development in maize flowers. In: Abraham-Ju Arez, J., Heeney, M., Feil, R., Lunn, J.E., Xiao, Y., Chuck, G., Whipple, C., Jackson, D., Bartlett, M., Kellogg, E., Danforth, D. (Eds.), Proc. Natl. Acad. Sci. USA 119, 1–10. https://doi.org/10.1073/pnas.2115871119/-/DCSupplemental.

Kong, L., Liu, Y., Zhi, P., Wang, X., Xu, B., Gong, Z., Chang, C., 2020. Origins and evolution of cuticle biosynthetic machinery in land plants. Plant Physiol. 184 (4), 1998–2010. https://doi.org/10.1104/pp.20.00913.

Kudoyarova, G.R., Dodd, I.C., Veselov, D.S., Rothwell, S.A., Veselov, S.Y., 2015. Common and specific responses to availability of mineral nutrients and water. J. Exp. Bot. 66, 2133–2144. https://doi.org/10.1093/jxb/erv017.

Li, M., Li, H., Zhu, Q., Liu, D., Li, Z., Chen, H., Luo, J., Gong, P., Ismail, A.M., Zhang, Z., 2024. Knockout of the sugar transporter OsSTP15 enhances grain yield by improving tiller number due to increased sugar content in the shoot base of rice (Oryza sativa L.). New Phytol. 241 (3), 1250–1265. https://doi.org/10.1111/nph.19411.

Li, Z., Wei, X., Tong, X., Zhao, J., Liu, X., Wang, H., et al., 2022. The OsNAC23-Tre6P-SnRK1a feed-forward loop regulates sugar homeostasis and grain yield in rice. Mol. Plant 15 (4), 706–722.

Ligrone, R., Duckett, J.G., Renzaglia, K.S., 2012. The origin of the sporophyte shoot in land plants: a bryological perspective. In: Annals of Botany, 110, pp. 935–941. https://doi.org/10.1093/aob/mcs176. Issue 5.

Liu, Y., Li, B., Chen, T., Tian, S., Zhang, Z., 2025. The synthesis, degradation and biological function of trehalose-6-phosphate. Stress Biology 5 (38), 1–13. https://doi.org/10.1007/s44154-025-00235-8.

Lucas, W.J., Groover, A., Lichtenberger, R., Furuta, K., Yadav, S.R., Helariutta, Y., He, X. Q., Fukuda, H., Kang, J., Brady, S.M., Patrick, J.W., Sperry, J., Yoshida, A., López-Millán, A.F., Grusak, M.A., Kachroo, P., 2013. The plant vascular system: evolution, development and functions. In: Journal of Integrative Plant Biology, 55, pp. 294–388. https://doi.org/10.1111/jipb.12041. Issue 4.

Lunn, J.E., 2007. Gene families and evolution of trehalose metabolism in plants. Funct. Plant Biol. 34, 550–563. https://doi.org/10.1071/FP06315.

Lunn, J.E., Delorge, I., Mar Ia Figueroa, C., Dijck, P. Van, Stitt, M., 2014. Trehalose metabolism in plants. Plant J. 79, 544–567. https://doi.org/10.1111/tpj.12509.

Mae-Lin Kerbler, S., Armijos-Jaramillo, V., Edward Lunn, J., Vicente, R., 2023. The trehalose 6-phosphate phosphatase family in plants. https://doi.org/10.1111/ppl.14096.

Margalha, L., Confraria, A., Baena-González, E., 2019. SnRK1 and TOR: modulating growth–defense trade-offs in plant stress responses. In: Journal of Experimental Botany, 70. Oxford University Press, pp. 2261–2274. https://doi.org/10.1093/jxb/erz066. Issue 8.

Martínez-Barajas, E., Delatte, T., Schluepmann, H., de Jong, G.J., Somsen, G.W., Nunes, C., et al., 2011. Wheat grain development is characterized by remarkable trehalose 6-phosphate accumulation pregrain filling: tissue distribution and relationship to SNF1-related protein kinase1 activity. Plant Physiol. 156 (1), 373–381.

Matthes, M.S., Best, N.B., Robil, J.M., Malcomber, S., Gallavotti, A., McSteen, P., 2019. Auxin EvoDevo: conservation and diversification of genes regulating auxin biosynthesis, transport, and signaling. Mol. Plant 12 (3), 298–320. https://doi.org/10.1016/J.MOLP.2018.12.012.

Miret, J.A., Griffiths, C.A., Paul, M.J., 2024. Sucrose homeostasis: mechanisms and opportunity in crop yield improvement. In: Journal of Plant Physiology, 294. Elsevier GmbH. https://doi.org/10.1016/j.jplph.2024.154188.

Morales-Herrera, S., Jourquin, J., Coppé, F., Lopez-Galvis, L., De Smet, T., Safi, A., Njo, M., Griffiths, C.A., Sidda, J.D., Mccullagh, J.S.O., Xue, X., Davis, B.G., Van der Eycken, J., Paul, M.J., Van Dijck, P., Beeckman, T., 2023. Trehalose-6- phosphate signaling regulates lateral root formation in Arabidopsis thaliana. Proc. Natl. Acad. Sci. USA 120 (40). https://doi.org/10.1073/pnas.2302996120.

Morales-Herrera, S., Paul, M.J., Van Dijck, P., Beeckman, T., 2024. SnRK1/TOR/T6P: three musketeers guarding energy for root growth. Trends Plant Sci. 29 (10), 1066–1076.

Nietzsche, M., Schießl, I., Börnke, F., 2014. The complex becomes more complex: Protein-protein interactions of SnRK1 with DUF581 family proteins provide a framework for cell- and stimulus type-specific SnRK1 signaling in plants. Front. Plant Sci. 5 (FEB). https://doi.org/10.3389/fpls.2014.00054.

Notaguchi, M., Okamoto, S., 2015. Dynamics of long-distance signaling via plant vascular tissues. https://doi.org/10.3389/fpls.2015.00161.

Nuccio, M.L., Wu, J., Mowers, R., Zhou, H.P., Meghji, M., Primavesi, L.F., et al., 2015. Expression of trehalose-6-phosphate phosphatase in maize ears improves yield in well-watered and drought conditions. Nat. Biotechnol. 33 (8), 862–869.

Nukarinen, E., Nägele, T., Pedrotti, L., Wurzinger, B., Mair, A., Landgraf, R., Börnke, F., Hanson, J., Teige, M., Baena-Gonzalez, E., Dröge-Laser, W., Weckwerth, W., 2016. Quantitative phosphoproteomics reveals the role of the AMPK plant ortholog SnRK1 as a metabolic master regulator under energy deprivation OPEN. https://doi.org/10.1038/srep31697.

Nunes, C., O'Hara, L.E., Primavesi, L.F., Delatte, T.L., Schluepmann, H., Somsen, G.W., et al., 2013. The trehalose 6-phosphate/SnRK1 signaling pathway primes growth recovery following relief of sink limitation. Plant Physiol. 162 (3), 1720–1732.

Oszvald, M., Primavesi, L.F., Griffiths, C.A., Cohn, J., Basu, S.S., Nuccio, M.L., Paul, M.J., 2018. Trehalose 6-phosphate regulates photosynthesis and assimilate partitioning in reproductive tissue. Plant Physiol. 176 (4), 2623–2638.

Patil, S.B., Barbier, F.F., Zhao, J., Zafar, S.A., Uzair, M., Sun, Y., Fang, J., Perez-Garcia, M.-D., Bertheloot, J., Sakr, S., Fichtner, F., Chabikwa, T.G., Yuan, S., Beveridge, C.A., Li, X., 2022. Sucrose promotes D53 accumulation and tillering in rice. New Phytol. 234, 122–136. https://doi.org/10.1111/nph.17834.

Patrick, J.W., Offler, C.E., 2001. Compartmentation of transport and transfer events in developing seeds. J. Exp. Bot. 52 (Compartmentation Special Issue), 551–564.

Paul, M.J., Foyer, C.H., 2001. Sink regulation of photosynthesis. J. Exp. Bot. 52, 1383–1400.

Paul, M.J., Primavesi, L.F., Jhurreea, D., Zhang, Y., 2008. Trehalose metabolism and signaling. Annu. Rev. Plant Biol. 59, 417–441.

Paul, M.J., Oszvald, M., Jesus, C., Rajulu, C., Griffiths, C.A., 2017. Increasing crop yield and resilience with trehalose 6-phosphate: targeting a feast–famine mechanism in cereals for better source–sink optimization. J. Exp. Bot. 68 (16), 4455–4462.

Paul, M.J., Watson, A., Griffiths, C.A., 2020. Trehalose 6-phosphate signalling and impact on crop yield. In: Biochemical Society Transactions, 48. Portland Press Ltd, pp. 2127–2137. https://doi.org/10.1042/BST20200286. Issue 5.

Peixoto, B., Baena-González, E., 2022. Management of plant central metabolism by SnRK1 protein kinases. J. Exp. Bot. 73 (20), 7068–7082. https://doi.org/10.1093/jxb/erac261.

Phan, T.L.C.H.B., Delorge, I., Avonce, N., Van Dijck, P., 2020. Functional characterization of class I trehalose biosynthesis genes in physcomitrella patens. Front. Plant Sci. 10. https://doi.org/10.3389/fpls.2019.01694.

Proost, S., Mutwil, M., 2018. CoNekT: an open-source framework for comparative genomic and transcriptomic network analyses. Nucleic Acids Res. 46, 133–140. https://doi.org/10.1093/nar/gky336.

Raven, J.A., Edwards, D., 2001. Roots: evolutionary origins and biogeochemical significance. J. Exp. Bot. 52 (Roots Special Issue), 381–401.

Reis-Barata, D., Confraria, A., Margalha, L., Peixoto, B., Lopes, F., Belda-Palazón, B., et al., 2025. TPS proteins coordinate plant growth with sugar availability via the SnRK1 kinase. bioRxiv 2025–08.

Renner, S.S., 2001. Erratum: how common is heterodichogamy?. In: Trends in Ecology and Evolution, 16. Elsevier Ltd, p. 721. https://doi.org/10.1016/s0169-5347(01)02377-1. Issue 12.

Rojas, B.E., Tonetti, T., Figueroa, C.M., 2023. Trehalose 6-phosphate metabolism in C4 species. Curr. Opin. Plant Biol. 72, 102347. https://doi.org/10.1016/J.PBI.2023.102347.

Salam, B.B., Barbier, F., Danieli, R., Teper-Bamnolker, P., Ziv, C., Spíchal, L., Aruchamy, K., Shnaider, Y., Leibman, D., Shaya, F., Carmeli-Weissberg, M., Gal-On, A., Jiang, J., Ori, N., Beveridge, C., Eshel, D., 2021. Sucrose promotes stem branching through cytokinin. Plant Physiol. 185, 1708–1721. https://doi.org/10.1093/plphys/kiab003.

Saliba, E., Hoernstein, S.N.W., Gessel, N. van, Sentimenti, A., Höß, K.M.V., Parsons, J., Decker, E.L., Huesgen, P.F., Simonsen, H.T., Reski, R., 2025. Functional characterization of target of rapamycin (TOR) signalling in physcomitrella. https://doi.org/10.1101/2025.11.04.686496.

Satoh-Nagasawa, N., Nagasawa, N., Malcomber, S., Sakai, H., Jackson, D., 2006. A trehalose metabolic enzyme controls inflorescence architecture in maize. Nature 441 (7090), 227–230. https://doi.org/10.1038/nature04725.

Schluepmann, H., Van Dijken, A., Smeekens, S., Paul, M., 2003. Trehalose 6-phosphate is indispensable for carbohydrate utilization and growth in Arabidopsis thaliana. Proc. Natl. Acad. Sci. USA 100 (11), 6849–6854. https://www.pnas.org.

Shi, L., Wu, Y., Sheen, J., 2018. TOR signaling in plants: conservation and innovation. In: Development (Cambridge, England), 145. https://doi.org/10.1242/dev.160887. Issue 13.

Singh, H., Singh, Z., Kashyap, R., Yadav, S.R., 2023. Lateral root branching: evolutionary innovations and mechanistic divergence in land plants. New Phytol. 238 (4), 1379–1385. https://doi.org/10.1111/nph.18864.

Sun, Y., Dong, L., Kang, L., Zhong, W., Jackson, D., Yang, F., 2024. Progressive meristem and single-cell transcriptomes reveal the regulatory mechanisms underlying maize inflorescence development and sex differentiation. Mol. Plant 17 (7), 1019–1037. https://doi.org/10.1016/j.molp.2024.06.007.

Supriya, L., Dake, D., Woch, N., Gupta, P., Gopinath, K., Padmaja, G., Muthamilarasan, M., 2025. Sugar sensors in plants: orchestrators of growth, stress tolerance, and hormonal crosstalk. J. Plant Physiol. 307, 154471. https://doi.org/10.1016/J.JPLPH.2025.154471.

Suzuki, H., Kato, H., Iwano, M., Nishihama, R., Kohchi, T., 2023. Auxin signaling is essential for organogenesis but not for cell survival in the liverwort Marchantia polymorpha. Plant Cell 35 (3), 1058–1075. https://doi.org/10.1093/plcell/koac367.

Thelander, M., Landberg, K., Muller, A., Cloarec, G., Cunniffe, N., Huguet, S., Soubigou-Taconnat, L., Brunaud, V., Coudert, Y., 2022. Apical dominance control by TAR-YUC-mediated auxin biosynthesis is a deep homology of land plants. Current Biology-CB 2022 (17). https://doi.org/10.1016/j.cub.2022.06.064ï.

Thelander, M., Olsson, T., Ronne, H., 2004. Snf1-related protein kinase 1 is needed for growth in a normal day-night light cycle. EMBO J. 23 (8), 1900–1910. https://doi.org/10.1038/sj.emboj.7600182.

Tran, T.M., Claeys, H., Abraham-Juárez, M.J., Vi, S.L., Xu, X., Michalski, K., Chou, T.H., Iohannes, S.D., Boumpas, P., Williams, Z.P., Sheppard, S., Griffiths, C., Paul, M.J., Furukawa, H., Jackson, D., 2025. Non-catalytic and catalytic TREHALOSE-6-PHOSPHATE SYNTHASES interact with RAMOSA3 to control maize development. https://doi.org/10.1101/2025.08.09.669499.

Van Dijken, A.J.H., Schluepmann, H., Smeekens, S.C.M., 2004. Arabidopsis trehalose-6-phosphate synthase 1 is essential for normal vegetative growth and transition to flowering. Plant Physiol. 135 (2), 969–977. https://doi.org/10.1104/pp.104.039743.

Van Houtte, H., Vandesteene, L., López-Galvis, L., Lemmens, L., Kissel, E., Carpentier, S., Feil, R., Avonce, N., Beeckman, T., Lunn, J.E., Van Dijck, P., 2013. Overexpression of the trehalase gene AtTRE1 leads to increased drought stress tolerance in arabidopsis and is involved in abscisic acid-induced stomatal closure. Plant Physiol. 161 (3), 1158–1171. https://doi.org/10.1104/pp.112.211391.

Van Leene, J., Eeckhout, D., Gadeyne, A., Matthijs, C., Han, C., De Winne, N., Persiau, G., De Slijke, E. Van, Persyn, F., Mertens, T., Smagghe, W., Crepin, N., Broucke, E., Van Damme, D., Pleskot, R., Rolland, F., De Jaeger, G., 2022. Mapping of the plant SnRK1 kinase signalling network reveals a key regulatory role for the class II T6P synthase-like proteins. Nat. Plants 8, 1245–1261. https://doi.org/10.1038/s41477-022-01269-w.

Vandesteene, L., Ramon, M., Le Roy, K., Van Dijck, P., Rolland, F., 2010. A single active Trehalose-6-P synthase (TPS) and a family of putative regulatory TPS-like proteins in arabidopsis. Mol. Plant 3 (2), 406–419. https://doi.org/10.1093/MP/SSP114.

Vardanega, I., Maika, J.E., Demesa-Arevalo, E., Lan, T., Kirschner, G.K., Imani, J., Acosta, I.F., Makowska, K., Hensel, G., Ranaweera, T., Shiu, S.H., Schnurbusch, T., von Korff, M., Simon, R., 2025. CLAVATA signalling shapes barley inflorescence by controlling activity and determinacy of shoot meristem and rachilla. Nat. Commun. 16 (1). https://doi.org/10.1038/s41467-025-59330-z.

Wahl, V., Ponnu, J., Schlereth, A., Arrivault, S., Langenecker, T., Franke, A., Feil, R., Lunn, J.E., Stitt, M., Schmid, M., 2013. Regulation of flowering by Trehalose-6-Phosphate signaling in Arabidopsis thaliana. Science 339 (6120), 704–707. https://doi.org/10.1126/science.1230406.

Wang, J., Guan, H., Dong, R., Liu, C., Liu, Q., Liu, T., Wang, L., He, C., 2019. Overexpression of maize sucrose non-fermenting-1-related protein kinase 1 genes, *ZmSnRK1s*, causes alteration in carbon metabolism and leaf senescence in *Arabidopsis thaliana*. Gene 691, 34–44. https://doi.org/10.1016/j.gene.2018.12.039.

Wang, Q., Yu, Y., Mei, D., Yang, Y., Huang, Y., Mao, X., Shang, X., Qu, Y., Fu, X., 2025. Differential methylation analysis of floral buds between two morphs unravels the contributions of key genes to flowering 2 time in heterodichogamous Cyclocarya paliurus. https://doi.org/10.1093/hr/uhaf296/8313026.

Wang, T., Miao, M., Zhao, J., Kumar, A., Li, X., 2025. Sugars Integrate External and Internal Signals in Regulating Shoot Branching. Plant Cell Environ 48, 8688–8701. https://doi.org/10.1111/pce.70163.

Weber, H., Borisjuk, L., Wobus, U., 2005. Molecular physiology of legume seed development. In: Annual Review of Plant Biology, 56, pp. 253–279. https://doi.org/10.1146/annurev.arplant.56.032604.144201.

Wingler, A., Henriques, R., 2022. Sugars and the speed of life-Metabolic signals that determine plant growth, development and death. Physiol. Plantarum 174, 1–10. https://doi.org/10.1111/ppl.13656.

Winter, D., Vinegar, B., Nahal, H., Ammar, R., Wilson, G.V., Provart, N.J., 2007. An "electronic fluorescent pictograph" Browser for exploring and analyzing large-scale biological data sets. PLoS One 2 (8). https://doi.org/10.1371/journal.pone.0000718.

Yadav, U.P., Ivakov, A., Feil, R., Duan, G.Y., Walther, D., Giavalisco, P., Piques, M., Carillo, P., Hubberten, H.M., Stitt, M., Lunn, J.E., 2014. The sucrose-trehalose 6-phosphate (Tre6P) nexus: specificity and mechanisms of sucrose signalling by. J. Exp. Bot. 65 (4), 1051–1068. https://doi.org/10.1093/jxb/ert457.

Yoon, J., Cho, L.H., Tun, W., Jeon, J.S., An, G., 2021. Sucrose signaling in higher plants. Plant Sci. 302, 110703. https://doi.org/10.1016/J.PLANTSCI.2020.110703.

Yu, S.M., Lo, S.F., Ho, T.H.D., 2015. Source–sink communication: regulated by hormone, nutrient, and stress cross-signaling. Trends Plant Sci. 20 (12), 844–857.

Zacharaki, V., Ponnu, J., Crepin, N., Langenecker, T., Hagmann, J., Skorzinski, N., Musialak-Lange, M., Wahl, V., Rolland, F., Schmid, M., 2022. Impaired KIN10 function restores developmental defects in the Arabidopsis trehalose 6-phosphate synthase1 (tps1) mutant. New Phytol. 235 (1), 220–233. https://doi.org/10.1111/nph.18104.

Zang, B., Li, H., Li, W., Deng, X.W., Wang, X., 2011. Analysis of trehalose-6-phosphate synthase (TPS) gene family suggests the formation of TPS complexes in rice. Plant Mol. Biol. 76 (6), 507–522. https://doi.org/10.1007/s11103-011-9781-1.

Zegers, J.M.S., Irisarri, I., de Vries, S., de Vries, J., 2024. Evolving circuitries in plant signaling cascades. In: Journal of Cell Science, 137. Company of Biologists Ltd. https://doi.org/10.1242/jcs.261712. Issue 17.

Zeng, L., Zacharaki, V., van Es, S.W., Wang, Y., Schmid, M., 2025. Mutations in the floral regulator gene HUA2 restore flowering to the Arabidopsis trehalose 6-phosphate synthase1 (tps1) mutant. Plant Physiol 198, kiaf225. https://doi.org/10.1093/plphys/kiaf225.

Zhai, Z., Keereetaweep, J., Liu, H., Feil, R., Lunn, J.E., Shanklin, J., 2018. Trehalose 6-Phosphate positively regulates fatty acid synthesis by stabilizing WRINKLED1. Plant Cell 30, 2616–2627.

Zhang, T.-Q., Chen, Y., Liu, Y., Lin, W.-H., Wang, J.-W., 2021. Single-cell transcriptome atlas and chromatin accessibility landscape reveal differentiation trajectories in the rice root. Nat. Commun. 12 (1), 2053. https://doi.org/10.1038/s41467-021-22352-4.

Zhang, Y., Primavesi, L.F., Jhurreea, D., Andralojc, P.J., Mitchell, R.A.C., Powers, S.J., Schluepmann, H., Delatte, T., Wingler, A., Paul, M.J., 2009. Inhibition of SNF1-Related protein Kinase1 activity and regulation of metabolic pathways by Trehalose-6-Phosphate 1[W][OA]. Plant Physiol. 149, 1860–1871. https://doi.org/10.1104/pp.108.133934.

Zhou, H., Shi, H., Yang, Y., Feng, X., Chen, X., Xiao, F., Lin, H., Guo, Y., 2024. Insights into plant salt stress signaling and tolerance. J. Genet. Genomics 51, 16–34. https://doi.org/10.1016/j.jgg.2023.08.007.